Evolution of environmentally mediated social interactions under isolation by distance

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Abstract. Many social interactions happen indirectly via modifications of environmental variables, e.g. through the depletion of renewable resources or the secretion of functional compounds. Here, we derive the selection gradient on a quantitative trait affecting the dynamics of such environmental variables that feedback on reproduction and survival in a patch-structured population that is finite, of constant size, and subject to isolation by distance. Our analysis shows that the selection gradient depends on how a focal individual influences the fitness of all future individuals in the population through modifications of the environmental variables they experience, weighted by the neutral relatedness between recipients and the focal. The evolutionarily relevant trait-driven environmental modifications are formalized as the extended phenotypic effects of an individual, which quantify how a trait change in the individual in the present affects the environmental variables in all patches at all future times. When the trait affects reproduction and survival through some payoff function, the selection gradient can be expressed in terms of extended phenotypic effects weighted by scaled-relatedness coefficients. We show how to compute extended phenotypic effects, relatedness, and scaled-relatedness coefficients using Fourier analysis, allowing us to investigate a broad class of environmentally mediated social interactions in a tractable way. We illustrate our approach by studying the evolution of a trait controlling the costly production of some lasting commons (e.g. a common-pool resource or a toxic compound) that can diffuse in space. We show that whether selection favours environmentally mediated altruism or spite depends on the spatial correlation between an individual's lineage and the commons originating from its patch. The sign of this correlation depends on interactions between dispersal patterns and the commons' renewal dynamics. More broadly, we suggest that selection can favour a wide range of social behaviours when these are mediated in space and time through environmental feedback.

Keywords: Adaptive dynamics, Metacommunity, Extended Phenotype, Altruism, Spite

1 Introduction

Organisms continually interact with one another in ways that can significantly impact their survival and reproduction. Such social interactions are incredibly diverse in nature, but still can usefully be classified as to whether they occur directly between individuals, such as grooming or fighting over resources, or as to whether they are indirectly mediated by environmental modifications, such as through the depletion or enrichment of resources, the release of pollutants, or the construction of nests and burrows [1]. Direct social interactions thus take place among contemporaries that are physically close to one another, while environmentally mediated interactions can extend much further in space and time. In fact, when modifications to the environment have long-lasting and long-ranging effects, indirect social interactions may occur between individuals whose lifetimes show little or even no overlap. This can lead to forms of trans-generational harming (e.g. when the overconsumption of a slowly renewable resource leads to stock collapse and poor harvest for future generations) or helping (e.g. when underconsumption ensures healthy stock maintenance).

The theory devoted to the evolution of quantitative traits that influence direct social interactions is well established (e.g. [2, 3, 4, 5, 6, 7]). One of the main contributions of this theory has been to highlight the importance of limited dispersal for determining how selection shapes social traits in populations that are spatially subdivided into finite groups [2, 3]. Under limited dispersal, stochastic demographic effects resulting from finite group (or patch or deme) size generate genetic associations whereby individuals expressing the same traits may be more or less likely to interact directly with one another than with individuals expressing alternative traits. The importance of such associations is enshrined in the fact that the selection gradient on a quantitative trait can be expressed as the marginal (or gradient) form of Hamilton's rule [2, 3]. This gradient captures the first-order effects of selection, which are sufficient to determine the trait values towards which a population converges under mutation-limited evolution ([5], i.e. to characterise convergence stability [8]).

The marginal form of Hamilton's rule is computationally attractive because all the necessary information about interactions is summarized in pairwise relatedness coefficients evaluated under neutrality (i.e. in the absence of selection or trait variation). This remarkable simplification makes the selection gradient tractable under realistic demographic assumptions, particularly in populations exhibiting isolation by distance (e.g. lattice models [3]). This has opened the door to understanding the evolution of multiple types of direct social interactions in such populations (e.g. helping and harming [9, 10, 11, 12, 13, 14, 15, 16]; sex ratio [17]; and dispersal [18, 19, 20, 21]).

In contrast, modelling the evolution of social interactions mediated by abiotic or biotic environmental variables is significantly more challenging in populations that are spatially subdivided into finite groups. This is because computing the selection gradient now also requires computing the joint distri-

bution of pairwise relatedness and environmental variables in the population (under neutrality [22, 3]). Generally, this distribution is the stationary solution to a high-dimensional stochastic dynamical system that is difficult to analyse or, in some cases, even characterise. The challenge is apparent from models that allow for trait-driven changes in local demography. Even in the island model of dispersal where spatial structure is only implicit [23], there is typically no analytical solution to the distribution of demographic states within groups, so that analyses of the selection gradient heavily rely on numerical methods (e.g. [24, 25, 22, 26, 27]). This "curse of dimensionality" becomes even more acute under isolation by distance as the size of the state space on which relevant environmental (or demographic) variables fluctuate blows up exponentially, with the selection gradient now requiring the distribution of states among as well as within groups (e.g. eq. 22 in [22]).

To circumvent this challenge, two approximations have been suggested. One is the pair approximation that has been developed for lattice-structured populations, where typically at most one individual lives in sites connected by stepping stone dispersal [28, 29, 30, 31, 32, 33, 34, 35]. Pair approximation is based on moment equations of the demographic state distribution and consists in ignoring third and higher order moments. Under this approximation, the selection gradient can be written in the form of Hamilton's marginal rule, thus allowing for a sharp understanding of some of the effects of demography on the evolution of social behaviour ([15, 16] see also [36]). However, using the pair approximation is not straightforward when considering arbitrarily complex dispersal patterns (e.g. [37]), patches with more than one individual, or trait-driven environmental state variables.

Another approximation relies on considering that the dynamics of environmental state variables are deterministic with a stable fixed point, so that there are no environmental stochastic fluctuations in the absence of genetic variation [38]. The selection gradient can then readily be expressed as Hamilton's marginal rule with inter-temporal fitness effects arising through trait-driven modifications to the environment at different temporal distances. In addition to being much simpler to compute than the original problem, this decomposition allows to delineate between the component of selection resulting from direct social interactions and that arising indirectly through changes in the environmental dynamics. So far, this approach has been applied only to the island model—hence, in the absence of isolation by distance [38, 39]. For populations showing isolation by distance, there exist general formulas for the selection gradient in terms of inter-temporal and now also spatial effects of trait expression on the fitness of all possible recipients [40, 41]. However, how environmental modifications mediate the long-lasting and long-ranging fitness effects due to trait expression remains implicit in these general formulas. To better understand selection resulting from indirect social interactions via environmental feedback, these fitness effects must be unpacked in terms of trait-driven environmental modifications at different temporal and spatial distances.

Here, we do just that: we fully characterise the selection gradient on a trait that impacts the deterministic dynamics of environmental state variables that can be abiotic or biotic, which feed back on

survival and reproduction under isolation by distance. Using Fourier analysis, we express this gradient in terms of extended phenotypic effects and relatedness coefficients scaled to local competition, both of which provide biological insights about the nature of selection and are straightforward to compute for a wide range of classical models of evolutionary theory (e.g. the Wright-Fisher model and the Cannings model). We use our results to investigate the evolution of environmentally mediated helping and harming through space and time. Our analyses indicate that indiscriminate spite where individuals suffer a cost to harm others living in the future readily evolves under isolation by distance.

2 Model

2.1 Spatial structure, life cycle, traits and environmental variables

We consider a population of homogeneous individuals that is subdivided among D homogeneous patches (or demes or groups), each carrying N adult individuals. The population is censused at discrete demographic time steps between which the following events occur in order: (a) reproduction and adult survival; (b) dispersal among patches; and (c) density-dependent regulation within patches such that each patch contains N adult individuals at the beginning of the next demographic time step.

Patches are arranged homogeneously in d dimensions, with D_j patches in dimension $j \in 1, \ldots, d$. For example, under a lattice structure in a one-dimensional habitat, $D = D_1$ patches are arranged on a circle, while in a two-dimensional habitat, $D = D_1 \times D_2$ patches are arranged on a torus. More generally, we denote by $\mathcal{G} = \{(i_1, i_2, ..., i_d) : 0 \leq i_j < D_j\}$ the set of all patches, which we endow with an abelian group structure (Box I).

Each patch is characterized by a quantitative state variable representing a biotic or abiotic environmental factor, which we refer to as an environmental state variable (e.g. the density of a common-pool resource, a pollutant, or the quality of the habitat). Meanwhile, each individual in the population is characterised by a genetically determined quantitative trait (e.g. the consumption of a resource, the release of a pollutant, or the investment into habitat maintenance) that influences the environment and the individual's fitness. We are interested in the evolution of this trait under the following assumptions.

(i) *Trait and environmentally mediated reproduction and survival*. By expressing the evolving trait, individuals can directly affect the survival and reproduction of any other individual in the population. For example, individuals may engage in costly fights for resources in other patches and return to their own to share these resources with patch neighbours. The effects of trait expression on others are assumed to be: (a) spatially invariant, i.e. the marginal effect of an individual from patch $\mathbf{i} = (i_1, i_2, ..., i_d) \in \mathcal{G}$ on the survival and/or reproduction of an individual in patch $\mathbf{j} = (j_1, j_2, ..., j_d) \in \mathcal{G}$ only depends on the

"distance" $\mathbf{j} - \mathbf{i}$ between the two patches (where $\mathbf{j} - \mathbf{i}$ is calculated from the abelian group operation, see Box I); and (b) spatially symmetric, i.e. the marginal effect of an individual from patch $\mathbf{i}$ on an individual in patch $\mathbf{j}$ is equal to the effect from $\mathbf{j}$ to $\mathbf{i}$. We refer to these two characteristics (a) and (b) together as spatial homogeneity. The survival and reproduction of an individual may also depend on the environmental state variable of each patch, also in a spatially homogeneous way (i.e. the marginal effect of the environmental state variable of a patch $\mathbf{i}$ on the survival and reproduction of an individual residing in patch $\mathbf{j}$ only depends on the distance $\mathbf{j} - \mathbf{i}$, and is equal to the effect from $\mathbf{j}$ to $\mathbf{i}$).

(ii) *Dispersal*. Each individual either stays in its natal patch or disperses to another patch. Dispersal occurs with non-zero probability so that patches are never completely isolated from one another. We assume that dispersal is spatially homogeneous, i.e. that the probability of dispersal from one patch $\mathbf{i}$ to another $\mathbf{j}$ depends only on the distance $\mathbf{k} = \mathbf{j} - \mathbf{i}$ between the two patches (spatial invariance), and is equal to the probability of dispersing the distance $\mathbf{i} - \mathbf{j}$ (spatial symmetry). We can thus write $m_{\mathbf{k}} = m_{-\mathbf{k}}$ for the probability that an individual disperses to a patch at distance $\mathbf{k}$ from its natal patch (with $\sum_{\mathbf{k} \in \mathcal{G}} m_{\mathbf{k}} = 1$).

(iii) *Trait and environmentally mediated environmental dynamics*. Through trait expression, individuals can affect environmental state variables from one demographic time step to the next. For example, the environmental variable may be a common-pool resource that individuals absorb locally, or a pollutant produced by individuals which then diffuses in the environment. Such trait effects on the environment are also spatially homogeneous (so that the marginal effect of an individual from patch $\mathbf{i}$ on the environmental state variable of patch $\mathbf{j}$ only depends on the distance $\mathbf{j} - \mathbf{i}$ and is equal to the effect from $\mathbf{j}$ to $\mathbf{i}$). These trait-driven environmental modifications can thus lead to inter-temporal, environmentally mediated social interactions.

2.2 The focal individual, its fitness, and environmental dynamics

The spatial homogeneity that underlies all processes described above (i-iii) means that the patch indexed as $\mathbf{0} \in \mathcal{G}$ can be taken as a representative patch, and that any individual in this patch can be taken as a representative individual from the population. We refer to this patch and to this individual as the focal patch and the focal individual, respectively. In the following, we introduce some notation to describe trait and environmental variation in the population relative to this focal individual (see Fig. 1C for a summary diagram of our model). We denote by $z_{\bullet}$ the realized value of the trait of the focal individual, and by $z_{\mathbf{k},t}$ ($\mathbf{k} \neq \mathbf{0}$) the realized average trait of individuals living in a patch $\mathbf{k} \in \mathcal{G}$ other than the focal at time (or "generation") t prior to the focal generation, e.g. $z_{1,1}$ is the average trait expressed in patch 1 one time point before the focal generation. We refer to this patch as patch "$\mathbf{k}, t$". Meanwhile, $z_{\mathbf{0},0}$ denotes the average phenotype among the patch neighbours of the focal individual in the focal generation (thus excluding the focal from the average). We use

$\mathbf{z}_{\mathbf{0},t} = (z_{\mathbf{0},t}, ..., z_{\mathbf{k},t}, ..., z_{\mathbf{D}_{-1},t})$ to denote the vector collecting all such realized phenotypes in $\mathcal{G}$ in lexicographic order, finishing with position $\mathbf{D}_{-1} = (D_1 - 1, D_2 - 1, ..., D_d - 1)$. Finally, we use $n_{\mathbf{k},t}$ to denote the environmental state variable in patch $\mathbf{k}$ at $t \geq 0$ generations prior to the focal generation, that we collect in $\mathbf{n}_{\mathbf{0},t} = (n_{\mathbf{0},t}, ..., n_{\mathbf{k},t}, ..., n_{\mathbf{D}_{-1},t})$ across all patches.

The fitness of the focal individual is determined by the function $w : \mathbb{R} \times \mathbb{R}^D \times \mathbb{R}^D \to \mathbb{R}_+$ such that

$$w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) \tag{1}$$

is the expected number of successful offspring (i.e. offspring that establish as adults, including the surviving self) produced over one demographic time by the focal individual with trait $z_\bullet$, when the trait average among other individuals at the different spatial positions is $\mathbf{z}_{\mathbf{0},0}$, and environmental state variables are $\mathbf{n}_{\mathbf{0},0}$. These state variables are obtained from the solution to the system of equations

$$n_{\mathbf{k},t} = g(\mathbf{z}_{\mathbf{k},t+1}, \mathbf{n}_{\mathbf{k},t+1}) \qquad \text{for all } \mathbf{k} \in \mathcal{G}, \tag{2}$$

where $g : \mathbb{R}^D \times \mathbb{R}^D \to \mathbb{R}$ is a transition map determining the dynamics of the environmental state variables $\mathbf{n}_{\mathbf{k},t}$ of all patches, which is a circular permutation of $\mathbf{n}_{\mathbf{0},t}$ with $n_{\mathbf{k},t}$ as first element (e.g. for a one-dimensional lattice, $\mathbf{n}_{0,t} = (n_{0,t}, n_{1,t}, ..., n_{0,t})$, $\mathbf{n}_{1,t} = (n_{1,t}, n_{2,t}, ..., n_{0,t})$, $\mathbf{n}_{2,t} = (n_{2,t}, n_{3,t}, ..., n_{0,t}, n_{1,t})$, and so on). The map g depends on (i) the traits in the whole population expressed at the previous generation via $\mathbf{z}_{\mathbf{k},t+1}$ (recall that t goes back in time), which is a circular permutation of the elements of $\mathbf{z}_{\mathbf{0},t+1}$ with $z_{\mathbf{k},t+1}$ as first element (e.g. for a one dimensional lattice where $d = 1$, $\mathbf{z}_{0,t+1} = (z_{0,t+1}, z_{1,t+1}, ..., z_{D-1,t+1})$, $\mathbf{z}_{1,t+1} = (z_{1,t+1}, z_{2,t+1}, ..., z_{0,t+1})$, $\mathbf{z}_{2,t+1} = (z_{2,t+1}, z_{3,t+1}, ..., z_{0,t+1}, z_{1,t+1})$, and so on); and (ii) the environmental state variables of all patches at the previous generation via $\mathbf{n}_{\mathbf{k},t+1}$. Due to the recursive nature of eq. (2), the environmental state variables in the focal generation, $\mathbf{n}_{\mathbf{0},0}$, depend on the whole history of traits $\mathbf{z}_{\mathrm{H}} = (\mathbf{z}_{\mathbf{0},1}, \mathbf{z}_{\mathbf{0},2}, ...)$ expressed in the population prior to the focal generation. As a result, the fitness of a focal individual eq. (1) may also depend on the traits expressed by all other previous individuals across space and time. To make this dependence explicit, we write the fitness of the focal individual as $w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}}))$.

We make the additional assumption that in a monomorphic population where all individuals express the same resident phenotype z, the deterministic environmental dynamics described by the map g have a unique hyperbolically stable equilibrium point, identical in each patch, and satisfying

$$\hat{n} = g(\mathbf{z}, \hat{\mathbf{n}}), \tag{3}$$

where $\mathbf{z} = (z, ..., z)$ and $\hat{\mathbf{n}} = (\hat{n}, ..., \hat{n})$ are vectors of dimension D whose entries are all equal to trait value z and environmental state variable $\hat{n}$, respectively. This is sometimes called the spatially homogeneous or flat solution in multi-patch ecological systems (p. 235 in [42]). The existence of such

a solution entails that, in the absence of genetic variation, all patches converge to the same environmental attractor $\hat{n}$, which may depend on the resident trait z. One useful property of a monomorphic population at such an equilibrium is that fitness must be one, i.e.

$$w(z, \mathbf{z}, \hat{\mathbf{n}}) = 1 \tag{4}$$

holds. This is because the total population size is constant and, consequently, each individual exactly replaces itself on average.

Equations (1) and (2) assume that fitness and environmental dynamics can be written as functions of trait averages within patches. That being said, this assumption does not limit us to only consider situations where effects within patches are additive. Indeed, because we are interested in convergence stability and thus in the first-order effects of selection (i.e. first-order effects of trait variation), expressions (1) and (2) are sufficient to model biological scenarios with non-additive effects among individuals within patches, for instance through complementarity or antagonism. Just a little bit of care may be required when defining these expressions from an individual-based model (p. 95 in [3]).

2.3 Evolutionary dynamics

We assume that the quantitative trait evolves through rare mutations of small phenotypic effects, such that the evolutionary dynamics proceed as a trait substitution sequence on the state space $\mathcal{Z} \subseteq \mathbb{R}$ (i.e. the process of "long-term evolution" described in [5] for finite populations). We are interested in characterising convergence stable trait values, which are local attractors of the trait substitution sequence. To do so, we base ourselves on the first-order effects of selection on the fixation probability of a mutant that arises as a single copy in a population monomorphic for a resident trait value [20, 43, 5]. Technical details about our derivations can be found in the appendices and in accompanying boxes. Our main findings are summarized below.

3 Results

3.1 Recipient-centered perspective: intra- and inter-temporal fitness effects

We show in Appendix A that a trait value z^* in the interior of $\mathcal{Z}$ is convergence stable if and only if

$$s(z^*) = 0 \quad \text{and} \quad \left.\frac{\mathrm{d}s(z)}{\mathrm{d}z}\right|_{z=z^*} < 0 \tag{5}$$

holds, where the function

$$s(z) = s_{\mathrm{w}}(z) + s_{\mathrm{e}}(z), \tag{6}$$

referred to as the selection gradient, can be written as the sum of two terms, given by

$$s_{\mathrm{w}}(z) = \frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}}))}{\partial z_\bullet} + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}}))}{\partial z_{\mathbf{k},0}} R_{\mathbf{k},0}, \text{ and} \tag{7a}$$

$$s_{\mathrm{e}}(z) = \sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}}))}{\partial z_{\mathbf{k},t}} R_{\mathbf{k},t}, \tag{7b}$$

which we interpret below. A z^* satisfying condition (5) constitutes a candidate end-point of evolution. More specifically, z^* is a mode of the stationary phenotypic distribution under the trait substitution sequence (eq. A-5 in Appendix and e.g. [5] for details).

Both $s_{\mathrm{w}}(z)$ and $s_{\mathrm{e}}(z)$ depend on marginal fitness effects, i.e. on derivatives of focal fitness, which here and hereafter are evaluated in a monomorphic population where all individuals express the resident trait value z, and where the environmental state variable in all patches is at the environmental equilibrium $\hat{n}$ (eq. 3). The quantity $R_{\mathbf{k},t}$ weighing fitness effects in eq. (7) is the relatedness between the focal individual and another randomly sampled individual from patch $\mathbf{k}, t$. It is defined as

$$R_{\mathbf{k},t} = \lim_{\mu\to 0} \frac{Q_{\mathbf{k},t} - \overline{Q}_t}{1 - \overline{Q}_0}, \tag{8}$$

where μ is the mutation rate at the evolving locus; $Q_{\mathbf{k},t}$ is the stationary probability that an allele sampled in the focal individual is identical by descent with a homologous allele sampled in another individual chosen at random from patch $\mathbf{k}, t$ under neutrality (i.e. in a population monomorphic for z); and $\overline{Q}_t = \sum_{\mathbf{k}\in\mathcal{G}} Q_{\mathbf{k},t}/D$ is the average probability of identity by descent between two homologous alleles sampled in two individuals living t generations apart. The probability of identity by descent $Q_{\mathbf{k},t}$, and thus $R_{\mathbf{k},t}$, may depend on the resident phenotype z but we leave this dependence implicit for readability.

Relatedness $R_{\mathbf{k},t}$ quantifies the extent to which an individual that is sampled in patch $\mathbf{k}, t$ is more (when $R_{\mathbf{k},t} > 0$) or less (when $R_{\mathbf{k},t} < 0$) likely than a randomly sampled individual to carry an allele identical by descent to one carried by the focal individual at a homologous locus. To illustrate this notion, consider a Wright-Fisher process (where there is no adult survival and individuals are semelparous), which is the reference model for probabilities of identity by descent under isolation by distance (e.g. [44, 45, 3]). For this model, the relatedness coefficients $R_{\mathbf{k},t}$ for $t = 1, 2, 3, \ldots$ are given by,

$$R_{\mathbf{k},t} = \frac{1}{ND + M} \sum_{\mathbf{h}\in\mathcal{G}\setminus\mathbf{0}} \frac{\mathcal{M}(\mathbf{h})^t}{1 - \mathcal{M}(\mathbf{h})^2} \overline{\chi}_{\mathbf{k}}(\mathbf{h}), \tag{9}$$

where $\mathcal{G} \setminus \mathbf{0}$ means the set $\mathcal{G}$ with element $\mathbf{0}$ removed; $M = \sum_{\mathbf{h} \in \mathcal{G} \setminus \mathbf{0}} \mathcal{M}(\mathbf{h})^2 / \left(1 - \mathcal{M}(\mathbf{h})^2\right)$; and

$$\mathcal{M}(\mathbf{h}) = \sum_{\mathbf{k} \in \mathcal{G}} m_{\mathbf{k}} \chi_{\mathbf{k}}(\mathbf{h}) \tag{10}$$

is the Fourier transform (or characteristic function) of the dispersal distribution (see Box I for definitions of character functions $\chi_{\mathbf{k}}(\mathbf{h})$ and inverses $\overline{\chi}_{\mathbf{k}}(\mathbf{h})$; Appendix B for an example of the characteristic function of a dispersal distribution; and [46] for a derivation of eq. 9). The relatedness coefficient between two individuals in the same generation, $R_{\mathbf{k},0}$, is given by eq. (9) with $t = 2$ (i.e. $R_{\mathbf{k},0} = R_{\mathbf{k},2}$). In a panmictic or randomly mixing population (where $m_{\mathbf{k}} = 1/D$ for all $\mathbf{k}$), relatedness between any two individuals is zero ($R_{\mathbf{k},t} = 0$ for all $\mathbf{k}$ and all t; as eq. 10 reduces to $\mathcal{M}(\mathbf{h}) = 1$ if $\mathbf{h} = \mathbf{0}$ and 0 otherwise using property I.F in Box I). But as soon as dispersal is non-uniform (i.e. where $m_{\mathbf{k}} \neq m_{\mathbf{j}}$ for some $\mathbf{k} \neq \mathbf{j}$), relatedness varies among individuals from different patches according to spatial and temporal distance. In particular, when dispersal is limited so that individuals have a tendency to remain in their natal patch, relatedness between the focal and individuals in the same patch from the same generation increases ($R_{\mathbf{0},0} > 0$). Because the average relatedness is zero (i.e. $\sum_{\mathbf{k} \in \mathcal{G}} R_{\mathbf{k},t}/D = 0$ holds from eq. 8), the focal individual must also be negatively related to individuals residing in at least one other patch (i.e. $R_{\mathbf{k},0} < 0$ must hold for some $\mathbf{k} \neq \mathbf{0}$). Which patches those are depends on patterns of dispersal. Under short-range dispersal, the focal individual tends to be positively related to individuals in patches nearby and negatively related to individuals further away (Fig. 2C and Fig. 3C). Under long-range dispersal, relatedness can be negative between individuals living in patches at intermediate distance (Fig. 2D and Fig. 3D).

In eq. (7), $\partial w/\partial z_{\bullet}$ is the effect of a trait change in the focal individual on its own fitness, and $\partial w/\partial z_{\mathbf{k},t}$ is the effect of a trait change in the whole set of individuals living in patch $\mathbf{k}, t$ on the fitness of the focal individual, weighted by relatedness $R_{\mathbf{k},t}$. As such, $s_{\mathrm{w}}(z)$ (eq. 7a) is the net effect of all intra-temporal effects on fitness, while $s_{\mathrm{e}}(z)$ (eq. 7b) is the net effect of all inter-temporal effects (i.e. all effects within and between demographic periods, respectively). More broadly, eq. (7) consists in the sum of effects on the fitness of a focal individual stemming from all individuals that currently live (eq. 7a) or have lived (eq. 7b) in the population. The perspective here is thus that the focal individual is the recipient of phenotypic effects, present and past. How past phenotypic effects are mediated by environmental dynamics is left implicit in eq. (7), contained in eq. (7b) through $\mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}})$. In the next section, we expose such environmental effects by unpacking eq. (7b) and shifting from a recipient-centered to an actor-centered perspective.

