

# The molding of intraspecific trait variation by selection under ecological inheritance

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## Abstract

Organisms continuously modify their environment, often impacting the fitness of future conspecifics due to ecological inheritance. When this inheritance is biased toward kin, selection favors modifications that increase the fitness of downstream individuals. How such selection shapes trait variation within populations remains poorly understood. Using mathematical modelling, we investigate the coevolution of multiple traits in a group-structured population when these traits affect the group environment, which is then bequeathed to future generations. We examine when such coevolution favors polymorphism as well as the resulting associations among traits. We find in particular that two traits become associated when one trait affects the environment while the other influences the likelihood that future kin experience this environment. To illustrate this, we model the coevolution of (a) the attack rate on a local renewable resource, which deteriorates environmental conditions, with (b) dispersal between groups, which reduces the likelihood that kin suffers from such deterioration. We show this often leads to the emergence of two highly differentiated morphs: one that readily disperses and depletes local resources, and another that maintains these resources and tends to remain philopatric. More broadly, we suggest that ecological inheritance can contribute to phenotypic diversity and lead to complex polymorphism.

**Keywords:** evolutionary ecology, polymorphism, niche construction, correlational selection, dispersal syndrome

## Introduction

By consuming, polluting or engineering, most if not all organisms modify and transform the environment they live in. Via such modifications, an individual impacts its own fitness as well as the fitness of conspecifics who share its environment. These fitness effects can extend to future generations when environmental modifications are transmitted to offspring under what is referred to as ecological inheritance (Bonduriansky, 2012; Bonduriansky & Day, 2020; Laland et al., 1996; Odling-Smee, 1988; Odling-Smee et al., 1996, 2003). For example, many plants continuously modify their substrate via plant–soil feedbacks that can stretch to downstream generations (Ehrenfeld et al., 2005; e.g., by producing and absorbing tannin, Kraus et al., 2003). *Pseudomonas aeruginosa* release long-lasting iron-scavenging siderophores, thus benefiting close-by conspecifics in the short and long term (Imperi et al., 2009; Ratledge & Dover, 2000), including individuals that are not living yet (Kümmerli & Brown, 2010). Ecological inheritance can of course also be harmful, for instance when individuals overconsume a slowly renewable resource or release pollutants that are difficult to degrade.

For natural selection to shape the intergenerational ecological effects of a trait, the genes underlying this trait must be statistically associated to the environment they transform (Brodie, 2005; Dawkins, 1982, 2004; Lehmann, 2007, 2008). This association entails that an environmental modification is more likely to be experienced by individuals in the future that carry the same genes as the individual who caused the initial modification. One simple and ubiquitous

way for a gene–environment association to emerge is via spatial structure. When the population is subdivided and dispersal between subpopulations is limited, individuals in the same local environment are more likely to share the same genes than individuals sampled at random in the population (i.e., they are related; Hamilton, 1964; Rousset, 2004). This is true of individuals living at the same but also at different generations (Lehmann, 2007). As a result, the intergenerational ecological modification made by an individual preferentially affects the fitness of its future relatives when dispersal is limited (Lehmann, 2008).

How directional selection steers the gradual evolution of traits with intergenerational ecological effects under limited dispersal has been well studied (Arnoldi et al., 2020; Lehmann, 2007, 2008; Mullon and Lehmann, 2018; Mullon et al., 2021; Sozou, 2009). One of the main insights from this theory is that populations in which dispersal is more limited are more likely to evolve traits that are costly to the individual but yield delayed ecological benefits, such as the preservation of a common good (Arnoldi et al., 2020; Lehmann, 2007, 2008; Silver & Di Paolo, 2006; Sozou, 2009; Krakauer et al., 2009; Mullon and Lehmann, 2018; Mullon et al., 2021; for review: Estrela et al., 2019). But while directional selection can explain trait variation between species (or completely isolated populations), it is not sufficient to investigate variation within species, which requires characterizing disruptive selection (Dercole & Rinaldi, 2008; Rousset, 2004). Consequently, these previous studies focused on directional selection do not address the question of how selection can favor the emergence

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of polymorphism in traits with intergenerational ecological effects.