3.2 Actor-centered perspective: environmentally mediated extended phenotypic effects

To understand natural selection on social traits, it is often helpful to see the focal individual as the actor, rather than the recipient, of phenotypic effects [47, 2, 3]. To shift to this perspective here, we can leverage the space-time homogeneity of our model to see that $\partial w/\partial z_{\mathbf{k},t}$ in eq. (7) is equivalent to the total effect of the focal individual on the fitness of the individuals in a patch at distance $\mathbf{k}$ at t steps in the future, and that relatedness $R_{\mathbf{k},t}$ (eq. 9) quantifies the extent to which an individual sampled in a patch at distance $\mathbf{k}$ at t steps in the future is more (or less) likely than a randomly sampled individual to carry an allele identical by descent to one in the focal individual at a homologous locus [48]. These considerations readily lead to an actor-centered perspective for selection on intra-temporal effects, $s_{\mathrm{w}}(z)$ (eq. 7a).

For selection on inter-temporal effects, $s_{\mathrm{e}}(z)$, we further need to unpack the phenotypic effects through the environmental dynamics in eq. (7b). To do so, we now let the time index t denote time forward so that $\mathbf{n}_{\mathbf{k},t}$ is the value of the environmental state variable in patch $\mathbf{k}$ at t time steps in the future of the focal generation ($t = 0$), and likewise let $\mathbf{z}_{\mathbf{k},t}$ denote the collection of population phenotypes at time t in the future. Environmental dynamics forward in time are characterised by rewriting eq. (2) as

$$n_{\mathbf{k},t+1} = \begin{cases} g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0}) & \text{for } t = 0 \\ g(\mathbf{z}_{\mathbf{k},t}, \mathbf{n}_{\mathbf{k},t}) & \text{for } t \geq 1 \end{cases}, \tag{11}$$

for all $\mathbf{k} \in \mathcal{G}$, where $\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}$ is equal to $\mathbf{z}_{\mathbf{k},0}$ except that the component $z_{\mathbf{0},0}$ in this vector is replaced with $z^{\mathrm{R}}_{\mathbf{0},0} = \frac{1}{N} z_{\bullet} + \frac{N-1}{N} z_{\mathbf{0},0}$, i.e. the average phenotype in the focal patch including the focal individual (e.g. for a one-dimensional lattice, $\mathbf{z}^{\mathrm{R}}_{k,0} = (z_{k,0}, z_{k+1,0}, \ldots, z_{D-1,0}, z^{\mathrm{R}}_{0,0}, z_{1,0}, \ldots, z_{k-1,0})$). Eq. (11) brings upfront the potential complexity of characterising the environmental consequences of a trait change in the focal individual. This is because the trait of the focal individual, $z_{\bullet}$, influences the environmental state variable of potentially any patch $\mathbf{k}$ over one generation, $n_{\mathbf{k},1}$, which can in turn have knock-on effects in the future on $n_{\mathbf{k},2}$, $n_{\mathbf{k},3}$, and so on throughout space in an interactive way. To broadly denote such effects, we write

$$e_{\mathbf{k},t} = \frac{\partial n_{\mathbf{k},t}}{\partial z_{\bullet}}, \tag{12}$$

for the extended phenotypic effect of the focal individual on the environmental state variable in patch $\mathbf{k}$ at t generations in the future. We show in Appendix C.1 that selection on inter-temporal effects $s_{\mathrm{e}}(z)$ (eq. 7b) can then be written in terms of these extended phenotypic effects as

$$s_{\mathrm{e}}(z) = \sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} \sum_{\mathbf{j}\in\mathcal{G}} \underbrace{e_{\mathbf{j}-\mathbf{k},t}}_{\substack{\text{effect of focal}\\ \text{on environment}\\ \text{in } \mathbf{j}-\mathbf{k},t}} \times \underbrace{\frac{\partial w(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j},0}}}_{\substack{\text{effect of environmental}\\ \text{perturbation in } \mathbf{j}-\mathbf{k},t\\ \text{on fitness in } \mathbf{k},t}} \times \underbrace{NR_{\mathbf{k},t}}_{\substack{\text{total genetic}\\ \text{value of } \mathbf{k},t\\ \text{for focal}}} . \tag{13}$$

As eq. (13) indicates, $s_{\mathrm{e}}(z)$ consists in the total effect of the focal individual on the fitness of individuals in each patch $\mathbf{k}, t$ in the future, via a change in the environmental state of possibly all patches $\mathbf{j}-\mathbf{k}, t$, where fitness is weighted by their relatedness $R_{\mathbf{k},t}$ to the focal individual. From the point of view of the focal individual, relatedness $R_{\mathbf{k},t}$ can be thought of as the "genetic value" of an individual randomly sampled in patch $\mathbf{k}, t$ in units of fitness. More specifically, $R_{\mathbf{k},t}$ can be interpreted as the number of units of its own fitness that the focal individual is willing to exchange with an individual from patch $\mathbf{k}, t$ against one unit of theirs without changing the mutant's probability of fixation at z^*. Selection thus favours the focal sacrificing some of its own fitness to increase fitness in patch $\mathbf{k}, t$ when $R_{\mathbf{k},t} > 0$ and to decrease fitness when $R_{\mathbf{k},t} < 0$. How such sacrifice impacts the environment encountered by recipients is quantified by the extended phenotypic effect $e_{\mathbf{j}-\mathbf{k},t}$ in eq. (13).

The remaining challenge is how to compute $e_{\mathbf{k},t}$, given the complex repercussions that a perturbation has in time and space (i.e. how to quantify a perturbation in the coupled dynamical system defined by eq. 11). We show in Appendix C.2 that this can be achieved through Fourier analysis using the following building blocks. First, we let

$$\psi_{\mathbf{k}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0})}{\partial z_{\bullet}} \tag{14}$$

be the focal individual's effect on the environmental state variable of patch $\mathbf{k}$ over one generation. Owing to our space-time homogeneity assumptions, this effect can equivalently be calculated as

$$\psi_{\mathbf{k}} = \begin{cases} \dfrac{1}{N}\dfrac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z^{\mathrm{R}}_{\mathbf{0},0}} & \text{for } \mathbf{k} = \mathbf{0} \\ \dfrac{1}{N}\dfrac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} & \text{otherwise} \end{cases} \tag{15}$$

which is often more useful in concrete applications (as it only requires characterising the environmental map of the focal patch, e.g. eq. 34 below, rather than for all $\mathbf{k}$ as in eq. 14). We write

$$\Psi(\mathbf{h}) = \sum_{\mathbf{k}\in\mathcal{G}} \psi_{\mathbf{k}}\chi_{\mathbf{k}}(\mathbf{h}) \tag{16}$$

for the Fourier transform of $\psi_{\mathbf{k}}$. Similarly, we let

$$c_{\mathbf{k}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0})}{\partial n_{\mathbf{0},0}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{k},0}} \tag{17}$$

be the effect of the environmental state variable of one patch on the environmental state variable of another at distance $\mathbf{k}$ over one generation, and

$$\mathcal{C}(\mathbf{h}) = \sum_{\mathbf{k}\in\mathcal{G}} c_{\mathbf{k}}\chi_{\mathbf{k}}(\mathbf{h}), \tag{18}$$

its Fourier transform. With the above notation, the extended phenotypic effect can be efficiently computed as the inverse Fourier transform

$$e_{\mathbf{k},t} = \frac{1}{D} \sum_{\mathbf{h} \in \mathcal{G}} \mathcal{E}_t(\mathbf{h}) \overline{\chi}_{\mathbf{k}}(\mathbf{h}) \tag{19}$$

of

$$\mathcal{E}_t(\mathbf{h}) = \mathcal{C}(\mathbf{h})^{t-1} \Psi(\mathbf{h}). \tag{20}$$

The form of eq. (20) indicates that $e_{\mathbf{k},t}$ can be thought of as a perturbation in the dynamics of an environmental state variable that ripples into the future (see Fig. 4 for a graphical illustration). This perturbation has its origin in a focal individual whose trait affects the environmental state variables of possibly multiple patches over one generation (captured by $\Psi(\mathbf{h})$ in eq. 20). This one-generational change then propagates through space over $t-1$ generations owing to the environmental dynamics, finally impacting the environment of individuals t generations downstream of the focal individual (captured by $\mathcal{C}(\mathbf{h})^{t-1}$ in eq. 20). In Box II, we generalize eqs. (13)-(20) to multi-dimensional environmental dynamics, i.e. when multiple environmental state variables can be affected by the evolving trait and whose dynamics can interact with one another.

Eq. (13) together with eqs. (15)-(20) constitute a basis to quantify and understand selection on traits that have inter-temporal effects through the environment under isolation by distance. These equations formalise the intuition behind inclusive fitness arguments for environmentally mediated social interactions, saying that natural selection tends to favor traits whose environmental effects benefit the fitness of relatives (i.e. individuals more likely to carry identical-by-descent genes). Here, the fundamental currency is individual fitness, and its exchange rate among individuals is given by relatedness. In many cases, however, it is not fitness that is directly impacted by traits or the environment, but rather some intermediate payoff, such as calories, the amount of prey caught, or the size of a breeding territory. In turn, this payoff influences survival and reproduction, which determine fitness. We explore such scenarios in the next section.

3.3 Payoff-mediated fitness: scaled relatedness or the genetic value of others in units of payoff

3.3.1 Payoff and fitness

Following much of evolutionary game theory (e.g. [6]), we now consider the case where fitness depends on some payoff function that summarizes social interactions between individuals. We let this function be $\pi : \mathbb{R} \times \mathbb{R}^D \times \mathbb{R}^D \to \mathbb{R}_+$, such that $\pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})$ is the payoff to the focal individual with phenotype $z_\bullet$ when the collection of average phenotypes among all other individuals is $\mathbf{z}_{\mathbf{0},0}$ and

the collection of environmental state variables across all patches is $\mathbf{n}_{\mathbf{0},0}$. We assume that the fitness of this focal individual can in turn be written as a function, $\tilde{w} : \mathbb{R}_+ \times \mathbb{R}_+ \times \mathbb{R}_+^{D-1} \to \mathbb{R}_+$ of, the payoff to self, the average payoff to a patch neighbour, and the average payoff to an individual from each patch other than the focal (of which there are $D-1$), i.e. as

$$w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) = \tilde{w}(\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})), \tag{21}$$

where

$$\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) = \left(\underbrace{\pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}_{\pi_\bullet}, \underbrace{\pi(z_{\mathbf{0},0}, \mathbf{z}^{\mathrm{n}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}_{\pi_{\mathbf{0}}}, \ldots, \underbrace{\pi(z_{\mathbf{j},0}, \mathbf{z}^{\mathrm{R}}_{\mathbf{j},0}, \mathbf{n}_{\mathbf{j},0})}_{\pi_{\mathbf{j}}}, \ldots \right) \tag{22}$$

is a vector of length $D+1$ collecting the payoff $\pi_\bullet$ to the focal individual, the average payoff $\pi_{\mathbf{0}}$ to a patch neighbour, and the average payoff $\pi_{\mathbf{j}}$ to an individual from each patch $\mathbf{j} \neq \mathbf{0}$. As an argument to $\pi_{\mathbf{0}}$ (in eq. 22), we used $\mathbf{z}^{\mathrm{n}}_{\mathbf{0},0}$ to denote a vector that is equal to the vector $\mathbf{z}_{\mathbf{0},0}$ except for its first entry, which is given by $z^{\mathrm{n}}_{\mathbf{0},0} = \frac{1}{N-1} z_\bullet + \left(\frac{N-2}{N-1}\right) z_{\mathbf{0},0}$, i.e. by the average trait among the neighbours of a neighbour of the focal individual. This captures the notion that the focal individual can influence the payoff of its neighbours.

Eq. (21) allows individual fitness to depend on the payoff of all the individuals of its generation in an arbitrary way. This said, in most practical applications the survival and fecundity of an individual depend only on its own payoff. In this case, fitness may be written as

$$\tilde{w}(\boldsymbol{\pi}) = \underbrace{s\left(\pi_\bullet\right)}_{\text{survival}} + \underbrace{\sum_{\mathbf{i} \in \mathcal{G}} m_{\mathbf{i}} \left[1 - s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] \frac{f(\pi_\bullet)}{\sum_{\mathbf{j} \in \mathcal{G}} m_{\mathbf{i}-\mathbf{j}} f^{\mathrm{R}}(\pi_{\mathbf{j}})}}_{\text{reproduction into spots left open by deaths}}, \tag{23}$$

where $s : \mathbb{R}_+ \to \mathbb{R}_+$ and $f : \mathbb{R}_+ \to \mathbb{R}_+$ are survival and fecundity functions, respectively, and quantities with R as superscript are defined such that $s^{\mathrm{R}}(\pi_{\mathbf{0}}) = \frac{1}{N} s(\pi_\bullet) + \frac{N-1}{N} s(\pi_{\mathbf{0}})$ is the average survival in the focal patch, otherwise $s^{\mathrm{R}}(\pi_{\mathbf{i}}) = s(\pi_{\mathbf{i}})$ for $\mathbf{i} \neq \mathbf{0}$; and $f^{\mathrm{R}}(\pi_{\mathbf{i}}) = \frac{1}{N} f(\pi_\bullet) + \frac{N-1}{N} f(\pi_{\mathbf{0}})$ is the average fecundity in the focal patch, otherwise $f^{\mathrm{R}}(\pi_{\mathbf{i}}) = f(\pi_{\mathbf{i}})$ for $\mathbf{i} \neq \mathbf{0}$. If we set survival to zero in eq. (23), we obtain the fitness function of the classical Wright-Fisher process (e.g. eq. 3 in [49], in the absence of environmental effects and for circular stepping-stone model). More generally, where s is a positive constant and payoff only influences fecundity f, eq. (23) implements a form of "death–birth" updating protocol (i.e. where individuals sampled at random to die are replaced by selecting individuals according to payoff, e.g. [33, 50]). Conversely, a "birth-death" updating is obtained by setting f to a positive constant and letting payoff influence survival s only. Eq. (23) will constitute a useful platform to explore more specific examples later, even though many of our results hold for the more general relationship between payoff and fitness given by eq. (21).

3.3.2 Selection under payoff-mediated fitness

We show in Appendix D that if fitness is of the form of eq. (21), the selection gradient can be written as

$$s(z) \propto \underbrace{\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet} + \sum_{\mathbf{k}\in\mathcal{G}} \kappa_{\mathbf{k},0} \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}}}_{\propto s_{\mathrm{w}}(z)} + \underbrace{\sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} N\kappa_{\mathbf{k},t} \sum_{\mathbf{j}\in\mathcal{G}} e_{\mathbf{k}-\mathbf{j},t} \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j},0}}}_{\propto s_{\mathrm{e}}(z)}, \tag{24}$$

where

$$\kappa_{\mathbf{k},t} = \begin{cases} \dfrac{R_{\mathbf{0},0} - \frac{1}{N-1}\lambda_{\mathbf{0}}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}}{1 - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}} & \text{for } t = 0 \text{ and } \mathbf{k} = \mathbf{0} \\[2ex] \dfrac{R_{\mathbf{k},0} - \frac{1}{N}\lambda_{\mathbf{k}}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j}-\mathbf{k},0}}{1 - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}} & \text{for } t = 0 \text{ and } \mathbf{k} \neq \mathbf{0} \\[2ex] \dfrac{R_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j}-\mathbf{k},t}}{1 - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}} & \text{otherwise,} \end{cases} \tag{25}$$

and

$$\lambda_{\mathbf{j}} = -\frac{\partial \tilde{w}(\boldsymbol{\pi})}{\partial \pi_{\mathbf{j}}} \Big/ \frac{\partial \tilde{w}(\boldsymbol{\pi})}{\partial \pi_\bullet}. \tag{26}$$

To understand eq. (24), it is first useful to interpret $\lambda_{\mathbf{j}}$ (eq. 26) as a coefficient of fitness interdependence through payoffs. Specifically, $\lambda_{\mathbf{j}}$ measures the effect on the fitness of the focal individual of a change in the payoff of an individual at distance $\mathbf{j}$, relative to the effect of the payoff of the focal individual on its own fitness. When positive, $\lambda_{\mathbf{j}}$ can thus be interpreted as the strength of competition as it indicates how much an increase in the payoffs of an individual at distance $\mathbf{j}$ reduces the fitness of the focal individual. With this in mind, the coefficient $\kappa_{\mathbf{k},t}$ (eq. 25) can be seen as a measure of relatedness scaled to competition (or scaled relatedness for short, e.g. [51, 52, 5]; with eq. 25 extending to isolation by distance the formalization of this concept by [53]). In fact, $\kappa_{\mathbf{k},t}$ can be interpreted as the number of units of its own payoff that the focal individual is willing to exchange with one randomly sampled individual from patch $\mathbf{k}, t$ against one unit of theirs without changing the mutant's probability of fixation at z^*. The scaled relatedness coefficient $\kappa_{\mathbf{k},t}$ can thus be seen as the genetic value of other individuals in patch $\mathbf{k}, t$ from the point of view of the focal individual in units of payoff.

From the considerations above, eq. (24) can be read as an inclusive fitness effect at the payoff level. That is, selection depends on how the focal individual influences its own payoff and the payoff of all other individuals across patches, now and in the future, weighted by their scaled relatedness $\kappa_{\mathbf{k},t}$. For recipients in the future ($t \geq 1$), payoff effects are mediated by how the focal individual perturbs the environment in each patch (via $e_{\mathbf{k}-\mathbf{j},t}$ in eq. 24), and in turn by how such environmental perturbation influences payoffs (via $\partial\pi/(\partial n_{\mathbf{j},0})$ in eq. 24).

We use Fourier analysis to compute scaled relatedness $\kappa_{\mathbf{k},t}$ in Appendix E for the fitness model eq. (23)

and arbitrary dispersal distribution $m_{\mathbf{k}}$. Our results are summarized in Box III. For example, we obtain that under a Wright-Fisher process,

$$\kappa_{\mathbf{k},t} = \begin{cases} -\dfrac{1}{DN-1} & \text{if } t = 0 \\ \dfrac{D(p_{\mathbf{k},t} - 1/D)}{DN-1} & \text{otherwise} \end{cases} \tag{27}$$

holds, where

$$p_{\mathbf{k},t} = \frac{1}{D} \sum_{\mathbf{h} \in \mathcal{G}} \mathcal{M}(\mathbf{h})^t \, \overline{\chi}_{\mathbf{k}}(\mathbf{h}) \tag{28}$$

is the probability that, under neutrality, a gene descending from the focal individual is in patch $\mathbf{k}$ at $t > 0$ steps in the future (which depends on the characteristic function $\mathcal{M}(\mathbf{h})$ of the dispersal distribution, eq. 10). The collection of these probabilities, $p_t = (p_{\mathbf{k},t})_{\mathbf{k} \in \mathcal{G}}$, can thus be seen as the distribution of a standard random walk on $\mathcal{G}$ with step distribution given by the dispersal distribution $m_{\mathbf{k}}$. When such a random walk leads to a probability $p_{\mathbf{k},t}$ that is greater than under a uniform distribution, i.e. when $p_{\mathbf{k},t} > 1/D$, eq. (27) indicates that scaled relatedness $\kappa_{\mathbf{k},t}$ is positive, so that selection favours environmental transformations that increase payoffs in patch $\mathbf{k}, t$. Conversely, selection favours environmental transformations that decrease payoffs in patches where $p_{\mathbf{k},t}$ is less than under a uniform distribution (i.e. $p_{\mathbf{k},t} < 1/D$). Which patches are those depends on the dispersal distribution (compare Fig. 2E with Fig. 2F for short and long-range dispersal in a 1D lattice, and Fig. 3E with Fig. 3F for short and long-range dispersal in a 2D lattice).

The selection gradient eq. (24) also shows that our formalization recovers a number of previous results of social evolution theory. To see these connections, assume that there are no ecologically meditated interactions, i.e. $\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) / \partial n_{\mathbf{0},0} = 0$, that $-C(z) = \partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) / \partial z_\bullet < 0$ is a net payoff cost to self, and that $B_{\mathbf{k}}(z) = \partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) / \partial z_{\mathbf{k},0}$ is a payoff benefit to individuals at distance $\mathbf{k}$, which is typical of models under the heading of the evolution of "cooperation" or "altruism". Further, suppose that individuals interact only with individuals at a single distance $\mathbf{k}$ so that the selection gradient is proportional to $-C(z) + \kappa_{\mathbf{k},0} B_{\mathbf{k}}(z)$. Then, eq. (24) entails that the cost-to-benefit ratio that needs to be overcome for such a helping behavior to be favored is

$$\kappa_{\mathbf{k},0} > C(z) / B_{\mathbf{k}}(z). \tag{29}$$

For a Wright-Fisher process, whose hallmark is no survival and fecundity effects, $\kappa_{\mathbf{k},0}$ reduces to $-1/(ND-1)$ (eq. 27). Thus, helping cannot spread regardless of population structure because condition (29) cannot be satisfied as long as $B_{\mathbf{k}}(z) > 0$ holds. Yet, we also see that harming recipients, i.e. $B_{\mathbf{k}}(z) < 0$, can be favored by selection when D is finite. This result was first derived for a lattice-structured population for $D \to \infty$ and $\mathbf{k} = \mathbf{0}$ by [54], and for finite D and any $\mathbf{k}$ under a circular one-dimensional habitat in [3] (chapter 8, and respectively generalized to any abelian group struc-

ture in [55] and [41]). More generally, the scaled relatedness coefficient given in Box III allows to recover established conditions for the spread of helping and harming behavior in lattice-structured populations under different biological assumptions, such as for survival effects or for fecundity effects with overlapping generations (e.g. [56, 11, 33, 50], see [41] for the explicit connections to this literature). Finally, in the presence of ecologically mediated interactions, so that $\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})/\partial n_{\mathbf{0},0} \neq 0$, eq. (24) recovers eq. (A.21) in [40] which holds for a Wright-Fisher process (to see correspondence, set $s_{\mathbf{k},t} = N\left(\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})/\partial n_{\mathbf{0},0}\right) e_{\mathbf{k},t}$ in eq. 24).

3.3.3 Local interactions

In eq. (24), payoffs can depend on the traits expressed and the environmental variables of all patches. In many instances, payoff effects can reasonably be assumed to be local, i.e. the payoff of an individual depends only on the traits and the environment of its patch. In this case, the payoff to the focal individual can be written as

$$\pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) = \pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0}), \tag{30}$$

and the selection gradient eq. (24) reduces to

$$s(z) \propto \underbrace{\frac{\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})}{\partial z_\bullet} + \frac{\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}}\kappa_{\mathbf{0},0}}_{\propto s_{\mathrm{w}}(z)} + \underbrace{\frac{\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})}{\partial n_{\mathbf{0},0}} NK}_{\propto s_{\mathrm{e}}(z)}, \tag{31}$$

where

$$K = \sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\kappa_{\mathbf{k},t} \tag{32}$$

summarizes selection on environmentally mediated social interactions (see Appendix F for derivation and eq. III.C in Box III for more details). When $K = 0$, selection is thus blind to the effects of the trait on the environment, even if the environment affects payoff (i.e. even if $\partial\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0})/(\partial n_{\mathbf{0},0}) \neq 0$). When $K > 0$, selection favours trait values that improve the environment (i.e. the payoff in the future increases). Conversely, when $K < 0$, selection favours trait values that deteriorate the environment (i.e. the payoff in the future decreases). Which of these outcomes unfolds depends on the interaction between extended phenotypic effects $e_{\mathbf{k},t}$ and scaled relatedness coefficients $\kappa_{\mathbf{k},t}$, with $K > 0$ when $e_{\mathbf{k},t}$ and $\kappa_{\mathbf{k},t}$ tend to be of the same sign (i.e. when $\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\kappa_{\mathbf{k},t} > 0$ holds), and $K > 0$ when they tend to be of opposite sign (i.e. when $\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\kappa_{\mathbf{k},t} < 0$ holds). In the next section, we explore how this interaction depends on dispersal and the way environmental state variables of different patches influence one another.

3.4 Inter-temporal helping and harming through a lasting commons

To gain more specific insights into how isolation by distance influences the way selection shapes environmentally mediated interactions, consider a scenario where the environmental variable is some lasting commons (e.g. a common-pool resource, a toxic compound) that can move in space, and whose production depends on the evolving trait that is individually costly to express. We assume that the commons is a "good" when the environmental variable takes positive values ($\hat{n} > 0$) and a "bad" when it takes negative values ($\hat{n} < 0$). We also assume that the trait leads to the former when $z > 0$ and to the latter when $z < 0$. The trait can thus be broadly thought of as environmentally mediated helping (increasing survival and reproduction to recipients) when $z > 0$, and as environmentally mediated harming (decreasing survival and reproduction to recipients) when $z < 0$.

Fitness and payoff respectively take the forms of eq. (23) and eq. (30). Specifically, we assume the payoff to the focal is given by

$$\pi(z_\bullet, z_{\mathbf{0},0}, n_{\mathbf{0},0}) = \exp\left(B n_{\mathbf{0},0}^{\alpha_\mathrm{B}} - C z_\bullet^{\alpha_\mathrm{C}}\right), \tag{33}$$

where $B > 0$ and $C > 0$ are parameters that respectively tune the effects of the environmental variable in the focal patch $n_{\mathbf{0},0}$ and of the modifying trait $z_\bullet$ of the focal individual on the payoff of the focal individual. These effects also depend on the shape parameters α_B and α_C, which we assume are positive integers, with α_B odd (e.g. $\alpha_\mathrm{B} = 1$) and α_C even (e.g. $\alpha_\mathrm{C} = 2$). Thus, the local commons increases (resp. decreases) payoffs when $n_{\mathbf{0},0} > 0$ (resp. $n_{\mathbf{0},0} < 0$) holds, but any trait expression, i.e. any $z_\bullet$ away from 0, is individually costly and reduces individual payoff. We also assume that costs increase more steeply than benefits, i.e. $\alpha_\mathrm{C} > \alpha_\mathrm{B}$ holds.

Meanwhile, how the trait modifies the commons is determined by the environmental map g (eq. 2). Here, we assume that g is given by

$$g(\mathbf{z}_{\mathbf{0},0}^\mathrm{R}, \mathbf{n}_{\mathbf{0},0}) = d_\mathbf{0}\left((1-\epsilon)n_{\mathbf{0},0} + P(z_{\mathbf{0},0}^\mathrm{R})\right) + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} d_\mathbf{j}\left((1-\epsilon)n_{\mathbf{j},0} + P(z_{\mathbf{j},0})\right), \tag{34}$$

which states that the commons changes from one demographic time point to the next due to three processes. First, the commons is modified or "produced" in a patch according to a function $P : \mathbb{R} \to \mathbb{R}$ of the average trait expressed in that patch, i.e. $z_{\mathbf{0},0}^\mathrm{R} = \frac{1}{N} z_\bullet + \frac{N-1}{N} z_{\mathbf{0},0}$ in the focal patch and $z_{\mathbf{j},0}$ otherwise (with $\mathbf{j} \neq \mathbf{0}$). We assume that the function P is such that (i) $P(0) = 0$ holds, and (ii) P is monotonically increasing with z, i.e. $P'(z) > 0$ for all $z \in \mathbb{R}$. Second, each unit of commons "diffuses" or moves with probability $d_\mathbf{j}$ to a patch at distance $\mathbf{j}$ from its source patch. The probability distribution defined by $d_\mathbf{j}$

can be thought of as the environmental equivalent of the dispersal probability distribution $m_{\mathbf{j}}$. We let

$$\mathcal{D}(\mathbf{h}) = \sum_{\mathbf{i}\in\mathcal{G}} d_{\mathbf{i}}\chi_{\mathbf{i}}(\mathbf{h}) \tag{35}$$

denote the characteristic function of this distribution for future use (i.e. $\mathcal{D}(\mathbf{h})$ is to $d_{\mathbf{j}}$ what $\mathcal{M}(\mathbf{h})$ is to $m_{\mathbf{j}}$, eq. 10). Third, a unit of commons decays with rate $0 < \epsilon \leq 1$ from one time step to the next. Plugging eq. (34) into eq. (3) indicates that in a monomorphic population for z, the dynamics of the commons stabilises to

$$\hat{n} = \frac{P(z)}{\epsilon}, \tag{36}$$

which is positive when $z > 0$ and negative when $z < 0$, and whose absolute value increases as the rate of decay ϵ decreases, as expected (note that the equilibrium $\hat{n}$, eq. 36, is unique because g is linear in P, and stable because $\epsilon > 0$).

With fitness of the form of eq. (23) and payoff of the form eq. (30), we can use eqs. (31) and (32) to characterise selection. With $\kappa_{\mathbf{k},t}$ given in Box III, all that remains to be computed are the extended phenotypic effects, $e_{\mathbf{k},t}$. Substituting eq. (34) into eqs. (15) and (17), we obtain $\psi_{\mathbf{k}} = P'(z)d_{\mathbf{k}}/N$, $c_{\mathbf{k}} = (1-\epsilon)d_{\mathbf{k}}$, which substituted into eqs. (16) and (18) in turn yield

$$\Psi(\mathbf{h}) = P'(z)\mathcal{D}(\mathbf{h})/N, \tag{37}$$

$$\mathcal{C}(\mathbf{h}) = (1-\epsilon)\mathcal{D}(\mathbf{h}). \tag{38}$$

Substituting eqs. (37) and (38) into eq. (20) then gives $\mathcal{E}_t(\mathbf{h}) = (1-\epsilon)^{t-1}P'(z)\mathcal{D}(\mathbf{h})^t/N$, which substituted into eq. (19) leads to

$$e_{\mathbf{k},t} = \frac{P'(z)}{N}(1-\epsilon)^{t-1}q_{\mathbf{k},t}, \tag{39}$$

for the extended phenotypic effect $e_{\mathbf{k},t}$ on patch $\mathbf{k}, t$, where

$$q_{\mathbf{k},t} = \frac{1}{D}\sum_{\mathbf{h}\in\mathcal{G}} \mathcal{D}(\mathbf{h})^t\overline{\chi}_{\mathbf{k}}(\mathbf{h}). \tag{40}$$

Equation eq. (39) can be understood as follows. By marginally changing its trait value, a focal individual produces $P'(z)/N$ additional units of commons. Each such unit decays with time according to $(1-\epsilon)^{t-1}$, and ends up in patch $\mathbf{k}, t$ according to $q_{\mathbf{k},t}$ (eq. 40), which can be interpreted as the probability that a non-decaying unit of the commons modified in the focal patch is located in patch $\mathbf{k}$ t generations in the future. In fact, the collection $q_t = (q_{\mathbf{k},t})_{\mathbf{k}\in\mathcal{G}}$ yields the distribution of a standard random walk in $\mathcal{G}$ with step distribution $d_{\mathbf{k}}$. Extended phenotypic effects thus depend critically on the way the commons moves in space as captured by $d_{\mathbf{k}}$ (see Fig. 5 for examples of $e_{\mathbf{k},t}$ in a 1D model).

In turn, how selection depends on extended phenotypic effects is found by substituting eq. (33) and

eq. (39) into eq. (31). From this, we obtain

$$s(z) \propto B\,\alpha_{\mathrm{B}} \left(\frac{P'(z)}{\epsilon}\right) \left(\frac{P(z)}{\epsilon}\right)^{\alpha_{\mathrm{B}}-1} \Omega - C\,\alpha_{\mathrm{C}}\, z^{\alpha_{\mathrm{C}}-1}, \tag{41}$$

where

$$\Omega = \sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} \epsilon(1-\epsilon)^{t-1} \kappa_{\mathbf{k},t}\, q_{\mathbf{k},t} \tag{42}$$

can be thought of as the expected genetic value in units of payoff of all the individuals in the future that are affected by a unit of the commons in the focal patch. Since the term multiplying Ω in eq. (41) is positive (recall that α_{B} is odd and hence $\alpha_{\mathrm{B}} - 1$ is even), the selection gradient increases with Ω, and the greater Ω is, the greater the z favoured by selection. In fact, the selection gradient reduces to $s(0) \propto \Omega$ at $z = 0$ (under our assumptions about parameters and $P(z)$). This shows that in a population where the trait is initially absent so that individuals have no effect on the commons, selection favours environmental modifications leading to a common good ($z > 0$) when $\Omega > 0$, or to a common bad ($z < 0$) when $\Omega < 0$. Put differently, selection favours environmentally mediated inter-temporal helping when, in the eyes of the focal individual, the recipient of such help on average has positive genetic value in units of payoff, and conversely, inter-temporal harming when it has negative genetic value.

Further insights can be generated if we assume that P is linear such that $P(z) = P_0 z$. In that case, the singular trait value z^* satisfies

$$z^* = \left[\frac{B}{C} \cdot \frac{\alpha_{\mathrm{B}}}{\alpha_{\mathrm{C}}} \cdot \left(\frac{P_0}{\epsilon}\right)^{\alpha_{\mathrm{B}}} \cdot \Omega\right]^{\frac{1}{\alpha_{\mathrm{C}}-\alpha_{\mathrm{B}}}}. \tag{43}$$

Such z^* is convergence stable under our assumption that the cost of expression increases faster than the benefits, i.e. $\alpha_{\mathrm{C}} > \alpha_{\mathrm{B}}$. From eq. (43) it is clear that the absolute value of z^* increases with the benefit-to-cost ratio B/C, with $\alpha_{\mathrm{B}}/\alpha_{\mathrm{C}}$, and with the environmental effect of the trait P_0. However, whether z^* is positive or negative, so whether helping or harming evolves, ultimately depends on the sign of Ω, i.e. whether the expected genetic value Ω of a modification to the commons is positive or negative in payoff units.

The impact of species dispersal and commons movement on Ω can be understood most easily by assuming that payoff influences fecundity under a Wright-Fisher process (i.e. $f' > 0$ and $s' = s = 0$ in Box III). We show in Appendix G.1 that in that case, Ω can be expressed as

$$\Omega = \frac{\epsilon D^2}{ND-1} \sum_{t=1}^{\infty} (1-\epsilon)^{t-1} \mathrm{cov}(p_t, q_t), \tag{44}$$

where $\mathrm{cov}(p_t, q_t)$ is the covariance between the distributions of the random walks, of genes $p_t = (p_{\mathbf{k},t})_{\mathbf{k}\in\mathcal{G}}$ (eq. 28), and of the commons $q_t = (q_{\mathbf{k},t})_{\mathbf{k}\in\mathcal{G}}$ (eq. 40). This covariance is positive when

there is a positive association between gene lineages and the commons these lineages modify. In other words, Ω is positive and helping is favoured when an environmental modification owing to the expression of a gene is most likely to be experienced by future carriers of that same gene and its identical-by-descent copies. Conversely, Ω tends to be negative and harming is favoured when this environmental modification is less likely to be experienced by future carriers.

While eq. (44) offers intuition on the biological conditions leading to positive or negative values of Ω, this quantity is more readily computed by noting that $\Omega = \epsilon KN/P'(z)$, where K is defined in eq. (32), and by substituting eqs. (37) and (38) into eq. (III.E) in Box III, to obtain

$$\Omega = \frac{\epsilon}{ND-1} \sum_{\mathbf{j} \in \mathcal{G} \setminus \mathbf{0}} \frac{\mathcal{D}(-\mathbf{j})\mathcal{M}(\mathbf{j})}{1-(1-\epsilon)\mathcal{D}(-\mathbf{j})\mathcal{M}(\mathbf{j})} \tag{45}$$

Figures 6AB give the sign of Ω under a binomial model for the distance of both the dispersal of the focal species and the movement of the commons (using the model detailed in Appendix G.4). These figures show that such model of dispersal allows for both positive and negative values of Ω and thus for the evolution of both inter-temporal helping and harming. Here, helping corresponds to altruism and harming to spite (*sensu* chapter 7 in [3]) since an individual can never obtain direct benefits from its own trait expression through the environment (as generations are non-overlapping under a Wright-Fisher process).

More generally, numerical explorations of Ω (Fig. 6AB) indicate that spite tends to be favoured by: (i) high levels of dispersal in the evolving species; (ii) high levels of movement of the commons; (iii) high environmental decay ϵ; and (iv) large differences in the dispersal distance of the species and of the commons (e.g. when individuals disperse short distances while the commons move far away from their original patch). This is because these conditions tend to lead to a negative association between gene lineages and the commons these lineages modify. Conversely, altruism tends to be favoured when dispersal and movement are weak, environmental decay is low, and the distributions of the species' dispersal and of the commons' movement are similar (Figure 6AB, white region). In fact, under weak dispersal and movement (so that $m_{\mathbf{0}} = 1-m$ and $d_{\mathbf{0}} = 1-d$ with m and d close to zero), we show in Appendix G.2 that regardless of the dispersal and movement distributions, we have

$$\Omega = \frac{1}{\epsilon}\left(\frac{D-1}{ND-1}\right)\left(1-\frac{m+d}{\epsilon}\right), \tag{46}$$

which is always positive when m and d are sufficiently small (i.e. smaller than ϵ). This is so because under these assumptions an individual's lineage and the commons originating from its patch will be strongly and locally associated.

We compared the singular strategy z^* found by substituting eq. (45) into eq. (43) with results from individual-based simulations. In these simulations, each offspring mutates with probability 10^{-4}, in

which case a normally distributed deviation with mean 0 and standard deviation 10^{-2} is added to the parental trait value. The only difference between these simulations and our analytical scenario is thus that multiple alleles can segregate due to mutation (rather than just two under a trait substitution sequence, see [5] for finite populations). Nevertheless, we find an excellent fit between the convergence stable z^* and the mean population trait value in simulations (Fig. 6C-E).

The case where payoff influences survival rather than fecundity ($s' > 0$ and $f' = 0$ in eq. 23) is illustrated in Fig. 7 (the expression of Ω for this case in terms of characteristic dispersal functions can be found in Appendix G.3). This analysis reveals that harming tends to be favoured when baseline survival s is low, especially when environmental decay is also low (Fig 7C). This is because, otherwise, an individual may harm itself in the future. But apart from this, selection is not fundamentally different when payoff influences survival rather than fecundity in this model (i.e. under a birth-death *vs.* death-birth process).

4 Discussion

Our analyses characterise in two main ways the selection gradient on a trait that impacts the deterministic dynamics of environmental state variables that can be abiotic or biotic, and that in turn feed back on survival and reproduction under isolation by distance.

First, we showed how selection on a trait due to its environmental effects can be understood in terms of how a focal actor influences the fitness of all future individuals via a modification to the environmental state variables these individuals experience (eq. 13 and eq. II.D for the case of multiple environmental variables). The relevant trait-driven environmental modifications are formalized as extended phenotypic effects that quantify how a trait change in an actor individual in the present affects the environmental state variables in all patches at all future times (the $e_{\mathbf{k},t}$ effects, eq. 19). While extended phenotypic effects are typically thought to directly benefit the actor or related contemporaries [57, 58], these effects in our model are all indirect, carrying over in space and time, thus influencing the fitness of future carriers of the actor's trait (when dispersal is limited). The associations between environmental and genetic variation that are necessary for selection to target trait-driven environmental modifications are given by the product between the extended environmental effects $e_{\mathbf{k},t}$ and the relatedness coefficients $R_{\mathbf{k},t}$ (see eq. 13), both of which can be efficiently computed using Fourier transforms (Fig. 4, eqs. 19-20 and II.E-II.F for a multivariate environment). These gene-environment associations indicate that selection favours traits or behaviours with environmental effects such that, when expressed by a focal individual, the environmental effects increase (or decrease) the fitness of future individuals that are more (or less) related to the focal than other individuals at that same future generation.

The second version of the selection gradient that we derived is based on the extra assumption that interactions between individuals are mediated through a payoff function (see eq. 23), as in most of traditional evolutionary game theory (e.g. [59, 60, 6]). Selection on a trait due to its environmental effects can still be viewed from an actor-centered perspective, but this time at the level of payoff rather than fitness. Specifically, selection can be quantified in terms of how a focal individual influences the payoff of all future individuals via a modification to the environment these individuals experience, weighted by the relatedness between these individuals and the focal, but now scaled to take competition into account (the term proportional to $s_{\mathrm{e}}(z)$ in eq. 24, with scaled relatedness given in eqs. 25-26). The concept of scaled relatedness is useful because it summarizes in a single quantity, here one for each spatial and temporal distance, all the consequence of interactions among related individuals for indirect selection [61, 51, 52, 5]. That is, scaled relatedness balances, on one hand, the positive effects of boosting the reproductive success of relatives in a particular spatial position, with, on the other hand, the negative effects of increasing competition for these relatives by affecting the reproduction and survival of others across the habitat. The increase of kin competition can be strong enough to offset the indirect benefits of social behaviour when social interactions occur among contemporaries (and generations do not overlap, e.g. [54, 3]). Because the strength of kin competition depends on the specifics of the life-cycle, such as whether generations overlap or not, whether payoff influences fecundity or survival, the evolution of direct social interactions is sensitive to such assumptions (see [51] for a review). This is notably the case under isolation by distance, where the evolution of altruism crucially depends on whether reproduction is modelled as a "birth-death" or "death-birth" process (e.g. [62, 63, 64]). The first is akin to iteroparous reproduction with fecundity effects and can sustain altruism, while the second is akin to iteroparous reproduction with survival effects, and here kin competition inhibits altruism (e.g. [56, 11, 13, 14]).

In contrast, we have found that in our model of environmentally mediated social interactions through a lasting commons, whether selection favours the evolution of helping or harming depends weakly on whether payoff influences survival or fecundity. There are two explanations for this. The first is that, because of environmental legacy, the effects on recipients are felt in the distant future, which decreases the competition among the focal's own offspring [65, 38]. The second explanation is that, in our model, individuals and their environmental effects can move in space independently, which further dissociates the positive and negative effects of interactions among relatives. In fact, this decoupling between benefits and costs means that natural selection can readily favor either altruism or spite in our model with non-overlapping generations. Which of these behaviours evolves depends on whether the combination of dispersal pattern and commons movement cause environmental effects to fall predominantly on individuals that are more or less related than average in the future.

Our findings on environmentally mediated spite merit further discussion as existing models suggest that the conditions for the evolution of spite are restrictive. By spite, we refer here to a trait or

behaviour whose expression decreases the individual fitness of both its actor and recipients. This is a strong form of spite (chapter 7 in [3]), which contrasts with the more commonly explored scenarios of weak spite (where the behavior directly increases the actor's fitness, e.g. [66, 67]). The evolution of strong spite typically relies on the existence of mechanisms by which individuals can evaluate their relatedness with social partners and thus behave according to some kin or type-recognition mechanism (e.g. [68, 69, 70, 71, 72]). By contrast, in our model, spite is indiscriminate: an individual deteriorates the environment of others in the future without paying attention to the identities of recipients, even if this comes at a cost now. With this in mind, it is noteworthy that spite can evolve even when local populations are not small (e.g. of local size 50, Fig. 6). More broadly, our results illustrate how environmentally mediated social interactions under isolation by distance can evolve to be as relevant for fitness as direct social interactions.

The two main assumptions of our model are that fitness and environmental effects are homogeneous in space and time, and that environmental dynamics are deterministic. These assumptions are common to previous mathematical models interested in environmental or ecological changes in space that are evolutionarily driven, and particularly to those where individuals produce an environmental commons that moves according to a diffusion process (e.g. [73, 74, 75, 76, 77]). These models further assume a separation of time scales between demography and the commons such that in between the reproduction, death or dispersal of any individual in the entire population, the dynamics of the commons reaches a stable distribution across the landscape. By contrast, here we have assumed that it is the mutation process, rather than the demographic process, that is slow compared to environmental dynamics. Reproduction, death or dispersal can occur on a similar time scale than environmental dynamics in our model, as is usually the case in ecological models (e.g. [78, 79]). As a result, even though environmental dynamics are described by a deterministic system (eq. 11, also as in most ecological models, [78, 79]), realised environmental dynamics fluctuate randomly on a similar time scale than unavoidable genetic fluctuations (owing to finite patch size). The next challenge would be to consider a fully stochastic system for the environmental variables (i.e. to extend eq. 11 to the dynamics of a probability distribution). This would be especially useful to investigate the effects of demographic stochasticity in response to trait evolution [22], allowing us to model, for instance, environmentally mediated evolutionary suicide or rescue. Our framework may nevertheless provide a suitable approximation to cases of demographic and environmental stochasticity (with eq. 11 giving the expectation in state variable at the next time step, conditional on the states of at the previous step). This approach has been shown to work well under the island model of dispersal provided patches were not too small and dispersal not too limited [38]. It would be interesting to investigate how this holds up under isolation by distance.

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Box I. Fourier analysis on finite abelian groups

We assume that the set of patches $\mathcal{G}$ is endowed with an abelian group structure, which allows us to consider more general spatial structures than just lattice models (e.g. hierarchical structures). The group $\mathcal{G}$ is defined as the direct product,

$$\mathcal{G} = \mathbb{Z}_{D_1} \times \ldots \times \mathbb{Z}_{D_d}, \tag{I.A}$$

where $\mathbb{Z}_{D_i} = \{0, \ldots, D_i - 1\}$ is the additive group of integers modulo D_i. The group $\mathcal{G}$ then consists of the set of all vectors $\mathbf{x} = (x_1, \ldots, x_d)$ with $x_i \in \mathbb{Z}_{D_i}$ together with addition (where addition between two vectors is component-wise). On such a group, the discrete Fourier transform $\mathcal{F}(\mathbf{x})$ of function f at $\mathbf{x}$ is given by

$$\mathcal{F}(\mathbf{x}) = \sum_{\mathbf{y} \in \mathcal{G}} f_{\mathbf{y}} \chi_{\mathbf{y}}(\mathbf{x}), \tag{I.B}$$

where the "character" function

$$\chi_{\mathbf{y}}(\mathbf{x}) = \prod_{i=1}^{d} \exp\left(\frac{2\pi\imath x_i y_i}{D_i}\right) = \exp\left(2\pi\imath \sum_{i=1}^{d} \frac{x_i y_i}{D_i}\right), \tag{I.C}$$

with $\imath = \sqrt{-1}$, is defined for all $\mathbf{x} = (x_1, \ldots, x_d) \in \mathcal{G}$ and $\mathbf{y} = (y_1, \ldots, y_d) \in \mathcal{G}$. Here, we followed the convention of population genetics (e.g. [44, 45, 3]) and defined the Fourier transform in terms of the character $\chi_{\mathbf{y}}(\mathbf{x})$ (instead its conjugate given in eq. I.E, which is more standard in engineering). As such, the Fourier transform gives the characteristic function when f is a probability distribution. For instance, $\mathcal{M}(\mathbf{h}) = \sum_{\mathbf{k} \in \mathcal{G}} m_{\mathbf{k}} \chi_{\mathbf{k}}(\mathbf{h})$ is the characteristic function of the dispersal distribution $m_{\mathbf{k}}$. The original function is found by using

$$f_{\mathbf{x}} = \mathcal{L}_{\mathbf{x}}(\mathcal{F}) = \frac{1}{D} \sum_{\mathbf{y} \in \mathcal{G}} \mathcal{F}(\mathbf{y}) \overline{\chi}_{\mathbf{x}}(\mathbf{y}), \tag{I.D}$$

where $\mathcal{L}_{\mathbf{x}}(\mathcal{F})$ is the inverse transform of $\mathcal{F}$ at $\mathbf{x}$, which is defined in terms of the conjugate of $\chi_{\mathbf{y}}(\mathbf{x})$:

$$\overline{\chi}_{\mathbf{x}}(\mathbf{y}) = \prod_{i=1}^{d} \exp\left(-\frac{2\pi\imath x_i y_i}{D_i}\right) = \exp\left(-2\pi\imath \sum_{i=1}^{d} \frac{x_i y_i}{D_i}\right) \tag{I.E}$$

(e.g. [80]). Another property that we use in our analysis is the orthogonality relation between characters:

$$\sum_{\mathbf{k} \in \mathcal{G}} \overline{\chi}_{\mathbf{k}}(\mathbf{i}) \overline{\chi}_{\mathbf{k}}(\mathbf{j}) = \sum_{\mathbf{k} \in \mathcal{G}} \overline{\chi}_{\mathbf{k}}(\mathbf{i} + \mathbf{j}) = \begin{cases} |\mathcal{G}| = D & \text{if } \mathbf{j} + \mathbf{i} = \mathbf{0} \\ 0 & \text{otherwise} \end{cases} \tag{I.F}$$

([80], p. 169).

Box II. Multi-dimensional environment

We generalize $s_{\mathrm{w}}(z)$ and $s_{\mathrm{e}}(z)$ to the case where there are $n_{\mathrm{e}} > 1$ environmental state variables. We denote by $\mathbf{n}_{\mathbf{k},t} = (n_{1,\mathbf{k},t}, n_{2,\mathbf{k},t}, ...n_{n_{\mathrm{e}},\mathbf{k},t})$ the vector of such variables in patch $\mathbf{k}, t$ (where $n_{i,\mathbf{k},t} \in \mathbb{R}$ is the value of the ith environment). The fitness of the focal individual is now given by

$$w(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0}) \qquad \text{with } w : \mathbb{R} \times \mathbb{R}^{D} \times \mathbb{R}^{Dn_{\mathrm{e}}} \to \mathbb{R}_{+}, \tag{II.A}$$

where $\vec{\boldsymbol{n}}_{\mathbf{0},0}$ is the values at $t = 0$ of $\vec{\boldsymbol{n}}_{\mathbf{0},t} = (\mathbf{n}_{\mathbf{0},t}, \mathbf{n}_{\mathbf{1},t}, ..., \mathbf{n}_{\mathbf{k},t}, ..., \mathbf{n}_{\mathbf{D}_{-1},t})$, whose elements are solutions of

$$n_{i,\mathbf{k},t+1} = g_i(\mathbf{z}_{\mathbf{k},t}, \vec{\boldsymbol{n}}_{\mathbf{k},t}) \qquad \text{for } i = 1, 2, .., n_{\mathrm{e}} \text{ and all } \mathbf{k} \in \mathcal{G}, \tag{II.B}$$

where g_i is the transition map for environmental variable i. We assume that in a monomorphic population z, there is a hyperbolically stable fixed point to environmental dynamics,

$$\hat{n}_i = g_i(\mathbf{z}, \hat{\vec{\mathbf{n}}}) \qquad \text{for } i = 1, 2, ..., n_{\mathrm{e}}, \tag{II.C}$$

where $\hat{\vec{\mathbf{n}}} = (\hat{\mathbf{n}}, ..., \hat{\mathbf{n}})$ is a vector of dimension D whose entries are all given by $\hat{\mathbf{n}} = (\hat{n}_1, ..., \hat{n}_{n_{\mathrm{e}}})$. With fitness given by eq. (II.A), selection on intra-temporal effects $s_{\mathrm{w}}(z)$ remains unchanged given by eq. (7a) with $w(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}}))$ substituted for $w(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_{\mathrm{H}})))$. For selection on inter-temporal effects $s_{\mathrm{e}}(z)$, carrying out *mutadis mutandis* the same calculations as we have for the one-dimensional case, yields

$$s_{\mathrm{e}}(z) = \sum_{t=1}^{\infty} \sum_{i=1}^{n_{\mathrm{e}}} \sum_{\mathbf{j} \in \mathcal{G}} \sum_{\mathbf{k} \in \mathcal{G}} e_{i,\mathbf{j}-\mathbf{k},t} \frac{\partial w(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0})}{\partial n_{i,\mathbf{j},0}} N R_{\mathbf{k},t}, \tag{II.D}$$

where $e_{i,\mathbf{k},t}$ is the extended phenotypic effect on environmental variable i in patch $\mathbf{k}, t$. This is computed as the inverse transform

$$e_{i,\mathbf{k},t} = \frac{1}{D} \sum_{\mathbf{h} \in \mathcal{G}} \mathcal{E}_{i,t}(\mathbf{h}) \overline{\chi}_{\mathbf{k}}(\mathbf{h}), \tag{II.E}$$

where $\mathcal{E}_{i,t}(\mathbf{h})$ is the i-th element of the vector $\vec{\mathcal{E}}_t(\mathbf{h}) = (\mathcal{E}_{1,t}(\mathbf{h}), \mathcal{E}_{2,t}(\mathbf{h}), ..., \mathcal{E}_{n_{\mathrm{e}},t}(\mathbf{h}))$, which is obtained from

$$\vec{\mathcal{E}}_t(\mathbf{h}) = \boldsymbol{C}(\mathbf{h})^{t-1} \vec{\Psi}(\mathbf{h}). \tag{II.F}$$

Here, the community matrix $\boldsymbol{C}(\mathbf{h})$ has its ij-th element given by $\mathcal{C}_{ij}(\boldsymbol{\theta}) = \sum_{\mathbf{k} \in \mathcal{G}} c_{i,\mathbf{0} \leftarrow j,\mathbf{k}} \chi_{\mathbf{k}}(\mathbf{h})$, where

$$c_{i,\mathbf{0} \leftarrow j,\mathbf{k}} = \frac{\partial g_i(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0})}{\partial n_{j,\mathbf{k},t}} \tag{II.G}$$

is the effect of environmental variable j in the focal patch on environmental variable i in patch $\mathbf{k}, t$. The vector $\vec{\Psi}(\mathbf{h})$ has i-th element given by $\Psi_i(\mathbf{h}) = \sum_{\mathbf{k} \in \mathcal{G}} \psi_{\mathbf{k},i} \chi_{\mathbf{k}}(\mathbf{h})$, which is the Fourier transform of

$$\psi_{i,\mathbf{k}} = \begin{cases} \dfrac{1}{N} \dfrac{\partial g_i(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0})}{\partial z^{\mathrm{R}}_{\mathbf{0},0}} & \text{for } \mathbf{k} = \mathbf{0} \\[2ex] \dfrac{1}{N} \dfrac{\partial g_i(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \vec{\boldsymbol{n}}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} & \text{otherwise.} \end{cases} \tag{II.H}$$

Under the infinite island model of dispersal, where $R_{\mathbf{k},t} = 0$, $e_{i,\mathbf{k},t} = 0$, and $c_{i,\mathbf{0} \leftarrow j,\mathbf{k}} = 0$ for all $\mathbf{k} \in \mathcal{G}$ except $\mathbf{k} = \mathbf{0}$, eq. (II.D) reduces to eqs. 15-16 of [38].