Intraspecific variation in ecologically relevant traits is nevertheless common, with potentially significant ecological effects (Araújo et al., 2011; Bolnick et al., 2003, 2011; Des Roches et al., 2018; Violle et al., 2012). Variation in predator traits can, for example, stabilize prey–predator dynamics (Okuyama, 2008), or lead to apparent mutualism between prey (Schreiber et al., 2011). So far, mathematical models that investigate the emergence of intraspecific variation owing to disruptive selection under limited dispersal assume that traits have immediate effects, which do not carry over between generations (e.g., Ajar, 2003; Day, 2001; Mullan et al., 2016; Ohtsuki et al., 2020; Schmid et al., 2022; Wakano & Lehmann, 2014). However, simulations indicate that polymorphism in traits that have lasting ecological effects can emerge or be maintained in spatially structured populations (Behar et al., 2014; Han et al., 2006; Joshi et al., 2020; Silver & Di Paolo, 2006). In particular, when harvesting of a common good evolves through social learning, agent-based simulations show that different harvesting strategies can coexist when learning is fast relative to the renewal of the good, suggesting a role for ecological inheritance (Joshi et al., 2020). More broadly, these simulation studies offer useful but partial insights into how intraspecific variation is molded under ecological inheritance and limited dispersal.

In this article, we extend current theory to better understand when gradual evolution leads to polymorphism in traits that have long-lasting environmental effects through disruptive selection. We investigate mathematically the coevolution of multiple traits in a group-structured population when these traits affect the group environment, which is then passed down to future generations. We use our model to investigate the type of between-traits within-individuals correlations that are favored by selection when polymorphism emerges. Our analyses reveal in particular that two traits tend to be correlated when one modifies the environment in a long-lasting manner while the other influences the likelihood that future relatives experience this environmental modification. To illustrate this, we model the coevolution of the attack rate on a local renewable resource, which deteriorates environmental conditions, with dispersal, which reduces the likelihood that relatives suffer from such deterioration. Beyond this specific example, we discuss the other pathways revealed by our model via which selection favors trait associations under ecological inheritance, with potential implications for dispersal and behavioral syndromes, phenotypic plasticity, and niche construction.

## Model and methods

### Life cycle, traits, and environmental dynamics

We consider a population of haploids distributed among a large number of patches. All patches carry the same number  $N$  of individuals and are uniformly connected by dispersal (according to the island model, Wright, 1931). Each patch is characterized by an environmental state or ecological variable  $\epsilon \in \mathbb{R}$  (e.g., abundance of a resource, pollution level, quality of a common good), and each individual by a phenotype  $z = (z_1, \dots, z_n) \in \mathbb{R}^n$  made of  $n$  genetically determined quantitative traits, where any trait  $z_p$  ( $p \in \{1, \dots, n\}$ , referred to as “trait  $p$ ” for short) can influence the state of the patch (e.g., attack rate on a resource, production of a pollutant,

investment into a common good). We census this population at discrete time points between which the following occurs (Figure 1A for diagram): (i) within patches, individuals interact with one another and with their environment whose state  $\epsilon$  can change as a result (we specify such interactions and how they depend on traits below); (ii) individuals reproduce, producing a large number of clonal offspring (large enough to ignore demographic stochasticity), and then die; (iii) independently of one another, each offspring either disperses to a randomly chosen patch or remains in its natal patch; and finally (iv) offspring compete locally in each patch for  $N$  spots. Patch state  $\epsilon$  and individual traits  $z$  can influence any vital rate, such as fecundity, offspring dispersal, or survival (or combination thereof). In addition, patch regulation may occur before and after dispersal, allowing for selection to be soft or hard (Christiansen, 1975; Débarre & Gandon, 2011; Wallace, 1975), as long as all patches carry  $N$  mature individuals by the end of the life cycle. Generations are nonoverlapping but as we detail next, individuals of different generations can interact with one another indirectly via the environment.

To allow individuals to transform their environment in a way that can be passed onto future generations, we write the state  $\epsilon_{t+1}$  of a patch at a generation  $t + 1$  as a function of the traits expressed by individuals in that patch at the previous generation  $t$ , as well as the previous state; specifically as

$$\epsilon_{t+1} = F(z_1, z_2, \dots, z_N, \epsilon), \quad (1)$$

where the vector  $z_i$  denotes the phenotype expressed by individual  $i \in \{1, \dots, N\}$  living in the patch at generation  $t$  and  $\epsilon$  is the state of the patch at generation  $t$  (Figure 1B for diagram). The environmental dynamics given by the map  $F$  (equation 1) unfold even in the absence of genetic variation (i.e., when  $z_i = z$  for all  $i$ ). We assume that these dynamics converge to a stable equilibrium, meaning that in a population monomorphic for  $z$  (i.e., where all individuals in the population express the same phenotype  $z$ ), all patches are eventually characterized by the same environmental equilibrium, which we denote by  $\hat{\epsilon}$  (this equilibrium will typically depend on  $z$ , but we do not write this dependence explicitly for short). This equilibrium satisfies

$$\hat{\epsilon} = F(z, z, \dots, z, \hat{\epsilon}), \quad (2)$$

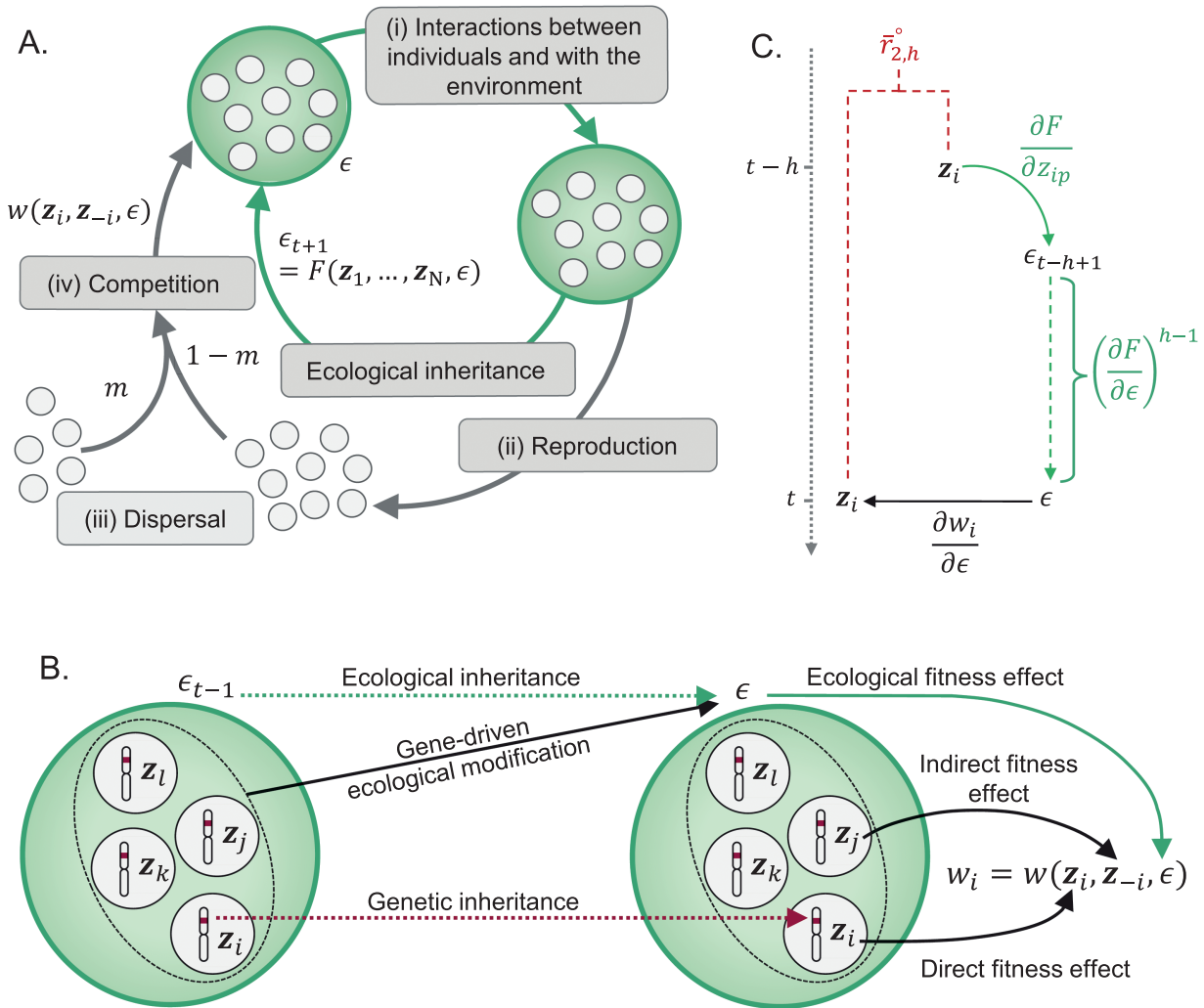
as well as the stability condition,

$$-1 < \left. \frac{\partial F}{\partial \epsilon} \right|_{\substack{\epsilon = \hat{\epsilon} \\ z_i = z}} < 1. \quad (3)$$

Here and hereafter, all derivatives are estimated where all individuals express the same phenotype  $z$  and all patches are characterized by the associated ecological equilibrium  $\hat{\epsilon}$ . So all derivatives should be seen as functions of the evolving traits  $z$ . The quantity  $\partial F / \partial \epsilon$  gives the effect of a perturbation in the state of a patch at one generation on the state at the next generation. This  $\partial F / \partial \epsilon$  can thus be thought of as the effect of ecological inheritance: the greater the absolute value of  $\partial F / \partial \epsilon$  is, the more consequential an environmental modification is to future generations.