Box III. Scaled-relatedness coefficients

With fitness given by eq. (23), we show in Appendix E that

$$\kappa_{\mathbf{k},t} = \begin{cases} \dfrac{\mathcal{L}_{\mathbf{k}}(F) - (1+s)\left[s'f + 2f'(1-s)\right]/(2D)}{N\left[s'f + f'(1-s)\right] + \mathcal{L}_{\mathbf{0}}(F) - (1+s)\left[s'f + 2f'(1-s)\right]/(2D)} & \text{if } t = 0 \\ \dfrac{\mathcal{L}_{\mathbf{k}}(G_t) - (1+s)\left[s'f + 2f'(1-s)\right]/(2D)}{N\left[s'f + f'(1-s)\right] + \mathcal{L}_{\mathbf{0}}(F) - (1+s)\left[s'f + 2f'(1-s)\right]/(2D)} & \text{otherwise,} \end{cases} \tag{III.A}$$

where as usual, all functions are evaluated at the resident trait value z, and $\mathcal{L}_{\mathbf{k}}(D)$ is the inverse Fourier transform of a function $D(\mathbf{h})$ at $\mathbf{k}$ (eq. I.B of Box I). The functions F and G_t are defined as

$$\begin{aligned} F(\mathbf{h}) &= -\frac{(1-s)\left[s'f - f'2s\right]\mathcal{M}(\mathbf{h})}{1+s+(1-s)\mathcal{M}(\mathbf{h})}, \\ G_t(\mathbf{h}) &= \frac{(1+s)\left[s'f + f'(1-s)(1+\mathcal{M}(\mathbf{h}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{h})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{h})}. \end{aligned} \tag{III.B}$$

For fecundity effects under a Wright-Fisher process ($s = s' = 0$), the above reduces to $F(\mathbf{h}) = 0$ and $G_t(\mathbf{h}) = f'\mathcal{M}(\mathbf{h})^t$, which yields eq. (27) of the main text when $f' = 1$ (i.e. the payoff is directly fecundity). Using eq. (III.A), we also show in Appendix F that the summary statistic K, for selection on environmentally mediated social interactions under local interactions (eq. 32), is given by

$$K = \frac{1}{H}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1+s)\left[s'f + f'(1-s)(1+\mathcal{M}(\mathbf{j}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{j}) - \mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]\Psi(-\mathbf{j})}{\left[1+s+(1-s)\mathcal{M}(\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]}, \tag{III.C}$$

where

$$H = (DN-1)\left[s'f + f'(1-s)\right] - \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1-s)\left[s'f - 2f's\right]\mathcal{M}(\mathbf{j})}{1+s+(1-s)\mathcal{M}(\mathbf{j})}. \tag{III.D}$$

For fecundity effects under a Wright-Fisher process ($s = s' = 0$) the summary statistic K simplifies to

$$K = \frac{1}{DN-1}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\mathcal{M}(\mathbf{j})\Psi(-\mathbf{j})}{1-\mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})}, \tag{III.E}$$

while for survival effects ($f' = 0$), it simplifies to

$$K = \frac{1}{(DN-1) - \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1-s)\mathcal{M}(\mathbf{j})}{1+s+(1-s)\mathcal{M}(\mathbf{j})}} \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1+s)\left[s+(1-s)\mathcal{M}(\mathbf{j}) - \mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]\Psi(-\mathbf{j})}{\left[1+s+(1-s)\mathcal{M}(\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]}. \tag{III.F}$$

Figures

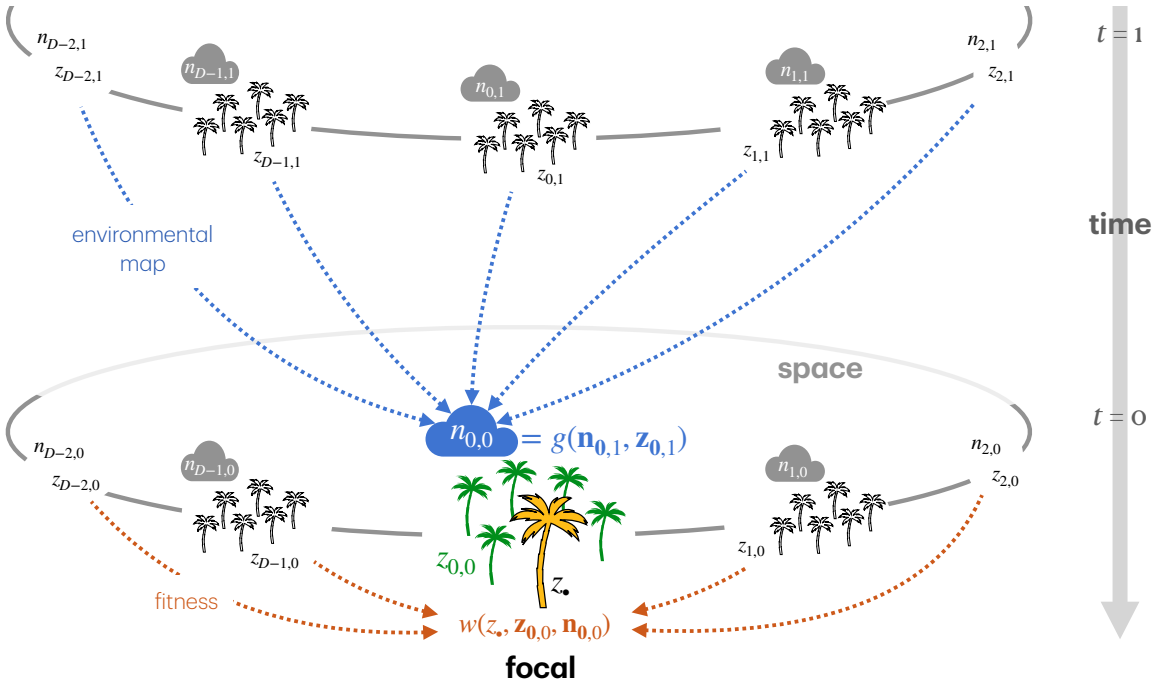

Figure 1: **A model for environmentally mediated social interactions in space and time.** Schematic description of our model for a one-dimensional lattice habitat (sections 2.1-2.2 for details). Each patch $k \in \{\ldots, D-1, 0, 1, \ldots\}$ at time $t \in \{0, 1, \ldots\}$ in the past is characterized by an environmental state variable $n_{k,t}$ (represented here by a cloud, e.g. water level, concentration of a pollutant, density of a resource), and the average trait value $z_{k,t}$ expressed by the individuals it carries (e.g. water absorption rate, detoxifying capacity, handling time; individuals represented here as palms). The environmental state $n_{0,0}$ of the focal patch $k = 0$ at $t = 0$ depends on all environmental states and traits of the previous generation according to the environmental map g (blue dashed arrows, eq. 2). In turn, the fitness of a focal individual with trait $z_\bullet$ (in yellow) depends on all environmental states and traits expressed in its own generation according to the fitness function w (orange arrows, eq. 1). The two functions g and w thus characterise how evolutionary and environmental dynamics interact with one another through dual inheritance of traits and environmental state variables.

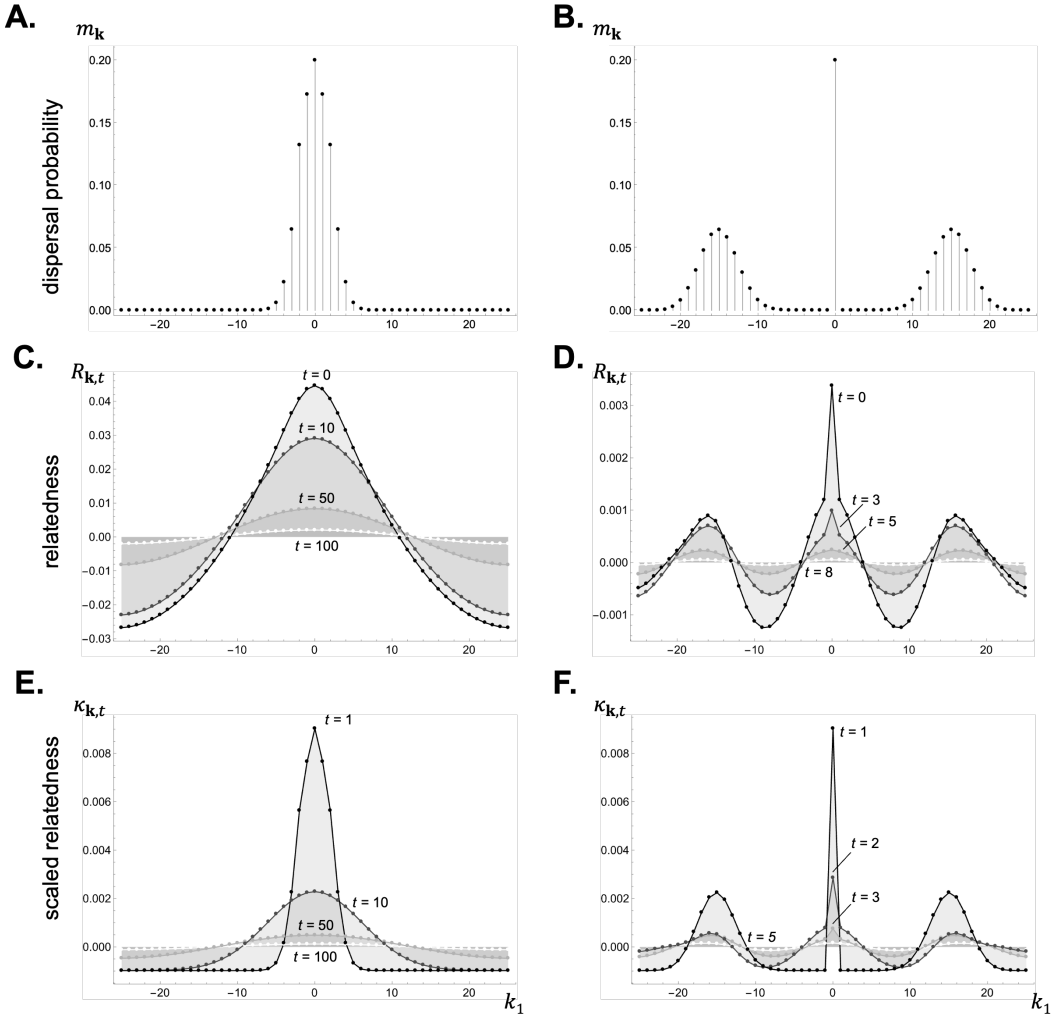

Figure 2: **Dispersal distribution, relatedness and scaled relatedness in a 1D lattice model under short and long range dispersal.** Panels **A-B**: Panels **A-B**: Dispersal distribution $m_{\mathbf{k}}$ in a lattice-structured population in a one-dimensional habitat (with $D_1 = 51$). An offspring leaves its natal patch with probability $1 - m_{\mathbf{0}} = m = 0.8$ and disperses to a patch at a Manhattan distance that follows a truncated binomial distribution (eq. A-6 in Appendix B.1) with mean $\overline{\lambda}_{\mathrm{m}} = 1.9$ in A, leading to short-range dispersal, and $\overline{\lambda}_{\mathrm{m}} = 15$ in B for long range dispersal. The distance dispersed along each dimension of the habitat is uniformally distributed across all dimensions and directions (Appendix B.1 for details). Panels **C-D:** Relatedness $R_{\mathbf{k},t}$ for dispersal distributions shown in A and B, respectively (using eq. 9 with patch size $N = 20$ and no adult survival $s = 0$). Panel C highlights how relatedness decays in time and space, becoming negative away from the focal deme when dispersal is short range, whereas in panel D, where dispersal is long range, relatedness is negative at intermediate and large distances thus leading to a multimodal distribution of relatedness values . Panels **E-F:** Scaled relatedness $\kappa_{\mathbf{k},t}$ for dispersal distributions shown in A and B, respectively, under a Wright-Fisher model with fecundity effects (using eq. 27 with patch size $N = 20$). The trend of scaled-relatedness is similar as that for relatedness. See Mathematica Notebook for how to generate these figures.

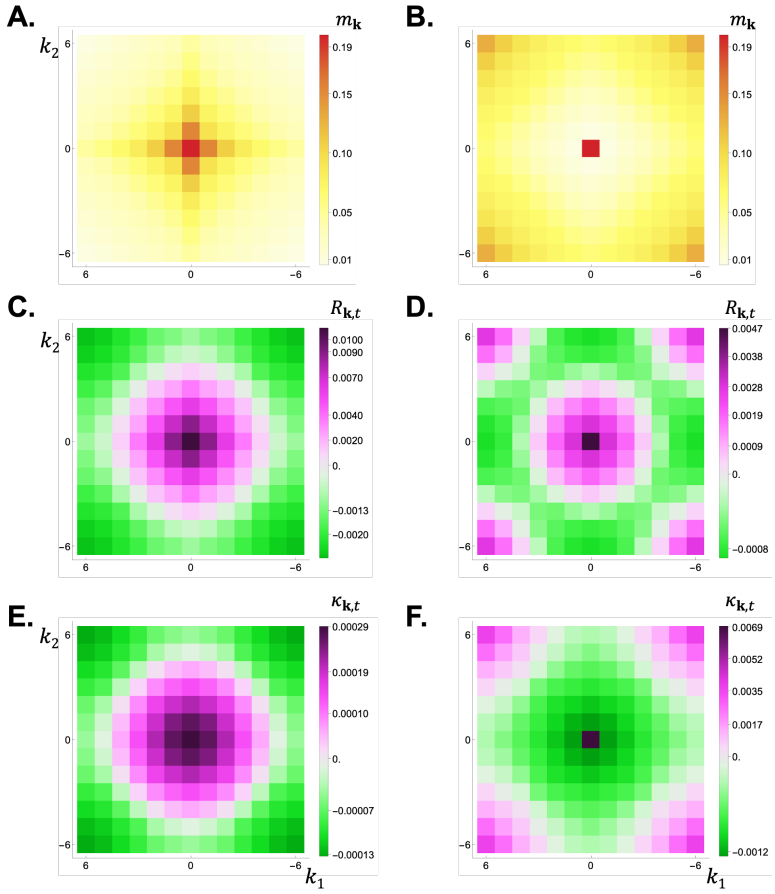

Figure 3: **Dispersal distribution, relatedness and scaled relatedness in a 2D lattice model under short and long range dispersal.** Panels **A-B:** Dispersal distribution $m_{\mathbf{k}}$ in a one-dimensional habitat (with $D_1 = D_2 = 13$). An offspring leaves its natal patch with probability $1 - m_{\mathbf{0}} = m = 0.8$ and disperses to a patch at a Manhattan distance that follows a truncated binomial distribution with mean $\overline{\lambda}_{\mathrm{m}} = 1.5$ in A, leading to short-range dispersal, and $\overline{\lambda}_{\mathrm{m}} = 11$ in B for long range dispersal (Appendix B.2 for details). Panels **C-D:** Relatedness $R_{\mathbf{k},0}$ from the dispersal distributions shown in A and B, respectively (using eq. 9 with patch size $N = 20$ and no adult survival $s = 0$). Panels **E-F:** Scaled relatedness, $\kappa_{\mathbf{k},10}$ in E and $\kappa_{\mathbf{k},1}$ in F, from the dispersal distributions shown in A and B, respectively, for a Wright-Fisher model (using eq. 27 with patch size $N = 20$. See Mathematica Notebook for how to generate these figures.).

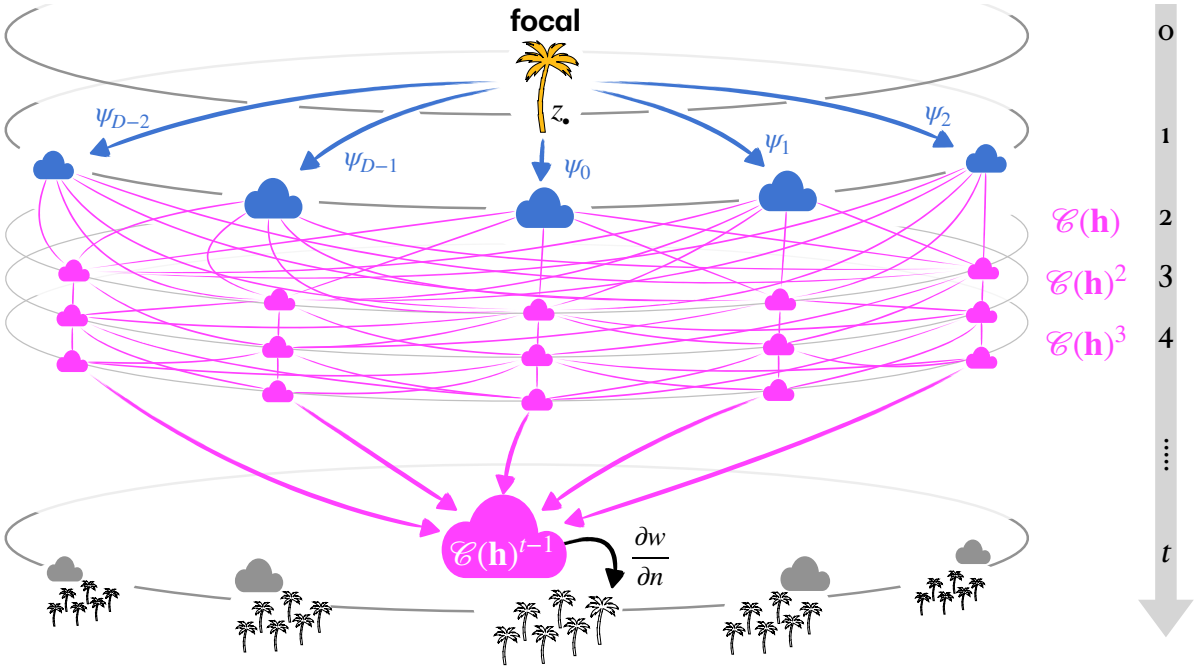

Figure 4: **Selection on environmentally mediated social interaction: extended phenotypic effects.** This illustrates the main idea of eqs. (13)-(20), which express selection on inter-temporal environmental effects in terms of the effect that a focal individual has on the fitness of all future individuals via modifications of environmental dynamics. Through the expression of its trait $z_\bullet$, a focal individual at time $t = 0$ perturbs the environmental state variable of each patch $\mathbf{k}$ at time $t = 1$ according to $\psi_{\mathbf{k}}$ (or its transform $\Psi(\mathbf{h})$, eqs. 15-16, blue arrows). These environmental effects then ripple through space over $t-1$ time steps according to the transform $\mathcal{C}(\mathbf{h})^{t-1}$ (eqs. 17-18), which quantifies the impact on the environmental state variable in each patch $\mathbf{k}$ at time t. Finally, the relevance of these inter-temporal environmental effects for selection depends on their relatedness weighted fitness effects (given by terms of the form $\partial w/(\partial n) \times NR_{\mathbf{k},t}$ in eq. 13).

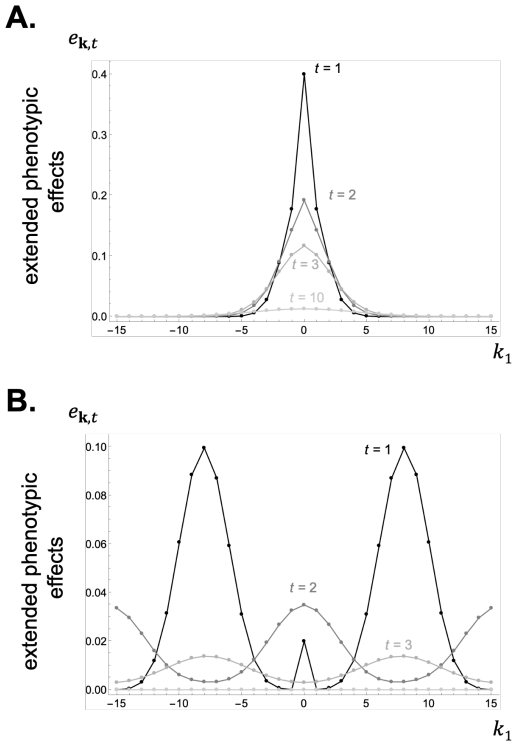

Figure 5: **Extended phenotypic effects in a 1D lattice model under short and long range movement of the commons.** Panel **A**: When the commons moves locally, extended phenotypic effects $e_{\mathbf{k},t}$ decay in time and space away from the focal deme (from eq. 39 with movement probability $d = 0.6$ and expected movement distance $\overline{\lambda}_{\mathrm{d}} = 1.54$, see Appendix G.4 for details on movement is modelled; production function $P(z) = Nz$, i.e. each unit of z contribute to one unit of resource; decay rate $\epsilon = 0.2$; other parameters: same as Fig. 2A). Panel **B**: In contrast, when the resource moves at greater distances, extended phenotypic effects $e_{\mathbf{k},t}$ are greatest further away from the focal deme (using eq. 39 with movement parameters $d = 0.98$ and $\overline{\lambda}_{\mathrm{d}} = 8$; production function $P(z) = Nz$; decay rate $\epsilon = 0.5$; other parameters: same as Fig. 2A). See Mathematica Notebook for how to generate these figures.

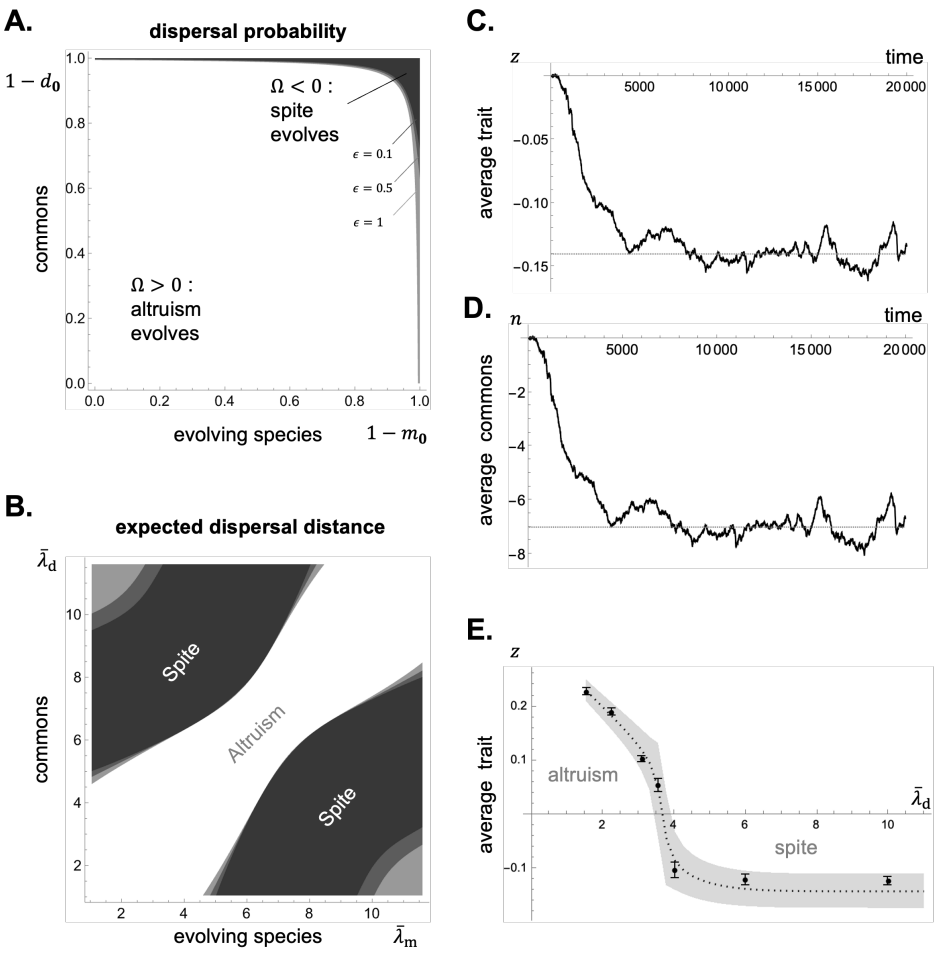

Figure 6: **Selection favours altruism or spite depending on dispersal of the evolving species and the commons in a 2D lattice model. A-B**. Regions of dispersal parameters leading to the evolution of altruism, $\Omega > 0$ (in white), or of spite, $\Omega < 0$ (in gray) for an example in 2D (with $D_1 = D_2 = 13$ and $N = 50$) under a Wright-Fisher life-cycle with fecundity effects (with Ω computed from eq. 45). **A**: Combination of dispersal probability of the evolving species $m = 1 - m_0$ (x-axis) and of the commons $d = 1 - d_0$ (y-axis) for different levels of environmental decay ϵ in different shades of gray ($\epsilon = 0.1, 0.5, 1$) with expected dispersal distance fixed ($\overline{\lambda}_m = 1.54$ and $\overline{\lambda}_d = 8$). This shows that spite is favoured by high levels of dispersal and high levels of environmental decay. **B**: Combination of expected dispersal distance of the evolving species $\overline{\lambda}_m$ (x-axis) and of the commons $\overline{\lambda}_d$ (y-axis) for different levels of environmental decay ϵ in different shades of gray (A for legend) with dispersal probability fixed ($m = 0.98$ and $d = 1$). This shows that spite is favoured by dispersal asymmetry between the evolving species and the commons. **C-D** Evolution of spite in individual based simulations under a Wright-Fisher life-cycle with fecundity effects (with $D_1 = D_2 = 13$, $N = 50$, $m = 0.3$, $\overline{\lambda}_m = 1.54$, $d = 1$, $\overline{\lambda}_d = 8$, $B = 2$, $\alpha_B = 1$, $C = 1$, $\alpha_C = 4$, $P(z) = Nz$; for mutation: the trait mutates during reproduction with probability 10^{-4}, in which case a normally distributed deviation with mean 0 and standard deviation 10^{-2} is added to the parental trait value). Panel C shows the average trait z in the population and D shows the average commons level or environmental variable n (with simulations in full and analytical prediction in dashed – from eq. 43 for z and 36 for n). **E** Observed *vs.* predicted equilibrium trait value in individual based simulations running for 20'000 generations under different expected dispersal distance of the commons $\overline{\lambda}_d$ leading to altruism ($z > 0$) and spite ($z < 0$). Other parameters: same as in C-D. Prediction is shown as a dashed line (from eq. 43) with grey region around for twice the standard deviation obtained from the stationary phenotypic distribution (from eq. A-5, see Mathematica Notebook for how to generate panels A, B and E). Observed values of the trait average in the population are shown as black dots for the average from generation 5000 to 15000, with error bars for standard deviation over the same 10000 generations. Simulations were initialised at the predicted convergence stable trait value.