The consequences of an environmental modification also depend on how the fitness of an individual varies with its local environment. To capture this in a general way, we assume the fitness  $w_i$  of individual  $i \in \{1, \dots, N\}$  from a focal patch can be written as a function,

$$w_i = w(z_i, \underbrace{(z_1, \dots, z_{i-1}, z_{i+1}, \dots, z_N)}_{=z_{-i}}, \epsilon), \quad (4)$$



**Figure 1.** (A) Life cycle (see section “Life cycle, traits, and environmental dynamics” for details). (B) Genetic and ecological inheritance. Diagram showing the dual pathways of inheritance in the model, where individuals inherit their genes from their parent (“Genetic inheritance”) but also their local environment (“Ecological inheritance”), which has been modified by the genetically determined traits of the parental generation (“Gene-driven ecological modification,” with  $\mathbf{z}$ , for the traits of individual  $i$ ). The fitness  $w_i$  of a focal individual  $i$  then depends on its own traits  $\mathbf{z}_i$  (“direct fitness effect”), on the traits of its neighbors  $\mathbf{z}_{-i}$  (“indirect fitness effect”), and on the state of the environment  $\epsilon$  (“ecological fitness effect”). (C) Diagram for the expected effect of a change in trait  $p$  on the fitness of an individual in the future via ecological inheritance, illustrating equation (11). A change in trait  $p$  in an individual at generation  $t-h$  modifies the environment of the next generation  $t-h+1$  by  $\frac{\partial F}{\partial z_{ip}}$  (solid green arrow). Due to ecological inheritance, this modification carries over downstream generations till generation  $t$  (according to a factor  $(\frac{\partial F}{\partial \epsilon})^{h-1}$ , dashed green arrow). This in turn influences the fitness of a focal individual living at that time according to  $\frac{\partial w_i}{\partial \epsilon}$  (solid black arrow). These two individuals separated by  $h$  generations belong to the same lineage (and thus express the same phenotype  $\mathbf{z}_i$ ) with probability  $\bar{r}_{2,h}^o$  (dashed red lines).

which gives the expected number of offspring produced by this individual  $i$  that are recruited across all patches (so counted over one full iteration of the life cycle, from steps (i) to (iv)), given (a) its phenotype,  $\mathbf{z}_i = (z_{i1}, \dots, z_{im})$  (with  $z_{ip}$  the value for trait  $p$ ); (b) the phenotypes expressed by its  $N-1$  patch-neighbors, collected in  $\mathbf{z}_{-i} = (z_{11}, \dots, z_{i-1,1}, z_{i+1,1}, \dots, z_{N,1})$ ; and (c) the environmental state of its patch,  $\epsilon$ . This formulation allows for the fitness of an individual to depend on interactions between its own traits, the traits of its neighbors, and the environment (Figure 1B). Since there is no class structure in our model (e.g., no age, sex, or stage structure), the fitness function is invariant to permutations within  $\mathbf{z}_{-i}$ , that is, it does not matter which specific neighbors express which phenotype, only the collection of phenotypes matters. Fitness may however depend on the number of such neighbors and thus on patch size,  $N$  (equation 33 for a specific example). Note

also that even though traits  $\mathbf{z}$  are genetically determined, the general formulation for environmental dynamics (equation 1) and individual fitness (equation 4) allows us to consider the evolution of plastic traits through reaction norms (as in, e.g., Lande, 2009). For instance, one could assume that the expression of a plastic trait is given by  $z_1 + z_2\epsilon$  and then investigate the joint evolution of  $z_1$  and  $z_2$ , where  $z_2$  captures plasticity to the local environment  $\epsilon$ .