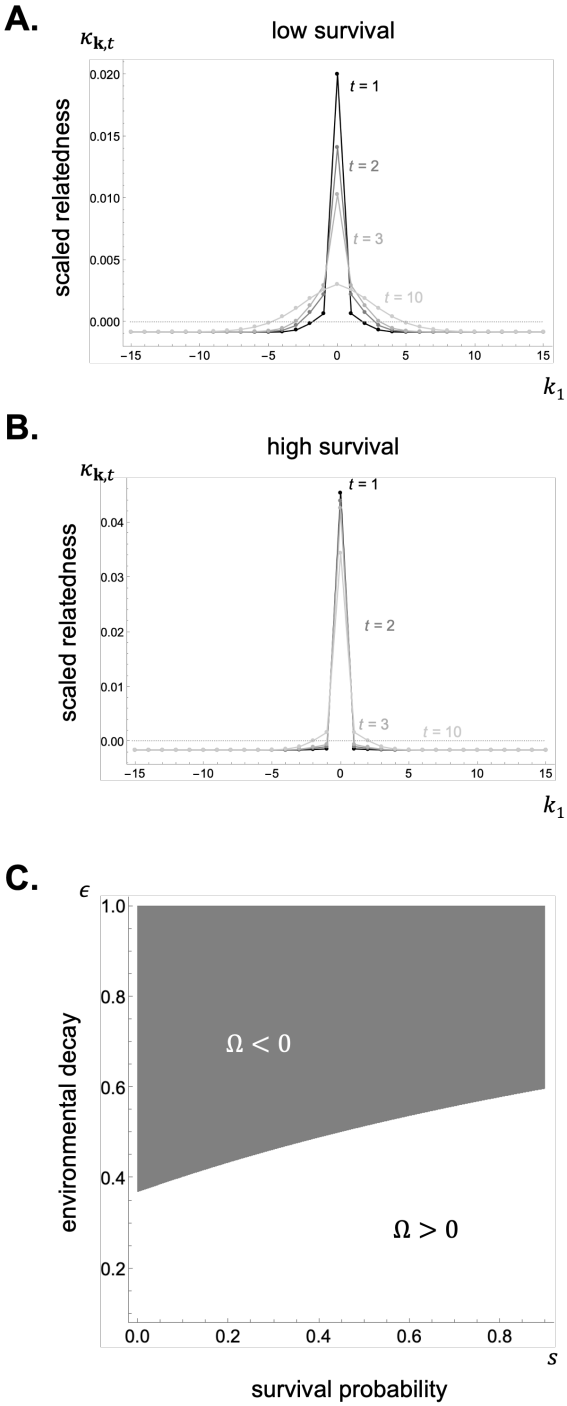

Figure 7: **Scaled relatedness and selection under survival effects in a 1D lattice model. A-B:** Scaled relatedness $\kappa_{\mathbf{k},t}$ in 1D under survival effects (from Box III with $s = 0$ in A and $s = 0.9$ in B; other parameters: same as in Fig. 5A). These shows that genetic value decays away from the focal deme especially quickly when baseline survival is high (compare A and B). Otherwise, these profiles of scaled relatedness are similar to to those in Fig. 5A, which suggests that selection act similarly when the trait affects survival or fecundity. **C.** Parameter region where selection favours the evolution of helping $\Omega > 0$ or harming $\Omega < 0$ under survival effects with adult survival probability s on the x-axis and environmental decay ϵ on the y-axis (Ω computed from eq. 42 using eq. A-121; other parameters: same as in Fig. 5B i.e. under long range movement of the commons. See Mathematica Notebook for how to generate these figures.

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Appendix A Convergence stability from fixation probability

Here, we show eq. (5) of the main text from considering the fixation probability of a single mutant with trait value $z+\delta$ into a population monomorphic for resident trait z. Let $\Pi(z+\delta, z)$ denote the fixation probability of this mutant, and by

$$\phi(z) = \left.\frac{\mathrm{d}\Pi(z+\delta, z)}{\mathrm{d}\delta}\right|_{\delta=0} \tag{A-1}$$

the derivative of the fixation probability with respect to mutant effect. Using this notation, a trait value z^* that is convergence stable under a trait substitution sequence is characterized by

$$\phi(z^*) = 0 \quad \text{and} \quad \left.\frac{\mathrm{d}\phi(z)}{\mathrm{d}z}\right|_{z=z^*} < 0 \tag{A-2}$$

[20, 3, 5]. Under our modeling assumptions, the perturbation of the fixation probability is given by

$$\phi(z) = \lim_{\mu\to 0}\left(\frac{1-\overline{Q}_0}{1-Q_{\mathbf{0},0}}\right) \times \left(\frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_\mathrm{H}))}{\partial z_\bullet} + \sum_{t=0}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_\mathrm{H}))}{\partial z_{\mathbf{k},t}} R_{\mathbf{k},t}\right), \tag{A-3}$$

(eq. 1 of [46] together with eq. A11 of [65]), which can be expressed as

$$\phi(z) = \underbrace{\lim_{\mu\to 0}\left(\frac{1-\overline{Q}_0}{1-Q_{\mathbf{0},0}}\right)}_{>0} s(z), \tag{A-4}$$

where $s(z)$ is given by eqs. (6)–(7b). Because the limit is always positive as long as $N > 1$ [3], the condition for convergence stability (A-2) is equivalently given by eq. (5).

The condition for convergence stability (A-2) also connects to the stationary probability density function $p(z)$ that trait value z is observed in the population under a trait substitution sequence process in a finite population. This probability density function is given by

$$p(z) = K \exp\left[2ND\int_l^z \phi(y)\,\mathrm{d}y\right], \tag{A-5}$$

(eq. 7. of [81], eq. 62 of [5]) where l is the lower boundary of the state space and $p(z)$ has a local maximum at z^* if conditions (A-2) are satisfied (e.g. [5] for details). The density function (A-5) is useful for instance to evaluate the expected phenotypic variance in the population and can thus be compared to results from individual based simulations (see eq. A-128 and Fig 6 for a concrete example). This $p(z)$ however requires to fully quantify $\phi(z)$, which depends on $\lim_{\mu\to 0}\left(\frac{1-\overline{Q}_0}{1-Q_{0,0}}\right)$, which is process specific. For instance, for the Wright-Fisher process, we have

$$\lim_{\mu\to 0}\left(\frac{1-\overline{Q}_0}{1-Q_{0,0}}\right) = \left(\frac{ND+M}{ND}\right)$$

(eq. A10 in [46]), where M is defined under eq. (9) in the main text.

Appendix B A distribution for short and long range dispersal

Here, we specify a dispersal distribution based on the Binomial distribution, which allows us to consider both short and long dispersal, and that we used to generate the various numerical examples of

our analysis.

Appendix B.1 One-dimensional habitat

Let us first consider a one-dimensional habitat consisting of a circular lattice, so that the set of patches is $\mathcal{G} = \mathbb{Z}_D = \{0, 1, \ldots, D-1\}$, i.e. the set of integers modulo D. We assume that D is odd, so that we can write $\mathbb{Z}_D = \{0, 1, \ldots, (D-1)/2, -(D-1)/2, -(D-1)/2+1, \ldots, -1\}$. We further assume that an individual disperses with probability m, and that it stays in its natal patch with probability $1-m$. If an individual disperses, it does so with equal probability either "clockwise" or "counterclockwise" a number $j \in \{1, 2, ..., (D-1)/2\}$ of steps, which we assume follows a zero-truncated binomial distribution with probability mass function

$$p_j(N_\mathrm{s}, q) = \frac{\binom{N_\mathrm{s}}{j} q^j (1-q)^{N_\mathrm{s}-j}}{1-(1-q)^{N_\mathrm{s}}}, \tag{A-6}$$

where $N_\mathrm{s} = (D-1)/2$ is the number of trials, and $q = 2\lambda_\mathrm{m}/(D-1)$ is the probability of success, such that $\lambda_\mathrm{m} = N_\mathrm{s} q$ is the mean of the non-truncated distribution. The mean number of steps an individual disperses conditional on dispersal is

$$\overline{\lambda}_\mathrm{m} = \frac{\lambda_\mathrm{m}}{1-\left(1-\frac{2\lambda_\mathrm{m}}{D-1}\right)^{(D-1)/2}}. \tag{A-7}$$

From these assumptions, the dispersal distribution is given by

$$m_j = m_{-j} = \begin{cases} 1-m, & \text{if } j = 0 \\ \frac{1}{2} m p_j(N_\mathrm{s}, q), & \text{if } j \in \{1, 2, ..., (D-1)/2\}. \end{cases} \tag{A-8}$$

The characteristic function of the dispersal distribution can then be written as

$$\begin{aligned} \mathcal{M}(k) &= \sum_{j=0}^{D-1} m_j \chi_j(k) \\ &= m_0 + \sum_{j=1}^{\frac{D-1}{2}} m_j \chi_j(k) + \sum_{j=1}^{\frac{D-1}{2}} m_{-j} \chi_{-j}(k) \\ &= m_0 + \sum_{j=1}^{\frac{D-1}{2}} m_j \left(\chi_j(k) + \overline{\chi}_j(k)\right) \\ &= (1-m) + m \sum_{j=1}^{\frac{D-1}{2}} p_j((D-1)/2, 2\lambda_\mathrm{m}/(D-1)) \left(\frac{\chi_j(k) + \overline{\chi}_j(k)}{2}\right) \\ &= (1-m) + m \sum_{j=1}^{\frac{D-1}{2}} p_j((D-1)/2, 2\lambda_\mathrm{m}/(D-1)) \cos\left(2\pi j k/D\right), \end{aligned} \tag{A-9}$$

where the third line uses the fact that the migration kernel is symmetric ($m_j = m_{-j}$ holds for $j \in \{1, 2, ..., (D-1)/2\}$) and the identity $\chi_{-j}(k) = \overline{\chi}_j(k)$, and the last line uses the trigonometric identity $\cos(x) = (\exp(\imath x) + \exp(-\imath x))/2$. Eq. (A-9) shows that the characteristic function of the dispersal distribution is determined by the parameters D, m, and λ_m.

Appendix B.2 Two-dimensional habitat

For the two-dimensional case, we assume that patches are arranged on a torus with the same number of patches in each dimension so that $\mathcal{G} = \{(k_1, k_2) : 0 \leq k_j < D^{1/2}\}$ for k_1 and k_2 modulo $D^{1/2}$. The dispersal distribution of the focal species $m_{\mathbf{k}}$ for $\mathbf{k} = (k_1, k_2) \in \mathcal{G}$, is constructed similarly as above. First, an individual disperses with probability m and with probability $1 - m$ stays in its natal patch. Second, conditional on dispersal, we sample the number of steps $j \in \{1, 2, ..., D^{1/2} - 1\}$ an individual disperses on the lattice (maximum $D^{1/2} - 1$) from a zero-truncated binomial distribution $p_j(N_\mathrm{s}, q)$ (eq. A-6) with parameters $N_\mathrm{s} = D^{1/2} - 1$ and $q = \lambda_\mathrm{m}/(D^{1/2} - 1)$. Accordingly, the mean number of steps an individual disperses conditional on dispersal here is

$$\overline{\lambda}_\mathrm{m} = \frac{\lambda_\mathrm{m}}{1 - \left(1 - \frac{\lambda_\mathrm{m}}{D^{1/2}-1}\right)^{D^{1/2}-1}}. \tag{A-10}$$

Third, we determine how this total number of steps j is divided between j_1 steps in dimension 1 and j_2 steps in dimension 2 (so that $j = j_1 + j_2$) assuming that dispersal in either dimension has the same distribution. We do so by sampling j_1 from a discrete uniform distribution unif$(j_\mathrm{min}, j_\mathrm{max})$, where

$$\begin{aligned} j_\mathrm{min} &= \max\left(0, j - \frac{D^{1/2} - 1}{2}\right) \\ j_\mathrm{max} &= \min\left(j, \frac{D^{1/2} - 1}{2}\right), \end{aligned} \tag{A-11}$$

and by setting $j_2 = j - j_1$. Finally, given the number of steps in each dimension j_1 and j_2, these are then equally likely to occur in either direction away from the focal patch.

Appendix C Extended phenotypic effects

Appendix C.1 Actor-centered representation of inter-temporal effects

Here, we derive eq. (13) of the main text. To this end, we first apply the chain rule to eq. (1) whereby we have for $t \geq 1$ that

$$\frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}(\mathbf{z}_\mathrm{H}))}{\partial z_{\mathbf{k},t}} = \sum_{\mathbf{j} \in \mathcal{G}} \left(N \frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j},0}} \right) e_{\mathbf{j}-\mathbf{k},t}, \tag{A-12}$$

where we have defined,

$$e_{\mathbf{j}-\mathbf{k},t} = \frac{1}{N} \frac{\partial n_{\mathbf{j},0}(\mathbf{z}_\mathrm{H})}{\partial z_{\mathbf{k},t}}, \tag{A-13}$$

which thanks to spatial homogeneity is equivalent to

$$e_{\mathbf{j}-\mathbf{k},t} = \frac{1}{N} \frac{\partial n_{\mathbf{j}-\mathbf{k},0}(\mathbf{z}_\mathrm{H})}{\partial z_{\mathbf{0},t}}. \tag{A-14}$$

The quantity $e_{\mathbf{j}-\mathbf{k},t}$ is the extended phenotypic effect of an individual residing in the focal patch at t time steps in the past on the value of the environmental variable in patch $\mathbf{j} - \mathbf{k}$ in the present. But since the map g (eq. 2) does not depend on time (i.e. environmental dynamics are homogeneous in time), $e_{\mathbf{j}-\mathbf{k},t}$ is also the effect of a focal individual residing in the focal patch on the value that the

environmental variable takes in patch $\mathbf{j}-\mathbf{k}$ at t time steps in the future. We can thus write

$$e_{\mathbf{j}-\mathbf{k},t} = \frac{\partial n_{\mathbf{j}-\mathbf{k},t}}{\partial z_\bullet}, \tag{A-15}$$

where $n_{\mathbf{k},t}$ now stands for the value of the environmental variable in patch $\mathbf{k}$ at t steps in the future. Substituting eq. (A-15) into eq. (A-12), which is in turn plugged into eq. (7b) obtains eq. (13), as required.

Appendix C.2 Extended phenotypic effects

We now derive eqs. (19)–(20) of the main text. For this, we first take the derivative on both sides of eq. (11) with respect to $z_\bullet$, which yields

$$\frac{\partial n_{\mathbf{k},t+1}}{\partial z_\bullet} = \delta_{t,0}\frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0})}{\partial z_\bullet} + \sum_{\mathbf{i}\in\mathcal{G}} \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},t}, \mathbf{n}_{\mathbf{k},t})}{\partial n_{\mathbf{i},t}}\frac{\partial n_{\mathbf{i},t}}{\partial z_\bullet}, \tag{A-16}$$

where $\delta_{t,0}$ is a Kronecker delta, and where we used the fact that $\partial g(\mathbf{z}_{\mathbf{k},t}, \mathbf{n}_{\mathbf{k},t})/\partial n_{\mathbf{i},t} = \partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},t}, \mathbf{n}_{\mathbf{k},t})/\partial n_{\mathbf{i},t}$, since all derivatives are evaluated at z and $\hat{n}$. This fact also entails that the derivatives of the transition map g are independent of time, which allows us to write

$$e_{\mathbf{k},t+1} = \delta_{t,0}\psi_{\mathbf{k}} + \sum_{\mathbf{i}\in\mathcal{G}} c_{\mathbf{k}-\mathbf{i}} e_{\mathbf{i},t}, \tag{A-17}$$

with

$$\psi_{\mathbf{k}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0})}{\partial z_\bullet} = \begin{cases} \dfrac{1}{N}\dfrac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z^{\mathrm{R}}_{\mathbf{0},0}} & \text{for } \mathbf{k}=\mathbf{0} \\[2ex] \dfrac{1}{N}\dfrac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} & \text{otherwise,} \end{cases} \tag{A-18}$$

and

$$c_{\mathbf{k}-\mathbf{i}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},t}, \mathbf{n}_{\mathbf{k},t})}{\partial n_{\mathbf{i},t}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{k},0}, \mathbf{n}_{\mathbf{k},0})}{\partial n_{\mathbf{i},0}} = \frac{\partial g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{k}-\mathbf{i},t}}, \tag{A-19}$$

where the second equality in equation (A-18) follows from spatial homogeneity and the chain rule of derivatives, the second equality in equation (A-19) follows from temporal homogeneity, and the last equality in equation (A-19) follows from spatial homogeneity. These expressions are useful in concrete applications since only $g(\mathbf{z}^{\mathrm{R}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})$ needs to be specified.

We can then by mean of Fourier analysis (see Box I) solve eq. (A-17), using the Fourier transforms $\mathcal{E}_t(\mathbf{h}) = \sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\chi_{\mathbf{k}}(\mathbf{h})$, $\mathcal{C}(\mathbf{h}) = \sum_{\mathbf{k}\in\mathcal{G}} c_{\mathbf{k}}\chi_{\mathbf{k}}(\mathbf{h})$ (eq. 18) and $\Psi(\mathbf{h}) = \sum_{\mathbf{k}\in\mathcal{G}} \psi_{\mathbf{k}}\chi_{\mathbf{k}}(\mathbf{h})$ (eq. 16). Then, from (A-17), and noting that $\chi_{\mathbf{k}}(\mathbf{h}) = \chi_{\mathbf{k}-\mathbf{i}}(\mathbf{h})\chi_{\mathbf{i}}(\mathbf{h})$, we have

$$\underbrace{\sum_{\mathbf{k}\in\mathcal{G}} e_{i,\mathbf{k},t+1}\chi_{\mathbf{k}}(\mathbf{h})}_{\mathcal{E}_{t+1}(\mathbf{h})} = \delta_{t,0}\underbrace{\sum_{\mathbf{k}\in\mathcal{G}} \psi_{\mathbf{k}}\chi_{\mathbf{k}}(\mathbf{h})}_{\Psi(\mathbf{h})} + \underbrace{\sum_{\mathbf{i}\in\mathcal{G}} e_{\mathbf{i},t}\chi_{\mathbf{i}}(\mathbf{h})}_{\mathcal{E}_t(\mathbf{h})}\underbrace{\sum_{\mathbf{k}\in\mathcal{G}} c_{\mathbf{k}-\mathbf{i}}\chi_{\mathbf{k}-\mathbf{i}}(\mathbf{h})}_{\mathcal{C}(\mathbf{h})}, \tag{A-20}$$

where the last underbrace holds by changing the dummy index of the sum. Therefore

$$\mathcal{E}_{t+1}(\mathbf{h}) = \delta_{t,0}\Psi(\mathbf{h}) + \mathcal{C}(\mathbf{h})\mathcal{E}_t(\mathbf{h}), \tag{A-21}$$

whose solution given the initial condition $\mathcal{E}_0(\mathbf{h}) = 0$ (as there are no extended phenotypic effects in the focal generation) is eq. (20), as required.

Appendix D Selection gradient in terms of scaled relatedness

Here, we derive eq. (24) which, recall, is premised on the fitness of the focal individual taking the form

$$w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) = \tilde{w}(\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})) \tag{A-22}$$

with payoff vector

$$\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}) = \left(\underbrace{\pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}_{\pi_\bullet}, \underbrace{\pi(z_{\mathbf{0},0}, \mathbf{z}^{\mathrm{n}}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}_{\pi_{\mathbf{0}}}, \ldots, \underbrace{\pi(z_{\mathbf{j},0}, \mathbf{z}^{\mathrm{R}}_{\mathbf{j},0}, \mathbf{n}_{\mathbf{j},0})}_{\pi_{\mathbf{j}}}, \ldots \right), \tag{A-23}$$

where $\mathbf{z}^{\mathrm{n}}_{\mathbf{0},0}$ is equivalent to $\mathbf{z}_{\mathbf{0},0}$ except for the first entry which is given by

$$z^{\mathrm{n}}_{\mathbf{0},0} = \frac{1}{N-1} z_\bullet + \frac{N-2}{N-1} z_{\mathbf{0},0}, \tag{A-24}$$

and $\mathbf{z}^{\mathrm{R}}_{\mathbf{j},0}$ is equal to $\mathbf{z}_{\mathbf{j},0}$ except that the entry with component $z_{\mathbf{0},0}$ in this vector is replaced with

$$z^{\mathrm{R}}_{\mathbf{0},0} = \frac{1}{N} z_\bullet + \frac{N-1}{N} z_{\mathbf{0},0}, \tag{A-25}$$

that is, with the average phenotype in the patch $\mathbf{0}, 0$ including the focal individual.

To simplify the operation of taking derivatives of fitness with respect to phenotypes later, we first express the derivatives of the payoff $\pi_{\mathbf{j}}$ appearing in eq. (A-23) with respect to its various arguments, in terms of the derivatives of the payoff to the focal individual. Applying the chain rule of derivatives and evaluating the derivatives at the resident phenotype, we readily obtain the following,

$$\frac{\partial \pi_\bullet}{\partial z_\bullet} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet}, \tag{A-26}$$

$$\frac{\partial \pi_\bullet}{\partial z_{\mathbf{0},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}}, \tag{A-27}$$

$$\frac{\partial \pi_{\mathbf{0}}}{\partial z_\bullet} = \frac{1}{N-1} \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}}, \tag{A-28}$$

$$\frac{\partial \pi_{\mathbf{j}}}{\partial z_\bullet} = \frac{1}{N} \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j},0}} \quad \text{for } \mathbf{j} \neq \bullet, \mathbf{0}, \tag{A-29}$$

$$\frac{\partial \pi_{\mathbf{0}}}{\partial z_{\mathbf{0},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet} + \left(\frac{N-2}{N-1} \right) \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}}, \tag{A-30}$$

$$\frac{\partial \pi_{\mathbf{j}}}{\partial z_{\mathbf{0},0}} = \left(\frac{N-1}{N} \right) \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j},0}} \quad \text{for } \mathbf{j} \neq \bullet, \mathbf{0}, \tag{A-31}$$

$$\frac{\partial \pi_{\mathbf{j}}}{\partial z_{\mathbf{j},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet} + \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} \quad \text{for } \mathbf{j} \neq \mathbf{0}, \tag{A-32}$$

$$\frac{\partial \pi_{\mathbf{k}}}{\partial z_{\mathbf{j},0}} = \frac{\partial \pi_{\mathbf{j}}}{\partial z_{\mathbf{k},0}} = \frac{\partial \pi_\bullet}{\partial z_{\mathbf{j}-\mathbf{k},0}} = \frac{\partial \pi_\bullet}{\partial z_{\mathbf{k}-\mathbf{j},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k}-\mathbf{j},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j}-\mathbf{k},0}} \quad \text{for } \mathbf{j} \neq \mathbf{0} \text{ and } \mathbf{k} \neq \bullet, \mathbf{j}, \tag{A-33}$$

where the equalities in the last expression all follow from our assumption of spatial homogeneity.

Similarly, we have for derivatives of payoffs with respect to environmental state variables,

$$\frac{\partial \pi_\bullet}{\partial n_{\mathbf{0},0}} = \frac{\partial \pi_{\mathbf{j}}}{\partial n_{\mathbf{j},0}} = \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{0},0}} \quad \text{for all } \mathbf{j} \in \mathcal{G}, \tag{A-34}$$

where the first and second equality are consequences of spatial homogeneity, and

$$\frac{\partial \pi_{\mathbf{k}}}{\partial n_{\mathbf{j},0}} = \frac{\partial \pi_{\bullet}}{\partial n_{\mathbf{j}-\mathbf{k},0}} = \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j}-\mathbf{k},0}} \text{ for } \mathbf{j} \neq \mathbf{0} \tag{A-35}$$

where the first equality is again a consequence of spatial homogeneity.

We can then write the derivatives of fitness that appear in the selection gradient (eqs. 7a–7b) in terms of the derivatives of the payoff to the focal individual (eqs. A-26–A-35) by applying the chain rule of derivatives to the right-hand side of eq. (A-22) and simplifying, as follows. First, the fitness derivative with respect to the focal individual's phenotype can be written as

$$\begin{aligned}
\frac{\partial w(z_{\bullet}, \mathbf{z}_{\mathbf{0}}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\bullet}} &= \frac{\partial \tilde{w}(\boldsymbol{\pi}(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}))}{\partial z_{\bullet}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi_{\bullet}}{\partial z_{\bullet}} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} \frac{\partial \pi_{\mathbf{0}}}{\partial z_{\bullet}} + \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \frac{\partial \pi_{\mathbf{k}}}{\partial z_{\bullet}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\bullet}} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} \frac{1}{N-1} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} \\
&+ \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \frac{1}{N} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}},
\end{aligned} \tag{A-36}$$

where the first equality follows from taking the derivative to both sides of eq. (A-22); the second equality follows from applying the chain rule; and the third equality follows from substituting eqs. (A-26)–(A-29).

Second, the fitness derivative with respect to the average phenotype of patch neighbours is

$$\begin{aligned}
\frac{\partial w(z_{\bullet}, \mathbf{z}_{\mathbf{0}}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} &= \frac{\partial \tilde{w}(\boldsymbol{\pi}(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}))}{\partial z_{\mathbf{0},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi_{\bullet}}{\partial z_{\mathbf{0},0}} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} \frac{\partial \pi_{\mathbf{0}}}{\partial z_{\mathbf{0},0}} + \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \frac{\partial \pi_{\mathbf{k}}}{\partial z_{\mathbf{0},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} + \frac{\partial \tilde{w}}{\partial \pi_{0}} \left[\frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\bullet}} + \left(\frac{N-2}{N-1} \right) \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} \right] \\
&+ \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \left(\frac{N-1}{N} \right) \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} + \frac{\partial \tilde{w}}{\partial \pi_{0}} \left[\frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\bullet}} + \left(1 - \frac{1}{N-1} \right) \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} \right] \\
&+ \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \left(1 - \frac{1}{N} \right) \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_{\bullet}} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} + \frac{\partial \tilde{w}}{\partial \pi_{0}} \left[\frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\bullet}} - \left(\frac{1}{N-1} \right) \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}} \right] \\
&+ \sum_{\mathbf{k} \in \mathcal{G}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}} - \sum_{\mathbf{k} \in \mathcal{G} \setminus \mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{k}}} \frac{1}{N} \frac{\partial \pi(z_{\bullet}, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{k},0}},
\end{aligned} \tag{A-37}$$

where the first equality follows from taking the derivative to both sides of eq. (A-22); the second equality follows from applying the chain rule; the third equality follows from substituting eqs. (A-27), (A-30) and (A-31); and the last equality follows from distributing and rearranging terms.

Third, the derivative with respect to the average phenotype in any patch $\mathbf{j} \neq \mathbf{0}$ is

$$\begin{aligned}
\frac{\partial w(z_\bullet, \mathbf{z_0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j},0}} &= \frac{\partial \tilde{w}(\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}))}{\partial z_{\mathbf{j},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_\bullet}\frac{\partial \pi_\bullet}{\partial z_{\mathbf{j},0}} + \frac{\partial \tilde{w}}{\partial \pi_\mathbf{j}}\frac{\partial \pi_\mathbf{j}}{\partial z_{\mathbf{j},0}} + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{j}} \frac{\partial \tilde{w}}{\partial \pi_\mathbf{k}}\frac{\partial \pi_\mathbf{k}}{\partial z_{\mathbf{j},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_\bullet}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j},0}} + \frac{\partial \tilde{w}}{\partial \pi_\mathbf{j}}\left(\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet} + \frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{0},0}}\right) \\
&+ \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{j}} \frac{\partial \tilde{w}}{\partial \pi_\mathbf{k}}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j}-\mathbf{k},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_\bullet}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j},0}} + \frac{\partial \tilde{w}}{\partial \pi_\mathbf{j}}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_\bullet} + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial \tilde{w}}{\partial \pi_\mathbf{k}}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial z_{\mathbf{j}-\mathbf{k},0}},
\end{aligned} \tag{A-38}$$

where the second equality follows from applying the chain rule; the third equality follows from using the definition of $\pi_\bullet$ (eq. A-23) and substituting eq. (A-32) and eq. (A-33); and the fourth and last equality follows from rearranging.

Finally, the derivative with respect to the state variable in patch $\mathbf{j}$ is

$$\begin{aligned}
\frac{\partial w(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j},0}} &= \frac{\partial \tilde{w}(\boldsymbol{\pi}(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0}))}{\partial n_{\mathbf{j},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_\bullet}\frac{\partial \pi_\bullet}{\partial n_{\mathbf{j},0}} + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial \tilde{w}}{\partial \pi_\mathbf{k}}\frac{\partial \pi_\mathbf{k}}{\partial n_{\mathbf{j},0}} \\
&= \frac{\partial \tilde{w}}{\partial \pi_\bullet}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j},0}} + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial \tilde{w}}{\partial \pi_\mathbf{k}}\frac{\partial \pi(z_\bullet, \mathbf{z}_{\mathbf{0},0}, \mathbf{n}_{\mathbf{0},0})}{\partial n_{\mathbf{j}-\mathbf{k},0}},
\end{aligned} \tag{A-39}$$

where the second equality follows from applying the chain rule; and the third equality follows from substituting eqs. (A-34)–(A-35).

We denote by

$$\lambda_\mathbf{j} = -\frac{\partial \tilde{w}}{\partial \pi_\mathbf{j}} \Big/ \frac{\partial \tilde{w}}{\partial \pi_\bullet} \tag{A-40}$$

the coefficient of fitness interdependence between individuals in the focal patch and individuals in patch $\mathbf{j}$.

We now express $s_\mathrm{w}(z)$ in terms of these coefficients of fitness interdependence and in terms of the derivatives of the fitness function with respect to the phenotypes of different actors. Substituting

eqs. (A-36)–(A-38) into eq. (7a), factoring $\partial\tilde{w}/\partial\pi_\bullet$, and making use of (A-40), we obtain:

$$
\begin{aligned}
s_{\mathrm{w}}(z) &= \frac{\partial w}{\partial z_\bullet} + \frac{\partial w}{\partial z_{\mathbf{0},0}} R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial w}{\partial z_{\mathbf{j},0}} R_{\mathbf{j},0} \\
&= \underbrace{\frac{\partial\tilde{w}}{\partial\pi_\bullet}\frac{\partial\pi}{\partial z_\bullet} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}\frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{k}}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}}_{\frac{\partial w}{\partial z_\bullet}} \\
&\quad + \underbrace{\left[\frac{\partial\tilde{w}}{\partial\pi_\bullet}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} + \frac{\partial\tilde{w}}{\partial\pi_0}\left(\frac{\partial\pi}{\partial z_\bullet} - \frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}}\right) + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{k}}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} - \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{k}}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\right]}_{\frac{\partial w}{\partial z_{\mathbf{0},0}}} R_{\mathbf{0},0} \\
&\quad + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \underbrace{\left[\frac{\partial\tilde{w}}{\partial\pi_\bullet}\frac{\partial\pi}{\partial z_{\mathbf{j},0}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}\frac{\partial\pi}{\partial z_\bullet} + \sum_{\mathbf{k}\in\mathcal{G}} \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{k}}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}\right]}_{\frac{\partial w}{\partial z_{\mathbf{j},0}}} R_{\mathbf{j},0} \\
&= \frac{\partial\tilde{w}}{\partial\pi_\bullet}\Bigg\{\frac{\partial\pi}{\partial z_\bullet} - \lambda_{\mathbf{0}}\frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \lambda_{\mathbf{k}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} \\
&\quad + \left[\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \lambda_{\mathbf{0}}\left(\frac{\partial\pi}{\partial z_\bullet} - \frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}}\right) + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \lambda_{\mathbf{k}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} - \sum_{\mathbf{k}\in\mathcal{G}} \lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\right] R_{\mathbf{0},0} \\
&\quad + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \left[\frac{\partial\pi}{\partial z_{\mathbf{j},0}} - \lambda_{\mathbf{j}}\frac{\partial\pi}{\partial z_\bullet} - \sum_{\mathbf{k}\in\mathcal{G}} \lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}\right] R_{\mathbf{j},0}\Bigg\} \\
&= \frac{\partial\tilde{w}}{\partial\pi_\bullet}\Bigg\{\frac{\partial\pi}{\partial z_\bullet} - \lambda_{\mathbf{0}}\frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \lambda_{\mathbf{k}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} \\
&\quad + \left[\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \lambda_{\mathbf{0}}\frac{\partial\pi}{\partial z_\bullet} - \lambda_{\mathbf{0}}\frac{1}{N-1}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \lambda_{\mathbf{k}}\frac{1}{N}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} - \lambda_{\mathbf{0}}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\right] R_{\mathbf{0},0} \\
&\quad + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \left[\frac{\partial\pi}{\partial z_{\mathbf{j},0}} - \lambda_{\mathbf{j}}\frac{\partial\pi}{\partial z_\bullet} - \lambda_{\mathbf{j}}\frac{\partial\pi}{\partial z_{\mathbf{0},0}} - \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{j}} \lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}\right] R_{\mathbf{j},0}\Bigg\}. \qquad \text{(A-41)}
\end{aligned}
$$

Collecting terms and simplifying, we further get

$$
\begin{aligned}
s_{\mathrm{w}}(z) = \frac{\partial\tilde{w}}{\partial\pi_\bullet}\Bigg\{&\frac{\partial\pi}{\partial z_\bullet}\left(1 - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}\right) + \frac{\partial\pi}{\partial z_{\mathbf{0},0}}\left[R_{\mathbf{0},0} - \lambda_{\mathbf{0}}\frac{1}{N-1}(1 - R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}\right] \\
&+ \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial\pi}{\partial z_{\mathbf{k},0}}\left[R_{\mathbf{k},0} - \frac{1}{N}\lambda_{\mathbf{k}}\left(1 - R_{\mathbf{0},0}\right)\right] - \underbrace{\sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{j}} \lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}} R_{\mathbf{j},0}}_{B}\Bigg\}. \qquad \text{(A-42)}
\end{aligned}
$$

To further simplify this expression, note that the underbraced term can be rewritten as

$$\begin{aligned}
\sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{j}}\lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}R_{\mathbf{j},0} &= \sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{k}\in\mathcal{G}}\lambda_{\mathbf{k}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}R_{\mathbf{j},0} - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}\frac{\partial\pi}{\partial z_{\mathbf{0},0}}R_{\mathbf{j},0} \\
&= \sum_{\mathbf{k}\in\mathcal{G}}\lambda_{\mathbf{k}}\sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\pi}{\partial z_{\mathbf{j}-\mathbf{k},0}}R_{\mathbf{j},0} - \frac{\partial\pi}{\partial z_{\mathbf{0},0}}\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0} \\
&= \sum_{\mathbf{k}\in\mathcal{G}}\lambda_{\mathbf{k}}\sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\pi}{\partial z_{\mathbf{j},0}}R_{\mathbf{j}-\mathbf{k},0} - \frac{\partial\pi}{\partial z_{\mathbf{0},0}}\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0} \\
&= \sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\pi}{\partial z_{\mathbf{j},0}}\sum_{\mathbf{k}\in\mathcal{G}}\lambda_{\mathbf{k}}R_{\mathbf{j}-\mathbf{k},0} - \frac{\partial\pi}{\partial z_{\mathbf{0},0}}\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0} \\
&= \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\pi}{\partial z_{\mathbf{j},0}}\sum_{\mathbf{k}\in\mathcal{G}}\lambda_{\mathbf{k}}R_{\mathbf{j}-\mathbf{k},0} \\
&= \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},0},
\end{aligned} \tag{A-43}$$

where the third line follows from the identity

$$\sum_{\mathbf{j}\in\mathcal{G}} f_{\mathbf{j}}g_{\mathbf{k}-\mathbf{j}} = \sum_{\mathbf{j}\in\mathcal{G}} f_{\mathbf{k}-\mathbf{j}}g_{\mathbf{j}}, \tag{A-44}$$

and the last line follows from changing the dummy variables and from the symmetry of the relatedness coefficients (i.e. the fact that $R_{-\mathbf{k},0} = R_{\mathbf{k},0}$ holds for all $\mathbf{k} \in \mathcal{G}$).

Substituting (A-43) into (A-42) and simplifying we obtain

$$\begin{aligned}
s_{\mathrm{w}}(z) &= \frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\left\{\frac{\partial\pi}{\partial z_{\bullet}}\left(1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right) + \frac{\partial\pi}{\partial z_{\mathbf{0},0}}\left[R_{\mathbf{0},0} - \lambda_{\mathbf{0}}\frac{1}{N-1}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right]\right. \\
&\quad \left. + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\left[R_{\mathbf{k},0} - \frac{1}{N}\lambda_{\mathbf{k}}\left(1-R_{\mathbf{0},0}\right) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},0}\right]\right\} \\
&= \frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\left(1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right)\left\{\frac{\partial\pi}{\partial z_{\bullet}} + \frac{R_{\mathbf{0},0} - \lambda_{\mathbf{0}}\frac{1}{N-1}\left(1-R_{\mathbf{0},0}\right) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}{1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}\frac{\partial\pi}{\partial z_{\mathbf{0},0}}\right. \\
&\quad \left. + \sum_{\mathbf{k}\in\mathcal{G}\setminus\mathbf{0}}\frac{R_{\mathbf{k},0} - \frac{1}{N}\lambda_{\mathbf{k}}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},0}}{1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\right\} \\
&= L\left\{\frac{\partial\pi}{\partial z_{\bullet}} + \sum_{\mathbf{k}\in\mathcal{G}}\kappa_{\mathbf{k},0}\frac{\partial\pi}{\partial z_{\mathbf{k},0}}\right\},
\end{aligned} \tag{A-45}$$

where the second equality follows from factoring $\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\left(1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right)$, and the final equality follows from defining

$$L = \frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\left(1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right), \tag{A-46}$$

$$\kappa_{\mathbf{0},0} = \frac{R_{\mathbf{0},0} - \frac{1}{N-1}\lambda_{\mathbf{0}}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}{1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}, \tag{A-47}$$

and

$$\kappa_{\mathbf{k},0} = \frac{R_{\mathbf{k},0} - \frac{1}{N}\lambda_{\mathbf{k}}(1-R_{\mathbf{0},0}) - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},0}}{1-\sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}}. \tag{A-48}$$

Eq. (A-45) corresponds to the expression for $s_{\mathrm{w}}(z)$ in eq. (24) of the main text, as required.

Note that in the infinite island model of dispersal, $R_{\mathbf{j},0} = 0$ for all $\mathbf{j} \neq \mathbf{0}$. In this case, $\kappa_{\mathbf{0},0}$ (eq. A-47) reduces to eq. 22 of [53] as it should. This provides a consistency check of our derivation.

Let us turn to express $s_{\mathrm{e}}(z)$ in terms of the coefficients of fitness interdependence. From eq. (13) and after substituting (A-39), factoring $\partial\tilde{w}/\partial\pi_{\bullet}$, and making use of eq. (A-40), we obtain

$$\begin{aligned}
s_{\mathrm{e}}(z) &= N\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{j}\in\mathcal{G}} e_{\mathbf{j}-\mathbf{k},t}R_{\mathbf{k},t}\frac{\partial w}{\partial n_{\mathbf{j},0}} \\
&= N\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{j}\in\mathcal{G}} e_{\mathbf{j}-\mathbf{k},t}R_{\mathbf{k},t}\left[\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\frac{\partial\pi}{\partial n_{\mathbf{j},0}} + \sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{i}}}\frac{\partial\pi}{\partial n_{\mathbf{j}-\mathbf{i},0}}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{j}\in\mathcal{G}} e_{\mathbf{j}-\mathbf{k},t}R_{\mathbf{k},t}\left[\frac{\partial\pi}{\partial n_{\mathbf{j},0}} - \sum_{\mathbf{i}\in\mathcal{G}}\lambda_{\mathbf{i}}\frac{\partial\pi}{\partial n_{\mathbf{j}-\mathbf{i},0}}\right]. \qquad \text{(A-49)}
\end{aligned}$$

By rearranging terms and applying the identity (A-44), we can rewrite this expression as

$$\begin{aligned}
s_{\mathrm{e}}(z) &= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\left[\sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{j},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{j}-\mathbf{k},t}R_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{i}\in\mathcal{G}}\lambda_{\mathbf{i}}\frac{\partial\pi}{\partial n_{\mathbf{j}-\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{j}-\mathbf{k},t}R_{\mathbf{k},t}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\left[\sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{j},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{j}-\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{i}\in\mathcal{G}}\lambda_{\mathbf{i}}\frac{\partial\pi}{\partial n_{\mathbf{j}-\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{j}-\mathbf{k},t}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\left[\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{i}-\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{j}-\mathbf{k},t}\sum_{\mathbf{i}\in\mathcal{G}}\lambda_{\mathbf{i}}\frac{\partial\pi}{\partial n_{\mathbf{j}-\mathbf{i},0}}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\left[\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{i}-\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{j}-\mathbf{k},t}\sum_{\mathbf{i}\in\mathcal{G}}\lambda_{\mathbf{j}-\mathbf{i}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\left[\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}R_{\mathbf{i}-\mathbf{k},t} - \sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\sum_{\mathbf{j}\in\mathcal{G}} R_{\mathbf{j}-\mathbf{k},t}\lambda_{\mathbf{j}-\mathbf{i}}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\left[R_{\mathbf{i}-\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}-\mathbf{i}}R_{\mathbf{j}-\mathbf{k},t}\right]. \qquad \text{(A-50)}
\end{aligned}$$

Using the symmetry of the relatedness coefficients and changing the summation indices we further get

$$\begin{aligned}
s_{\mathrm{e}}(z) &= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\left[R_{\mathbf{k}-\mathbf{i},t} - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k}+\mathbf{i},t}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\sum_{t=1}^{\infty}\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k}-\mathbf{i},t}\left[R_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}\right] \\
&= N\frac{\partial\tilde{w}}{\partial\pi_{\bullet}}\left(1 - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}\right)\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}e_{\mathbf{k}-\mathbf{i},t}\frac{R_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}}{1 - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}} \\
&= LN\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{i}\in\mathcal{G}}\frac{\partial\pi}{\partial n_{\mathbf{i},0}}e_{\mathbf{k}-\mathbf{i},t}\kappa_{\mathbf{k},t}, \qquad \text{(A-51)}
\end{aligned}$$

where the second-to-last line follows from multiplying and dividing by $1 - \sum_{\mathbf{j}\in\mathcal{G}}\lambda_{\mathbf{j}}R_{\mathbf{j},0}$, and the last

line follows from identifying L (A-46) and defining

$$\kappa_{\mathbf{k},t} = \frac{R_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j}-\mathbf{k},t}}{1 - \sum_{\mathbf{j}\in\mathcal{G}} \lambda_{\mathbf{j}} R_{\mathbf{j},0}} \text{ for } t > 0. \tag{A-52}$$

Eq. (A-51) corresponds to the expression for $s_{\mathrm{e}}(z)$ in eq. (24) of the main text, as required.

Adding the intra- (eq. A-45) and inter-temporal (eq. A-51) components of the selection gradient, we obtain

$$\begin{aligned} s(z) &= s_{\mathrm{w}}(z) + s_{\mathrm{e}}(z) \\ &= L\left\{\frac{\partial\pi}{\partial z_{\bullet}} + \sum_{\mathbf{k}\in\mathcal{G}\mathbf{0}} \kappa_{\mathbf{k},0}\frac{\partial\pi}{\partial z_{\mathbf{k},0}} + N\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\sum_{\mathbf{i}\in\mathcal{G}} \frac{\partial\pi}{\partial n_{\mathbf{i},0}} e_{\mathbf{k}-\mathbf{i},t}\kappa_{\mathbf{k},t}\right\}, \end{aligned} \tag{A-53}$$

overall.

For derivations to come, it will turn out to be convenient to have scaled relatedness written in terms of the partial derivatives of $\tilde{w}$ with respect to the payoffs of different individuals. From eqs. (A-47), (A-48) and (A-52) and the definition of the coefficients of fitness interdependence (A-40) we have after rearrangements and multiplying numerators and denominators by $\partial\tilde{w}/\partial\pi_{\bullet}$:

$$\kappa_{\mathbf{0},0} = \frac{R_{\mathbf{0},0}\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}\left[\frac{1}{N-1}(1-R_{\mathbf{0},0}) + R_{\mathbf{0},0}\right] + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j},0}}{\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j},0}}, \tag{A-54}$$

$$\kappa_{\mathbf{k},0} = \frac{R_{\mathbf{k},t}\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{k}}}\frac{1}{N}(1-R_{\mathbf{0},0}) + \sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j}-\mathbf{k},0}}{\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j},0}} \text{ for } \mathbf{k}\neq\mathbf{0}, \tag{A-55}$$

and

$$\kappa_{\mathbf{k},t} = \frac{R_{\mathbf{k},t}\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j}-\mathbf{k},t}}{\frac{\partial\tilde{w}}{\partial\pi_{\bullet}} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j},0}} \text{ for } t > 0. \tag{A-56}$$

Appendix E Explicit expressions for scaled relatedness

In this appendix, we derive an explicit expression for scaled relatedness $\kappa_{\mathbf{k},t}$ as shown eq. (III.A) shown in Box III, which is based on the assumption that individual fitness can be written as eq. (23); that is

$$\tilde{w}(\boldsymbol{\pi}) = s(\pi_{\bullet}) + \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}\left[1 - s^{\mathrm{R}}(\pi_{\mathbf{i}})\right]\frac{f(\pi_{\bullet})}{\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} f^{\mathrm{R}}(\pi_{\mathbf{j}})}, \tag{A-57}$$

where

$$s^{\mathrm{R}}(\pi_{\mathbf{i}}) = \begin{cases} \frac{1}{N}s(\pi_{\bullet}) + \frac{N-1}{N}s(\pi_{\mathbf{0}}) & \text{if } \mathbf{i} = \mathbf{0} \\ s(\pi_{\mathbf{i}}) & \text{otherwise} \end{cases} \tag{A-58}$$

and

$$f^{\mathrm{R}}(\pi_{\mathbf{i}}) = \begin{cases} \frac{1}{N}f(\pi_{\bullet}) + \frac{N-1}{N}f(\pi_{\mathbf{0}}) & \text{if } \mathbf{i} = \mathbf{0} \\ f(\pi_{\mathbf{i}}) & \text{otherwise.} \end{cases} \tag{A-59}$$

We proceed in three steps. First, we calculate payoff derivatives and the coefficients of fitness interdependence in terms of demographic parameters (Appendix E.1). Second, we calculate expressions for the scaled relatedness coefficients in terms of relatedness coefficients (Appendix E.2). Third, starting from these expressions, we calculate expressions for the scaled relatedness coefficients in terms of demographic parameters, obtaining eq. (III.A) shown in Box III (Appendix E.3). Finally, in Appendix

E.4, we use these results to get an expression for L (A-46) in terms of demographic parameters, which can be useful to have the magnitude (not just the sign) of the selection gradient.

Appendix E.1 Payoff derivatives and coefficients of fitness interdependence

Using the quotient rule of derivatives, and evaluating expressions at the resident trait value, the derivative of $\tilde{w}$ (A-57) with respect to the payoff of the focal individual $\pi_\bullet$ can be written as

$$\begin{aligned}
\frac{\partial \tilde{w}}{\partial \pi_\bullet} &= \frac{\partial s\left(\pi_\bullet\right)}{\partial \pi_\bullet} + \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{\partial}{\partial \pi_\bullet}\left\{\frac{\left[1-s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right)}{\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} f^{\mathrm{R}}(\pi_{\mathbf{j}})}\right\} \\
&= s' + \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{\frac{\partial}{\partial \pi_\bullet}\left\{\left[1-s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right)\right\} \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} f^{\mathrm{R}}(\pi_{\mathbf{j}}) - \left[1-s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right) \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} \frac{\partial f^{\mathrm{R}}(\pi_{\mathbf{j}})}{\partial \pi_\bullet}}{\left[\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} f^{\mathrm{R}}(\pi_{\mathbf{j}})\right]^2} \\
&= s' + \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{\frac{\partial}{\partial \pi_\bullet}\left\{\left[1-s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right)\right\} f - (1-s) f \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} \frac{\partial f^{\mathrm{R}}(\pi_{\mathbf{j}})}{\partial \pi_\bullet}}{f^2} \\
&= s' + \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{\frac{\partial}{\partial \pi_\bullet}\left\{\left[1-s^{\mathrm{R}}\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right)\right\}}{f} - \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{(1-s) \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} \frac{\partial f^{\mathrm{R}}(\pi_{\mathbf{j}})}{\partial \pi_\bullet}}{f},
\end{aligned}$$

where we have set $s' = \partial s\left(\pi_\bullet\right)/\partial \pi_\bullet$, and used the fact that $\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} = 1$ for all $\mathbf{i}$.

Substituting (A-58), noting that

$$\frac{\partial s^{\mathrm{R}}(\pi_{\mathbf{i}})}{\partial \pi_\bullet} = \begin{cases} \frac{1}{N} s' & \text{if } \mathbf{i} = \mathbf{0} \\ 0 & \text{otherwise} \end{cases} \tag{A-60}$$

and

$$\frac{\partial f^{\mathrm{R}}(\pi_{\mathbf{i}})}{\partial \pi_\bullet} = \begin{cases} \frac{1}{N} f' & \text{if } \mathbf{i} = \mathbf{0} \\ 0 & \text{otherwise} \end{cases} \tag{A-61}$$

hold, and setting $f' = \partial f\left(\pi_\bullet\right)/\partial \pi_\bullet$, we further get

$$\begin{aligned}
\frac{\partial \tilde{w}}{\partial \pi_\bullet} &= s' + m_{\mathbf{0}} \frac{\frac{\partial}{\partial \pi_\bullet}\left\{\left[1 - \frac{1}{N} s(\pi_\bullet) - \frac{N-1}{N} s(\pi_{\mathbf{0}})\right] f\left(\pi_\bullet\right)\right\}}{f} + \sum_{\mathbf{i}\in\mathcal{G}\setminus\mathbf{0}} m_{\mathbf{i}} \frac{\frac{\partial}{\partial \pi_\bullet}\left\{\left[1-s\left(\pi_{\mathbf{i}}\right)\right] f\left(\pi_\bullet\right)\right\}}{f} \\
&\quad - \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{(1-s) \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{i}-\mathbf{j}} \frac{\partial f^{\mathrm{R}}(\pi_{\mathbf{j}})}{\partial \pi_\bullet}}{f} \\
&= s' + m_{\mathbf{0}} \frac{(1-s) f' - \frac{1}{N} s' f}{f} + \sum_{\mathbf{i}\in\mathcal{G}\setminus\mathbf{0}} m_{\mathbf{i}} \frac{(1-s) f'}{f} - \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} \frac{(1-s) m_{\mathbf{i}} \frac{1}{N} f'}{f} \\
&= s' - m_{\mathbf{0}} \frac{1}{N} s' + m_{\mathbf{0}} \frac{(1-s) f'}{f} + \sum_{\mathbf{i}\in\mathcal{G}\setminus\mathbf{0}} m_{\mathbf{i}} \frac{(1-s) f'}{f} - \frac{1}{N}(1-s) \frac{f'}{f} \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}^2 \\
&= s'\left(1 - m_{\mathbf{0}} \frac{1}{N}\right) + (1-s) \frac{f'}{f} \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}} - \frac{1}{N}(1-s) \frac{f'}{f} \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}^2 \\
&= \left(1 - \frac{1}{N} m_{\mathbf{0}}\right) s' + \left(1 - \frac{1}{N} \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}^2\right)(1-s) \frac{f'}{f} \\
&= s' + (1-s) \frac{f'}{f} - \frac{1}{N}\left(s' m_{\mathbf{0}} + (1-s) \frac{f'}{f} \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}^2\right).
\end{aligned} \tag{A-62}$$

Applying the same line of arguments produces

$$\frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} = -\frac{N-1}{N}\left[m_{\mathbf{0}}s' + \left(\sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}^2\right)(1-s)\frac{f'}{f}\right] \tag{A-63}$$

and

$$\frac{\partial \tilde{w}}{\partial \pi_{\mathbf{j}}} = -m_{\mathbf{j}}s' - \left(\sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}m_{\mathbf{i}-\mathbf{j}}\right)(1-s)\frac{f'}{f} \text{ for } \mathbf{j} \neq \mathbf{0}, \tag{A-64}$$

where, as usual, all functions are evaluated at the resident trait value z and equilibrium $\hat{n}$.

Introducing the notation

$$P_{\mathbf{j}} = \sum_{\mathbf{i}\in\mathcal{G}} m_{\mathbf{i}}m_{\mathbf{i}-\mathbf{j}}, \tag{A-65}$$

which is the probability that an offspring born in patch $\mathbf{j}$ competes with an offspring of the focal individual (i.e. that they both migrate to the same patch), the derivatives in eqs. (A-62)–(A-64) can be more compactly written as

$$\frac{\partial \tilde{w}}{\partial \pi_{\bullet}} = s' + (1-s)\frac{f'}{f} - \frac{1}{N}\left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right) \tag{A-66}$$

$$\frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} = -\frac{N-1}{N}\left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right) \tag{A-67}$$

$$\frac{\partial \tilde{w}}{\partial \pi_{\mathbf{j}}} = -\left(s'm_{\mathbf{j}} + (1-s)\frac{f'}{f}P_{\mathbf{j}}\right) \text{ for } \mathbf{j} \neq \mathbf{0}. \tag{A-68}$$

In terms of these derivatives, the coefficients of fitness interdependence (A-40) can then be written as

$$\lambda_{\mathbf{0}} = -\frac{\partial \tilde{w}/\partial \pi_{\mathbf{0}}}{\partial \tilde{w}/\partial \pi_{\bullet}} = \left(\frac{N-1}{N}\right)\frac{s'fm_{\mathbf{0}} + f'(1-s)P_{\mathbf{0}}}{s'f + f'(1-s) - \left[s'fm_{\mathbf{0}} + f'(1-s)P_{\mathbf{0}}\right]/N}, \tag{A-69}$$

$$\lambda_{\mathbf{j}} = -\frac{\partial \tilde{w}/\partial \pi_{\mathbf{j}}}{\partial \tilde{w}/\partial \pi_{\bullet}} = \frac{s'fm_{\mathbf{j}} + f'(1-s)P_{\mathbf{j}}}{s'f + f'(1-s) - \left[s'fm_{\mathbf{0}} + f'(1-s)P_{\mathbf{0}}\right]/N} \text{ for } \mathbf{j} \neq \mathbf{0}. \tag{A-70}$$

Appendix E.2 Scaled-relatedness in terms of relatedness coefficients

To calculate and simplify the scaled-relatedness coefficients, it is convenient to start from expressions (A-54) – (A-56). First, note that using eqs. (A-66) and (A-67), and rearranging terms yields

$$\begin{aligned}
\frac{\partial \tilde{w}}{\partial \pi_{\bullet}} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}}R_{\mathbf{0},0} &= s' + (1-s)\frac{f'}{f} - \left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right)\left(\frac{1}{N} + \frac{N-1}{N}R_{\mathbf{0},0}\right) \\
&= s' + (1-s)\frac{f'}{f} - \left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right)\left(R_{\mathbf{0},0} + \frac{1}{N}\left(1 - R_{\mathbf{0},0}\right)\right) \\
&= s' + (1-s)\frac{f'}{f} - \left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right)R_{\mathbf{0},0} \\
&\quad - \left(s'm_{\mathbf{0}} + (1-s)\frac{f'}{f}P_{\mathbf{0}}\right)\frac{1}{N}\left(1 - R_{\mathbf{0},0}\right).
\end{aligned} \tag{A-71}$$

Then, using (A-71) and (A-68), rearranging, and factoring, the common denominator of $\kappa_{\mathbf{0},0}$ (A-54), $\kappa_{\mathbf{k},0}$ (A-55), and $\kappa_{\mathbf{k},t}$ (A-56) can then be written as

$$\begin{aligned}
&\frac{\partial \tilde{w}}{\partial \pi_\bullet} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}} R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{j}}} R_{\mathbf{j},0} \\
&= s' + (1-s)\frac{f'}{f} - \left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right) \frac{1}{N}\left(1 - R_{\mathbf{0},0}\right) - \sum_{\mathbf{j}\in\mathcal{G}} \left(s' m_{\mathbf{j}} + (1-s)\frac{f'}{f} P_{\mathbf{j}}\right) R_{\mathbf{j},0} \\
&= s' \left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} R_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right] + \frac{f'}{f}(1-s)\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} R_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right]. \qquad \text{(A-72)}
\end{aligned}$$

Similarly, using (A-67) yields

$$\begin{aligned}
\frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}}\left(\frac{1}{N-1}(1-R_{\mathbf{0},0}) + R_{\mathbf{0},0}\right) &= -\frac{N-1}{N}\left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right)\left(\frac{1}{N-1}(1-R_{\mathbf{0},0}) + R_{\mathbf{0},0}\right) \\
&= -\left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right)\left(\frac{1}{N}(1-R_{\mathbf{0},0}) + \frac{N-1}{N} R_{\mathbf{0},0}\right) \\
&= -\left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right)\left(R_{\mathbf{0},0} - \frac{1}{N} R_{\mathbf{0},0} + \frac{1}{N}\left(1-R_{\mathbf{0},0}\right)\right).
\end{aligned}$$

Using this expression together with (A-66) and (A-68), the numerator of $\kappa_{\mathbf{0},0}$ (A-54) can be simplified as follows:

$$\begin{aligned}
&R_{\mathbf{0},0}\frac{\partial \tilde{w}}{\partial \pi_\bullet} + \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{0}}}\left(\frac{1}{N-1}(1-R_{\mathbf{0},0}) + R_{\mathbf{0},0}\right) + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\partial \tilde{w}}{\partial \pi_{\mathbf{j}}} R_{\mathbf{j},0} \\
&= R_{\mathbf{0},0}\left(s' + (1-s)\frac{f'}{f}\right) - \frac{1}{N}\left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right) R_{\mathbf{0},0} \\
&- \left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right)\left(R_{\mathbf{0},0} - \frac{1}{N} R_{\mathbf{0},0} + \frac{1}{N}\left(1-R_{\mathbf{0},0}\right)\right) - \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \left(s' m_{\mathbf{j}} + (1-s)\frac{f'}{f} P_{\mathbf{j}}\right) R_{\mathbf{j},0}, \\
&= R_{\mathbf{0},0}\left(s' + (1-s)\frac{f'}{f}\right) - \left(s' m_{\mathbf{0}} + (1-s)\frac{f'}{f} P_{\mathbf{0}}\right)\frac{1}{N}\left(1-R_{\mathbf{0},0}\right) - \sum_{\mathbf{j}\in\mathcal{G}} \left(s' m_{\mathbf{j}} + (1-s)\frac{f'}{f} P_{\mathbf{j}}\right) R_{\mathbf{j},0} \\
&= s'\left[R_{\mathbf{0},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} R_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right] + \frac{f'}{f}(1-s)\left[R_{\mathbf{0},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} R_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right].
\end{aligned} \qquad \text{(A-73)}$$

Now, substituting (A-72) and (A-73) into (A-54), and then multiplying numerator and denominator by f, yields

$$\kappa_{\mathbf{0},0} = \frac{s' f\left[R_{\mathbf{0},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} R_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right] + f'(1-s)\left[R_{\mathbf{0},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} R_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right]}{s' f\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} R_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right] + f'(1-s)\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} R_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-R_{\mathbf{0},0})}{N}\right)\right]}. \qquad \text{(A-74)}$$

To obtain similar expressions for $\kappa_{\mathbf{k},0}$ (A-55), and $\kappa_{\mathbf{k},t}$ (A-56), we first use eqs. (A-66)–(A-68) to write

$$
\begin{aligned}
&R_{\mathbf{k},t}\frac{\partial\tilde{w}}{\partial\pi_\bullet}+\sum_{\mathbf{j}\in\mathcal{G}}\frac{\partial\tilde{w}}{\partial\pi_\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}\\
&=R_{\mathbf{k},t}\frac{\partial\tilde{w}}{\partial\pi_\bullet}+R_{-\mathbf{k},t}\frac{\partial\tilde{w}}{\partial\pi_\mathbf{0}}+\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}\\
&=R_{\mathbf{k},t}\left(\frac{\partial\tilde{w}}{\partial\pi_\bullet}+\frac{\partial\tilde{w}}{\partial\pi_\mathbf{0}}\right)+\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}\\
&=R_{\mathbf{k},t}\left[s'+(1-s)\frac{f'}{f}-\frac{1}{N}\left(s'm_\mathbf{0}+(1-s)\frac{f'}{f}P_\mathbf{0}\right)-\frac{N-1}{N}\left(s'm_\mathbf{0}+(1-s)\frac{f'}{f}P_\mathbf{0}\right)\right]+\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_\mathbf{j}}R_{\mathbf{j}-\mathbf{k},t}\\
&=R_{\mathbf{k},t}\left[s'+(1-s)\frac{f'}{f}-\left(s'm_\mathbf{0}+(1-s)\frac{f'}{f}P_\mathbf{0}\right)\right]-\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\left[s'm_\mathbf{j}+(1-s)\frac{f'}{f}P_\mathbf{j}\right]R_{\mathbf{j}-\mathbf{k},t}\\
&=R_{\mathbf{k},t}\left[s'+(1-s)\frac{f'}{f}\right]-\sum_{\mathbf{j}\in\mathcal{G}}\left[s'm_\mathbf{j}+(1-s)\frac{f'}{f}P_\mathbf{j}\right]R_{\mathbf{j}-\mathbf{k},t}\\
&=s'\left[R_{\mathbf{k},t}-\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}R_{\mathbf{j}-\mathbf{k},t}\right]+\frac{f'}{f}(1-s)\left[R_{\mathbf{k},t}-\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}R_{\mathbf{j}-\mathbf{k},t}\right].
\end{aligned}
\tag{A-75}
$$

and

$$
\begin{aligned}
\frac{\partial\tilde{w}}{\partial\pi_\mathbf{k}}\frac{1}{N}(1-R_{\mathbf{k},0})&=-\left(s'm_\mathbf{k}+(1-s)\frac{f'}{f}P_\mathbf{k}\right)\frac{1}{N}(1-R_{\mathbf{k},0})\\
&=-s'm_\mathbf{k}\frac{(1-R_{\mathbf{k},0})}{N}-\frac{f'(1-s)}{f}P_\mathbf{k}\frac{(1-R_{\mathbf{k},0})}{N}
\end{aligned}
\tag{A-76}
$$

Substituting (A-72), (A-76), and (A-75) into (A-55), and then multiplying numerator and denominator by f, yields

$$
\kappa_{\mathbf{k},0}=\frac{s'f\left[R_{\mathbf{k},t}-\left(\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}R_{\mathbf{j}-\mathbf{k},0}+m_\mathbf{k}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]+f'(1-s)\left[R_{\mathbf{k},t}-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}R_{\mathbf{j}-\mathbf{k},0}+P_\mathbf{k}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]}{s'f\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}R_{\mathbf{j},0}+m_\mathbf{0}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]+f'(1-s)\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}R_{\mathbf{j},0}+P_\mathbf{0}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]}\text{ for }\mathbf{k}\neq\mathbf{0}.
\tag{A-77}
$$

Likewise, substituting (A-72), and (A-75) into (A-56), and then multiplying numerator and denominator by f, yields

$$
\kappa_{\mathbf{k},t}=\frac{s'f\left[R_{\mathbf{k},t}-\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}R_{\mathbf{j}-\mathbf{k},t}\right]+f'(1-s)\left[R_{\mathbf{k},t}-\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}R_{\mathbf{j}-\mathbf{k},t}\right]}{s'f\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}R_{\mathbf{j},0}+m_\mathbf{0}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]+f'(1-s)\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}R_{\mathbf{j},0}+P_\mathbf{0}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right]}\text{ for }t>0.
\tag{A-78}
$$

Appendix E.3 Scaled-relatedness in terms of demographic parameters

Substituting eq. (8) into eqs. (A-74), (A-77), and (A-78), and then cancelling common terms, we obtain

$$
\kappa_{\mathbf{0},0}=\frac{s'f\lim_{\mu\to0}\left[Q_{\mathbf{0},0}-\left(\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}Q_{\mathbf{j},0}+m_\mathbf{0}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]+f'(1-s)\lim_{\mu\to0}\left[Q_{\mathbf{0},0}-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}Q_{\mathbf{j},0}+P_\mathbf{0}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]}{s'f\lim_{\mu\to0}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}m_\mathbf{j}Q_{\mathbf{j},0}+m_\mathbf{0}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]+f'(1-s)\lim_{\mu\to0}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_\mathbf{j}Q_{\mathbf{j},0}+P_\mathbf{0}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]},
\tag{A-79}
$$

$$\kappa_{\mathbf{k},0} = \frac{s' f \lim\limits_{\mu\to 0}\left[Q_{\mathbf{k},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},0} + m_{\mathbf{k}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] + f'(1-s) \lim\limits_{\mu\to 0}\left[Q_{\mathbf{k},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},0} + P_{\mathbf{k}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]}{s' f \lim\limits_{\mu\to 0}\left[1 - \left(\sum\limits_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] + f'(1-s) \lim\limits_{\mu\to 0}\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} Q_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]}, \tag{A-80}$$

for $\mathbf{k} \neq \mathbf{0}$, and

$$\kappa_{\mathbf{k},t} = \frac{s' f \lim\limits_{\mu\to 0}\left[Q_{\mathbf{k},t} - \sum\limits_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},t}\right] + f'(1-s) \lim\limits_{\mu\to 0}\left[Q_{\mathbf{k},t} - \sum\limits_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},t}\right]}{s' f \lim\limits_{\mu\to 0}\left[1 - \left(\sum\limits_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] + f'(1-s) \lim\limits_{\mu\to 0}\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}} Q_{\mathbf{j},0} + P_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]}. \tag{A-81}$$

for $t > 0$.

To simplify eqs. (A-79)–(A-81), we first note that, from eqs. (A.42), (A.48), and (A.51) in [41], we have[1]

$$\lim_{\mu\to 0} \frac{1}{1-Q_{\mathbf{0},0}}\left[1 - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] = \frac{1}{N}\left[N + \mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right) - \frac{1+s}{2D}\right], \tag{A-82}$$

$$\lim_{\mu\to 0} \frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{0},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j},0} + m_{\mathbf{0}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] = \frac{1}{N}\left[\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right) - \frac{1+s}{2D}\right], \tag{A-83}$$

$$\lim_{\mu\to 0} \frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{k},0} - \left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},0} + m_{\mathbf{k}} \frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] = \frac{1}{N}\left[\mathcal{L}_{\mathbf{k}}\left(F^{\mathrm{s}}\right) - \frac{1+s}{2D}\right] \text{ for } \mathbf{k} \neq \mathbf{0}, \tag{A-84}$$

$$\lim_{\mu\to 0} \frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{k},t} - \sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}} Q_{\mathbf{j}-\mathbf{k},t}\right] = \frac{1}{N}\left[\mathcal{L}_{\mathbf{k}}\left(G^{\mathrm{s}}_t\right) - \frac{1+s}{2D}\right] \text{ for } t \neq 0, \tag{A-85}$$

where $\mathcal{L}_{\mathbf{k}}(\mathcal{F})$ is the inverse transform of $\mathcal{F}$ at $\mathbf{k}$ as defined in eq. (I.B), and where the functions F^{s} and G^{s}_t are defined at $\mathbf{h}$ as

$$F^{\mathrm{s}}(\mathbf{h}) = -\frac{(1-s)\mathcal{M}(\mathbf{h})}{1+s+(1-s)\mathcal{M}(\mathbf{h})}, \tag{A-86}$$

$$G^{\mathrm{s}}_t(\mathbf{h}) = \frac{(1+s)\left[s+(1-s)\mathcal{M}(\mathbf{h})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{h})} \tag{A-87}$$

(see eqs. (A.47) and (A.49) in [41]).

[1] Eq. (A.51) in [41] applies for all $\mathbf{k} \in \mathcal{G}$, the condition " if $\mathbf{k} > \mathbf{0}$" therein is not necessary. Also, the term $-s/N$ in the last line of eq (A.48) of [41] contains a typo and should be replaced by s/N.

Likewise, from eqs. (A.32), (A.38), and (A.41)[2] in [41], we have

$$\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_{\mathbf{j}}Q_{\mathbf{j},0}+P_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]=\frac{1}{N}\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right] \tag{A-88}$$

$$\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{0},0}-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_{\mathbf{j}}Q_{\mathbf{j},0}+P_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]=\frac{1}{N}\left[\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right] \tag{A-89}$$

$$\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{k},0}-\left(\sum_{\mathbf{j}\in\mathcal{G}}P_{\mathbf{j}}Q_{\mathbf{j}-\mathbf{k},0}+P_{\mathbf{k}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]=\frac{1}{N}\left[\mathcal{L}_{\mathbf{k}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]\text{ for }\mathbf{k}\neq\mathbf{0}, \tag{A-90}$$

$$\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[Q_{\mathbf{k},t}-\sum_{\mathbf{j}\in\mathcal{G}}P_{\mathbf{j}}Q_{\mathbf{j}-\mathbf{k},t}\right]=\frac{1}{N}\left[\mathcal{L}_{\mathbf{k}}\left(G^{\mathrm{f}}_{t}\right)-\frac{1+s}{D}\right]\text{ for }t\neq 0, \tag{A-91}$$

where the functions F^{f} and G^{f}_t are defined at $\mathbf{h}$ as

$$F^{\mathrm{f}}(\mathbf{h}) = \frac{2s\mathcal{M}(\mathbf{h})}{1+s+(1-s)\mathcal{M}(\mathbf{h})}, \tag{A-92}$$

$$G^{\mathrm{f}}_t(\mathbf{h}) = \frac{(1+s)(1+\mathcal{M}(\mathbf{h}))\left[s+(1-s)\mathcal{M}(\mathbf{h})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{h})} \tag{A-93}$$

(see eqs. (A.37) and (A.39)[3] in [41]).

We can now proceed to simplify eqs. (A-79)–(A-81). First, multiplying the numerator and denominator of (A-79) by $\lim_{\mu\to 0}1/(1-Q_{\mathbf{0},0})$, substituting eqs. (A-82), (A-83), (A-88), and (A-89), and then multiplying numerator and denominator by N, we obtain

$$\kappa_{\mathbf{0},0}=\frac{s'f\left[\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}{s'f\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}. \tag{A-94}$$

Second, proceeding similarly with eq. (A-80) (by substituting eqs. (A-82), (A-84), (A-88), and (A-90)), we obtain

$$\kappa_{\mathbf{k},0}=\frac{s'f\left[\mathcal{L}_{\mathbf{k}}\left(F^{\mathrm{s}}\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[\mathcal{L}_{\mathbf{k}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}{s'f\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}\quad\text{for }\mathbf{k}\neq\mathbf{0}. \tag{A-95}$$

Third, proceeding similarly with eq. (A-81) with $t>0$ (by substituting eqs. (A-82), (A-85), (A-88), and (A-91)) we obtain

$$\kappa_{\mathbf{k},t}=\frac{s'f\left[\mathcal{L}_{\mathbf{k}}\left(G^{\mathrm{s}}_t\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[\mathcal{L}_{\mathbf{k}}\left(G^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}{s'f\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{s}}\right)-\frac{1+s}{2D}\right]+f'(1-s)\left[N+\mathcal{L}_{\mathbf{0}}\left(F^{\mathrm{f}}\right)-\frac{1+s}{D}\right]}\quad\text{for }t>0. \tag{A-96}$$

Finally, noting that eq. (A-94) is equal to eq. (A-95) with $\mathbf{k}=\mathbf{0}$, substituting eqs. (A-86)–(A-92), and rearranging yields eq. (III.A) of Box II, that is:

$$\kappa_{\mathbf{k},t}=\begin{cases}\dfrac{\mathcal{L}_{\mathbf{k}}(F)-(1+s)\left[s'f+2f'(1-s)\right]/(2D)}{N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-(1+s)\left[s'f+2f'(1-s)\right]/(2D)} & \text{if } t=0\\[2ex] \dfrac{\mathcal{L}_{\mathbf{k}}(G_t)-(1+s)\left[s'f+2f'(1-s)\right]/(2D)}{N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-(1+s)\left[s'f+2f'(1-s)\right]/(2D)} & \text{otherwise,}\end{cases} \tag{A-97}$$

[2]Eq. (A.41) in [41] applies for for all $\mathbf{k}\in\mathcal{G}$, the condition " if $\mathbf{k}\neq\mathbf{0}$" therein is not necessary.

[3]Eq.(A.39) in [41] contains a typo in that the the second parenthesis is not closed and the term $(1+\psi_{\mathbf{h}}$ should read $(1+\psi_{\mathbf{h}})$.

where the functions F and G_t are given by

$$\begin{aligned} F(\mathbf{h}) &= -\frac{(1-s)\left[s'f-2sf'\right]\mathcal{M}(\mathbf{h})}{1+s+(1-s)\mathcal{M}(\mathbf{h})}, \\ G_t(\mathbf{h}) &= \frac{(1+s)\left[s'f+f'(1-s)(1+\mathcal{M}(\mathbf{h}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{h})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{h})}, \end{aligned} \tag{A-98}$$

as required.

Note that one can also write eq. (A-97) as

$$\kappa_{\mathbf{k},t} = \begin{cases} \dfrac{\mathcal{L}_{\mathbf{k}}(F)-G_0(\mathbf{0})/D}{N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-G_0(\mathbf{0})/D} & \text{if } t=0 \\ \dfrac{\mathcal{L}_{\mathbf{k}}(G_t)-G_0(\mathbf{0})/D}{N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-G_0(\mathbf{0})/D} & \text{otherwise,} \end{cases} \tag{A-99}$$

since, for all t,

$$G_t(\mathbf{0}) = \frac{(1+s)\left[s'f+f'(1-s)(1+\mathcal{M}(\mathbf{0}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{0})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{0})} = G_0(\mathbf{0}) = \frac{(1+s)\left[s'f+2f'(1-s)\right]}{2} \tag{A-100}$$

holds.

Appendix E.4 Explicit expression for L

Finally, we evaluate L in eq. (A-46), which is needed if one aims to evaluated the trait stationary density function (A-5). Substituting the definition of the coefficients of fitness interdependence (A-40) into eq. (A-46), simplifying, and rearranging, we obtain

$$\begin{aligned} L &= \frac{\partial\tilde{w}}{\partial\pi_\bullet} + \frac{\partial\tilde{w}}{\partial\pi_{\mathbf{0}}}R_{\mathbf{0},0} + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\frac{\partial\tilde{w}}{\partial\pi_{\mathbf{j}}}R_{\mathbf{j},0} \\ &= s'\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}}R_{\mathbf{j},0} + m_{\mathbf{0}}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right] + \frac{f'}{f}(1-s)\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}}R_{\mathbf{j},0} + P_{\mathbf{0}}\frac{(1-R_{\mathbf{0},0})}{N}\right)\right], \end{aligned} \tag{A-101}$$

where the second equality follows from our previous derivation in eq. (A-72).

Substituting eq. (8), we get

$$\begin{aligned} L = \frac{1}{f}\Bigg(& s'f\lim_{\mu\to 0}\frac{1}{1-\overline{Q}_0}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}}Q_{\mathbf{j},0} + m_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] \\ & + f'(1-s)\lim_{\mu\to 0}\frac{1}{1-\overline{Q}_0}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}}Q_{\mathbf{j},0} + P_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]\Bigg), \end{aligned} \tag{A-102}$$

which can be computed as

$$\begin{aligned} L = \frac{1}{f}\lim_{\mu\to 0}\left(\frac{1-Q_{\mathbf{0},0}}{1-\overline{Q}_0}\right)\Bigg(& s'f\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} m_{\mathbf{j}}Q_{\mathbf{j},0} + m_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right] \\ & + f'(1-s)\lim_{\mu\to 0}\frac{1}{1-Q_{\mathbf{0},0}}\left[1-\left(\sum_{\mathbf{j}\in\mathcal{G}} P_{\mathbf{j}}Q_{\mathbf{j},0} + P_{\mathbf{0}}\frac{(1-Q_{\mathbf{0},0})}{N}\right)\right]\Bigg), \end{aligned} \tag{A-103}$$

where the term in the outmost parenthesis is the same as the denominator of eq. (A-79). Then in force

of the denominator of eq. (A-97) and noting that the factor $1/N$ in eq. (A-82) and eq. (A-88) does not cancel as it does in the numerator and denominator of eq. (A-97) allows us to write

$$L = \lim_{\mu\to 0}\left(\frac{1-Q_{\mathbf{0},0}}{1-\overline{Q}_0}\right)\times\frac{1}{fN}\left(N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-\frac{(1+s)\left[s'f+2f'(1-s)\right]}{2D}\right). \tag{A-104}$$

For a Wright-Fisher process where $s' = s = 0$ (and hence, also $\mathcal{L}_{\mathbf{0}}(F) = 0$), we have

$$L = \lim_{\mu\to 0}\left(\frac{1-Q_{\mathbf{0},0}}{1-\overline{Q}_0}\right)\times\frac{f'}{fN}\left(N-\frac{1}{D}\right) = \lim_{\mu\to 0}\left(\frac{1-Q_{\mathbf{0},0}}{1-\overline{Q}_0}\right)\times\frac{f'}{f}\left(\frac{ND-1}{ND}\right). \tag{A-105}$$

Appendix F Explicit coefficient for the selection gradient

Here, we derive eq. (III.C) of Box III of the main text. First, we simplify the expression for $\kappa_{\mathbf{k},t}$ for $t > 0$ given in the the second line of eq. (A-99). Using the definition of the inverse Fourier transform given in eq. (I.D), and simplifying we obtain

$$\begin{aligned}
\kappa_{\mathbf{k},t} &= \frac{\mathcal{L}_{\mathbf{k}}(G_t) - G_t(\mathbf{0})/D}{N\left[s'f+f'(1-s)\right]+\mathcal{L}_{\mathbf{0}}(F)-G_0(\mathbf{0})/D} \\
&= \frac{\frac{1}{D}\sum_{\mathbf{j}\in\mathcal{G}} G_t(\mathbf{j})\overline{\chi}_{\mathbf{k}}(\mathbf{j}) - \frac{1}{D}G_t(\mathbf{0})\overline{\chi}_{\mathbf{k}}(\mathbf{0})}{N\left[s'f+f'(1-s)\right]+\frac{1}{D}\sum_{\mathbf{j}\in\mathcal{G}} F(\mathbf{j}) - G_0(\mathbf{0})/D} \\
&= \frac{\frac{1}{D}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} G_t(\mathbf{j})\overline{\chi}_{\mathbf{k}}(\mathbf{j})}{N\left[s'f+f'(1-s)\right]+\frac{1}{D}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} F(\mathbf{j}) - \frac{s'f+f'(1-s)}{D}} \\
&= \frac{\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} G_t(\mathbf{j})\overline{\chi}_{\mathbf{k}}(\mathbf{j})}{(ND-1)\left[s'f+f'(1-s)\right]+\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} F(\mathbf{j})},
\end{aligned} \tag{A-106}$$

where we have used $\overline{\chi}_{\mathbf{k}}(\mathbf{0}) = 1$ for all $\mathbf{k}\in\mathcal{G}$, the identity $G_t(\mathbf{0}) = G_0(\mathbf{0})$ for all t (A-100), and the fact that

$$F(\mathbf{0}) - G_0(\mathbf{0}) = -\left[s'f+f'(1-s)\right] \tag{A-107}$$

holds.

Substituting the simplified expression for $\kappa_{\mathbf{k},t}$ (A-106) together with the expression for $e_{\mathbf{k},t}$ (19) into eq. (32), and setting

$$H = (ND-1)\left[s'f+f'(1-s)\right] + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} F(\mathbf{j}), \tag{A-108}$$

yields

$$\begin{aligned}
K &= \sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}} e_{\mathbf{k},t}\kappa_{\mathbf{k},t} \\
&= \frac{1}{H}\sum_{t=1}^{\infty}\sum_{\mathbf{k}\in\mathcal{G}}\left[\frac{1}{D}\sum_{\mathbf{i}\in\mathcal{G}}\mathcal{C}(\mathbf{i})^{t-1}\Psi(\mathbf{i})\overline{\chi}_{\mathbf{k}}(\mathbf{i})\right]\left[\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} G_t(\mathbf{j})\overline{\chi}_{\mathbf{k}}(\mathbf{j})\right] \\
&= \frac{1}{H}\sum_{t=1}^{\infty}\sum_{\mathbf{i}\in\mathcal{G}}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\mathcal{C}(\mathbf{i})^{t-1}\Psi(\mathbf{i})G_t(\mathbf{j})\frac{1}{D}\sum_{\mathbf{k}\in\mathcal{G}}\overline{\chi}_{\mathbf{k}}(\mathbf{i})\overline{\chi}_{\mathbf{k}}(\mathbf{j}) \\
&= \frac{1}{H}\sum_{t=1}^{\infty}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}\mathcal{C}(-\mathbf{j})^{t-1}\Psi(-\mathbf{j})G_t(\mathbf{j}),
\end{aligned} \tag{A-109}$$

where the last equality follows from using eq. (I.F). Substituting eq. (III.B) into (A-109) and solving

the geometric series yields

$$K = \frac{1}{H}\sum_{t=1}^{\infty}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \mathcal{C}(-\mathbf{j})^{t-1}\Psi(-\mathbf{j})\frac{(1+s)\left[s'f + f'(1-s)(1+\mathcal{M}(\mathbf{j}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{j})\right]^t}{1+s+(1-s)\mathcal{M}(\mathbf{j})} \tag{A-110}$$
$$= \frac{1}{H}\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1+s)\left[s'f + f'(1-s)(1+\mathcal{M}(\mathbf{j}))\right]\left[s+(1-s)\mathcal{M}(\mathbf{j}) - \mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]\Psi(-\mathbf{j})}{\left[1+s+(1-s)\mathcal{M}(\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\right]\left[1-\mathcal{C}(-\mathbf{j})\mathcal{M}(\mathbf{j})\right]},$$

which is the final expression presented in eq. (III.C).

To go from the first to the second line of eq. (A-110), the relevant geometric series must converge, which happens if the moduli of $\mathcal{M}(\mathbf{j})$ and $\mathcal{C}(\mathbf{j})$ are smaller than one (i.e. $|\mathcal{M}(\mathbf{j})| < 1$ and $|\mathcal{C}(\mathbf{j})| < 1$) for all $\mathbf{j} \in \mathcal{G}\setminus\mathbf{0}$, i.e. if the complex numbers $\mathcal{M}(\mathbf{j})$ and $\mathcal{C}(\mathbf{j})$ are within the unit circle. To see this is true, consider first that by the property of characteristic functions of probability distribution, we have $\mathcal{M}(\mathbf{0}) = 1$, and $|\mathcal{M}(\mathbf{j})| < 1$ for $\mathbf{j} \in \mathcal{G}\setminus\mathbf{0}$ (p. 182 in [82]). Second, $|\mathcal{C}(\mathbf{j})| < 1$ from our assumption that the dynamical system eq. (2) has an hyperbolically stable equilibrium point. Indeed, stability means that all the eigenvalues of the Jacobian matrix of eq. (2) have modulus smaller than one (e.g. p. 103 of [83]). But these eigenvalues are in fact given by the coefficients $\mathcal{C}(\mathbf{j})$. To see this, first note that from eq. (2) the Jacobian of this discrete-time dynamical system around the equilibrium $\hat{n}$ defined by eq. (3) is given by

$$\mathbf{J} = \begin{pmatrix} \frac{\partial g(\mathbf{z_0}_{,t},\mathbf{n_0}_{,t})}{\partial n_{\mathbf{0}}} & \frac{\partial g(\mathbf{z_0}_{,t},\mathbf{n_0}_{,t})}{\partial n_{\mathbf{1}}} & \frac{\partial g(\mathbf{z_0}_{,t},\mathbf{n_0}_{,t})}{\partial n_{\mathbf{2}}} & \cdots & \frac{\partial g(\mathbf{z_0}_{,t},\mathbf{n_0}_{,t})}{\partial n_{\mathbf{D_{-1}}}} \\ \frac{\partial g(\mathbf{z_1}_{,t},\mathbf{n_1}_{,t})}{\partial n_{\mathbf{0}}} & \frac{\partial g(\mathbf{z_1}_{,t},\mathbf{n_1}_{,t})}{\partial n_{\mathbf{1}}} & \frac{\partial g(\mathbf{z_1}_{,t},\mathbf{n_1}_{,t})}{\partial n_{\mathbf{2}}} & \cdots & \frac{\partial g(\mathbf{z_1}_{,t},\mathbf{n_1}_{,t})}{\partial n_{\mathbf{D_{-1}}}} \\ \frac{\partial g(\mathbf{z_2}_{,t},\mathbf{n_2}_{,t})}{\partial n_{\mathbf{0}}} & \frac{\partial g(\mathbf{z_2}_{,t},\mathbf{n_2}_{,t})}{\partial n_{\mathbf{1}}} & \frac{\partial g(\mathbf{z_2}_{,t},\mathbf{n_2}_{,t})}{\partial n_{\mathbf{2}}} & \cdots & \frac{\partial g(\mathbf{z_2}_{,t},\mathbf{n_2}_{,t})}{\partial n_{\mathbf{D_{-1}}}} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial g(\mathbf{z_{D_{-1}}}_{,t},\mathbf{n_{D_{-1}}}_{,t})}{\partial n_{\mathbf{0}}} & \frac{\partial g(\mathbf{z_{D_{-1}}}_{,t},\mathbf{n_{D_{-1}}}_{,t})}{\partial n_{\mathbf{1}}} & \frac{\partial g(\mathbf{z_{D_{-1}}}_{,t},\mathbf{n_{D_{-1}}}_{,t})}{\partial n_{\mathbf{2}}} & \cdots & \frac{\partial g(\mathbf{z_{D_{-1}}}_{,t},\mathbf{n_{D_{-1}}}_{,t})}{\partial n_{\mathbf{D_{-1}}}} \end{pmatrix}, \tag{A-111}$$

where all derivatives are evaluated at z and $\hat{n}$. Now, recalling the notations defined in eq. (A-19), the entries of this matrix are of the form

$$c_{\mathbf{k}-\mathbf{i}} = \frac{\partial g(\mathbf{z_k}_{,t},\mathbf{n_k}_{,t})}{\partial n_{\mathbf{i},t}} = \frac{\partial g(\mathbf{z_{k-i}}_{,t},\mathbf{n_{k-i}}_{,t})}{\partial n_{\mathbf{0},t}} = \frac{\partial g(\mathbf{z_0}_{,t},\mathbf{n_0}_{,t})}{\partial n_{\mathbf{k}-\mathbf{i},t}}, \tag{A-112}$$

which is the same as eq. (A-19) since all phenotypes vectors, here and there, are set to $(z, ..., z)$ when computing the derivative. From the first equality in the previous equation, the Jacobian (A-111) can be written as

$$\mathbf{J} = \begin{pmatrix} c_{\mathbf{0}} & c_{\mathbf{-1}} & c_{\mathbf{-2}} & \cdots \\ c_{\mathbf{1}} & c_{\mathbf{0}} & c_{\mathbf{-1}} & \cdots \\ \vdots & \vdots & \vdots & \cdots \\ c_{D_{-1}} & c_{D_{-2}} & c_{D_{-3}} & \ddots \end{pmatrix}, \tag{A-113}$$

where we defined $D_{-2} = \mathbf{D}_{-1} - \mathbf{1}$, $D_{-3} = \mathbf{D}_{-1} - \mathbf{2}$, etc. Written in this form, it is clear that the Jacobian (A-113) is a $\mathcal{G}$-group circulant matrix (e.g. p. 50 of [84]), with eigenvalues given by the Fourier transform of $c_{\mathbf{j}}$ (Theorem 8 in [84]). Hence, the $\mathbf{k}$-th eigenvalue of $\mathbf{J}$ is $\mathcal{C}(\mathbf{k}) = \sum_{\mathbf{j}\in\mathcal{G}} c_{\mathbf{j}}\chi_{\mathbf{j}}(\mathbf{k})$.

Appendix G Public good diffusion example

Appendix G.1 Fecundity effects

Here, we derive eq. (44) of the main text, which considers fecundity effects and no generational overlap ($s' = s = 0$). Substituting eq. (27) into eq. (42) yields

$$\begin{aligned}\Omega &= \epsilon \sum_{t=1}^{\infty} \sum_{\mathbf{k}\in\mathcal{G}} (1-\epsilon)^{t-1} q_{\mathbf{k},t} \left(\frac{D p_{\mathbf{k},t} - 1}{ND-1} \right) \\ &= \frac{\epsilon}{ND-1} \sum_{t=1}^{\infty} (1-\epsilon)^{t-1} \left(D \sum_{\mathbf{k}\in\mathcal{G}} q_{\mathbf{k},t} p_{\mathbf{k},t} - \sum_{\mathbf{k}\in\mathcal{G}} q_{\mathbf{k},t} \right) \\ &= \frac{\epsilon D}{ND-1} \sum_{t=1}^{\infty} (1-\epsilon)^{t-1} \left(\sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} q_{\mathbf{k},t} - \frac{1}{D} \right), \end{aligned} \tag{A-114}$$

where we have used the fact that $q_{\mathbf{k},t}$ is a probability distribution over $\mathcal{G}$ for all t and hence that $\sum_{\mathbf{k}\in\mathcal{G}} q_{\mathbf{k},t} = 1$ holds for all t.

Eq. (A-114) can be written in terms of the population covariance of $p_{\mathbf{k},t}$ and $q_{\mathbf{k},t}$ in the following way. Recall that the population covariance of two vectors $x = (x_1, \ldots, x_n)$ and $y = (y_1, \ldots, y_n)$ of length n is given by

$$\mathrm{cov}(x, y) = \frac{1}{n} \sum_{j=1}^{n} x_j y_j - \bar{x}\bar{y} \tag{A-115}$$

where $\bar{x} = \frac{1}{n}\sum_{j=1}^{n} x_j$ and $\bar{y} = \frac{1}{n}\sum_{j=1}^{n} y_j$. Using this definition of population covariance, and denoting by $p_t = (p_{\mathbf{0},t}, \ldots, p_{\mathbf{D}_{-1},t})$ and $q_t = (q_{\mathbf{0},t}, \ldots, q_{\mathbf{D}_{-1},t})$ the vectors collecting all $p_{\mathbf{k},t}$'s and $q_{\mathbf{k},t}$'s in lexicographic order, we can write

$$\begin{aligned}\mathrm{cov}(p_t, q_t) &= \frac{1}{D} \sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} q_{\mathbf{k},t} - \left(\frac{1}{D} \sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} \right) \left(\frac{1}{D} \sum_{\mathbf{k}\in\mathcal{G}} q_{\mathbf{k},t} \right) \\ &= \frac{1}{D} \sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} q_{\mathbf{k},t} - \frac{1}{D^2} \\ &= \frac{1}{D} \left(\sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} q_{\mathbf{k},t} - \frac{1}{D} \right) \\ D\mathrm{cov}(p_t, q_t) &= \sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} q_{\mathbf{k},t} - \frac{1}{D}, \end{aligned} \tag{A-116}$$

where the second line follows from the fact that both $p_{\mathbf{k},t}$ and $q_{\mathbf{k},t}$ are probability distributions over $\mathcal{G}$ for all t and hence satisfy $\sum_{\mathbf{k}\in\mathcal{G}} p_{\mathbf{k},t} = \sum_{\mathbf{k}\in\mathcal{G}} q_{\mathbf{k},t} = 1$ for all t. Substituting (A-116) into (A-114) we finally obtain

$$\Omega = \frac{\epsilon D^2}{ND-1} \sum_{t=1}^{\infty} (1-\epsilon)^{t-1} \mathrm{cov}(p_t, q_t), \tag{A-117}$$

as required.

Appendix G.2 Fecundity effects: Weak dispersal

Here, we derive eq. (46) of the main text, following the common approach to evaluate a weak migration approximation (chapter 3 in [3]). To do so, we first set $m_{\mathbf{0}} = (1-m)$ and $d_{\mathbf{0}} = (1-d)$, where m and d are the net dispersal probabilities of the focal species and the environmental variable, and

write $m_{\mathbf{i}} = m g^{\mathrm{m}}_{\mathbf{i}}$ and $d_{\mathbf{i}} = d g^{\mathrm{d}}_{\mathbf{i}}$. The characteristic functions of the dispersal distributions can then be expressed as $\mathcal{M}(\mathbf{j}) = 1 - m x^{\mathrm{m}}(\mathbf{j})$ and $\mathcal{D}(\mathbf{j}) = 1 - d x^{\mathrm{d}}(\mathbf{j})$, where $x^{\mathrm{m}}(\mathbf{j}) = 1 - \sum_{\mathbf{i}\neq\mathbf{0}} g^{\mathrm{m}}_{\mathbf{i}} \chi_{\mathbf{i}}(\mathbf{j})$ and $x^{\mathrm{d}}(\mathbf{j}) = 1 - \sum_{\mathbf{i}\neq\mathbf{0}} g^{\mathrm{d}}_{\mathbf{i}} \chi_{\mathbf{i}}(\mathbf{j})$. Substituting these expressions into the summand of eq. (45), and Taylor expanding around $m = 0$ and $d = 0$, we get

$$\frac{\mathcal{D}(-\mathbf{j})\mathcal{M}(\mathbf{j})}{1-(1-\epsilon)\mathcal{D}(-\mathbf{j})\mathcal{M}(\mathbf{j})} = \frac{\epsilon - m x^{\mathrm{m}}(\mathbf{j}) - d x^{\mathrm{d}}(\mathbf{j})}{\epsilon^2} + \text{h.o.t.}, \tag{A-118}$$

where "h.o.t." refers to higher order terms, e.g. terms proportional to m^2, md, d^2, etc. Substituting $x^{\mathrm{m}}(\mathbf{j}) = [1 - \mathcal{M}(\mathbf{j})]/m$ and $x^{\mathrm{d}}(\mathbf{j}) = [1 - \mathcal{D}(\mathbf{j})]/d$, we can write eq. (45) as

$$\Omega = \frac{1}{ND-1} \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\mathcal{M}(\mathbf{j}) + \mathcal{D}(\mathbf{j}) + \epsilon - 2}{\epsilon^2} + \text{h.o.t.}. \tag{A-119}$$

Neglecting the higher order terms and using $\mathcal{M}(\mathbf{j}) = \sum_{\mathbf{k}\in\mathcal{G}} m_{\mathbf{k}} \chi_{\mathbf{k}}(\mathbf{j})$, and $\mathcal{D}(\mathbf{j}) = \sum_{\mathbf{k}\in\mathcal{G}} d_{\mathbf{k}} \chi_{\mathbf{k}}(\mathbf{j})$ produces

$$\begin{aligned}
\Omega &= \frac{1}{ND-1} \left[\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \sum_{\mathbf{k}\in\mathcal{G}} \left(\frac{m_{\mathbf{k}} + d_{\mathbf{k}}}{\epsilon^2} \right) \chi_{\mathbf{k}}(\mathbf{j}) + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \left(\frac{\epsilon - 2}{\epsilon^2} \right) \right] \\
&= \frac{1}{ND-1} \left[\sum_{\mathbf{k}\in\mathcal{G}} \left(\frac{m_{\mathbf{k}} + d_{\mathbf{k}}}{\epsilon^2} \right) \left(\sum_{\mathbf{j}\in\mathcal{G}} \chi_{\mathbf{k}}(\mathbf{j}) - 1 \right) + \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \left(\frac{\epsilon - 2}{\epsilon^2} \right) \right] \\
&= \frac{1}{ND-1} \left[\left(\frac{m_{\mathbf{0}} + d_{\mathbf{0}}}{\epsilon^2} \right) (D-1) + (D-1) \left(\frac{\epsilon - 2}{\epsilon^2} \right) \right] \\
&= \left(\frac{D-1}{ND-1} \right) \left(\frac{\epsilon - m - d}{\epsilon^2} \right),
\end{aligned} \tag{A-120}$$

where the penultimate equality follows from the facts that $\sum_{\mathbf{k}\in\mathcal{G}} \chi_{\mathbf{k}}(\mathbf{j}) = D$ if $\mathbf{j} = \mathbf{0}$ and zero otherwise (recall eq. I.F), and that $\sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}}(1) = D - 1$.

Appendix G.3 Survival effects

We now consider the case where there are survival but no fecundity effects ($f' = 0$). Writing Ω as $\Omega = \epsilon KN/P'(z)$, substituting eqs. (37) and (38) into eq. (III.F) in Box III, and simplifying we obtain

$$\begin{aligned}
\Omega = &\frac{1}{(DN-1) - \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1-s)\mathcal{M}(\mathbf{j})}{1+s+(1-s)\mathcal{M}(\mathbf{j})}} \\
&\times \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{(1+s)\left[s + (1-s)\mathcal{M}(\mathbf{j}) - (1-\epsilon)\mathcal{M}(\mathbf{j})\mathcal{D}(-\mathbf{j})\right]\mathcal{D}(-\mathbf{j})}{\left[1+s+(1-s)\mathcal{M}(\mathbf{j})\right]\left[1-(1-\epsilon)\mathcal{D}(-\mathbf{j})\right]\left[1-(1-\epsilon)\mathcal{M}(\mathbf{j})\mathcal{D}(-\mathbf{j})\right]},
\end{aligned} \tag{A-121}$$

which remains a somewhat complicated expression. In the limit $s \to 1$, eq. (A-121) simplifies to

$$\Omega = \frac{1}{ND-1} \sum_{\mathbf{j}\in\mathcal{G}\setminus\mathbf{0}} \frac{\mathcal{D}(-\mathbf{j})}{1-(1-\epsilon)\mathcal{D}(-\mathbf{j})}. \tag{A-122}$$

This can be thought as a special case where investment into the common-pool resource occurs in a population of immortal individuals that therefore become mortal through endogeneously induced deaths. Finally, we not that for a spatially symmetric dispersal distribution we can set $\mathcal{D}(-\mathbf{j}) = \mathcal{D}(\mathbf{j})$.

Appendix G.4 Species dispersal and commons movement

In our example, we assumed that the evolving species dispersed according to a model based on the Binomial distribution, which is detailed in Appendix B. Hence, the characteristic function used for a one-dimensional habitat is given by eq. (A-9), while for two dimensional, it is based on Appendix B.2.

We assume that the way the commons moves in space follows the same model as the evolving species. We write d for the commons' probability of movement (instead of m), and $\overline{\lambda}_{\mathrm{d}}$ for the mean number of steps a unit of commons moves conditional on leaving the patch (instead of $\overline{\lambda}_{\mathrm{m}}$). The characteristic function of the movement in one dimension then is like eq. (A-9), i.e.

$$\mathcal{D}(k) = (1-d) + d \sum_{j=1}^{\frac{D-1}{2}} p_j((D-1)/2, 2\lambda_{\mathrm{d}}/(D-1)) \cos(2\pi jk/D) \tag{A-123}$$

where λ_{d} is such that

$$\overline{\lambda}_{\mathrm{d}} = \frac{\lambda_{\mathrm{d}}}{1 - \left(1 - \frac{2\lambda_{\mathrm{d}}}{D-1}\right)^{(D-1)/2}}. \tag{A-124}$$

Appendix G.5 Stationary distribution

Here, we specify the stationary distribution of the trait substitution sequence for our example, i.e. we specify eq. (A-5), which we used in Fig. 6E for the interval. Plugging eq. (41) into eq. (A-53), which is in turn substituted into eq. (A-4) gives

$$\phi(z) = \underbrace{\lim_{\mu\to 0}\left(\frac{1-\overline{Q}_0}{1-Q_{\mathbf{0},0}}\right)}_{>0} \times L \times \pi(z,z,\hat{n}) \times \left(BP'(z)\alpha_{\mathrm{B}}\left(\frac{P(z)}{\epsilon}\right)^{\alpha_{\mathrm{B}}-1}\Omega - C\alpha_C z^{\alpha_{\mathrm{C}}-1}\right), \tag{A-125}$$

thus characterising the term within parenthesis of eq. (A-5). For the Wright-Fisher process, we have from eq. (A-105) that

$$L = \lim_{\mu\to 0}\left(\frac{1-Q_{\mathbf{0},0}}{1-\overline{Q}_0}\right) \times \frac{1}{\pi(z,z,\hat{n})}\left(\frac{ND-1}{ND}\right), \tag{A-126}$$

where we used the fact that for our example payoff is fecundity and so $f' = 1$ in eq. (A-105). Thus, the perturbation of the fixation probability reduces to

$$\phi(z) = \left(\frac{ND-1}{ND}\right)\left(BP'(z)\alpha_{\mathrm{B}}\left(\frac{P(z)}{\epsilon}\right)^{\alpha_{\mathrm{B}}-1}\Omega - C\alpha_C z^{\alpha_{\mathrm{C}}-1}\right). \tag{A-127}$$

Assuming further that $P(z) = P_0 z$, we find by substituting eq. (A-127) into eq. (A-5) that the stationary distribution is given by

$$p(z) = C_{\mathrm{p}} \exp\left[2(ND-1)\left(B\left(\frac{P_0 z}{\epsilon}\right)^{\alpha_{\mathrm{B}}}\epsilon\,\Omega - Cz^{\alpha_{\mathrm{C}}}\right)\right], \tag{A-128}$$

where C_{p} is a constant of proportionality such that $\int p(z)\,\mathrm{d}z = 1$.