### Evolutionary dynamics

We are interested in the coevolution of the  $n$  traits, and particularly in whether such coevolution leads to polymorphism. To investigate this, we assume that traits evolve via the input of rare genetic mutations with weak phenotypic effects. Under these assumptions, evolutionary dynamics take place in two steps (Dercole & Rinaldi, 2008; Metz et al., 1995; Rousset,

2004), which can be inferred from the invasion fitness (i.e., the geometric growth rate),  $W(\zeta, z)$ , of a rare allele coding for a deviant phenotype  $\zeta = (\zeta_1, \dots, \zeta_n)$  in a population otherwise monomorphic for  $z = (z_1, \dots, z_n)$  (Ferriere & Gatto, 1995; Otto & Day, 2007; Tuljapurkar, 1989; Tuljapurkar et al., 2003). Our general approach, which is based on a sensitivity analysis of  $W(\zeta, z)$ , is detailed in [Supplementary Appendix A](#). We summarize here how such an analysis can be used to understand how selection leads to polymorphism under ecological inheritance.

**Directional selection**

First, the population evolves under directional selection whereby selected mutants rapidly sweep the population before a new mutation arises, so that the population can be thought of as “jumping” from one monomorphic state to another. Trait dynamics during this phase are characterized by the selection gradient vector,

$$s(z) = \begin{pmatrix} s_1(z) \\ \vdots \\ s_p(z) \\ \vdots \\ s_n(z) \end{pmatrix}, \tag{5}$$

which points in the direction favored by selection in phenotypic space (the space of all possible phenotypes, here  $\mathbb{R}^n$  or a subset thereof), that is,

$$s_p(z) = \left. \frac{\partial W(\zeta, z)}{\partial \zeta_p} \right|_{\zeta=z}. \tag{6}$$

Specifically, selection favors an increase in trait  $p$  when  $s_p(z) > 0$  and conversely a decrease when  $s_p(z) < 0$ . The population may thus eventually converge to a singular phenotype,  $z^* = (z_1^*, \dots, z_n^*)$ , which is such that each entry of the selection gradient is zero at  $z^*$ , that is,

$$s(z^*) = \mathbf{0}, \tag{7}$$

where  $\mathbf{0}$  is a vector of zeroes of size  $n$ . For the population to converge to  $z^*$ , it is sufficient that the Jacobian matrix,

$$\mathbf{J}(z^*) = \begin{pmatrix} J_{11}(z^*) & \dots & J_{1n}(z^*) \\ \vdots & \ddots & \vdots \\ J_{n1}(z^*) & \dots & J_{nn}(z^*) \end{pmatrix}, \tag{8}$$

with  $(p, q)$  entry

$$(\mathbf{J}(z^*))_{pq} = \left. \frac{\partial s_p(z)}{\partial z_q} \right|_{z=z^*, \epsilon_i=\hat{\epsilon}}, \tag{9}$$

is negative-definite (i.e., the symmetric real part of  $\mathbf{J}(z^*)$ ,  $[\mathbf{J}(z^*) + \mathbf{J}(z^*)^T]/2$ , has only negative eigenvalues, Débarre et al., 2014; Geritz et al., 2016; Leimar, 2005, 2009). Such a phenotype is an attractor of evolutionary dynamics and typically referred to as (strongly) convergence stable (Leimar, 2009).

**Directional selection under ecological inheritance**

The selection gradient  $s(z)$  (equation 6) is defined in terms of the invasion fitness  $W(\zeta, z)$  of a genetic mutant, which can be seen as a measure of fitness at the level of the gene that codes for a deviant phenotype. To reveal directional selection

on the intergenerational effects of traits through ecological inheritance requires expressing  $s(z)$  in terms of *individual* (or personal) fitness, that is, in terms of  $w_i$  (equation 4, e.g., Lehmann, 2007, 2008; Mullon and Lehmann, 2018). We briefly go over these previous findings in the context of our model here.

The selection gradient on a trait  $p$  with intergenerational effects (given by equation 1) can be expressed in terms of individual fitness (equation 4) as

$$s_p(z) = \underbrace{\frac{\partial w_i}{\partial z_{ip}} + (N-1)r_2^\circ \frac{\partial w_i}{\partial z_{jp}}}_{\text{intragenerational effects}} + \underbrace{\frac{\partial w_i}{\partial \epsilon} E^\circ \left[ \frac{\partial \epsilon}{\partial z_p} \right]}_{\text{inter}} \tag{10}$$

(equations 13-15 in Mullon and Lehmann, 2018, equation 2 in Lehmann, 2007, equation 4 in Lehmann, 2008, and equation 4.11 in Sozou, 2009—[Supplementary Appendix B](#) here for a rederivation of this result). Equation (10) consists of three weighted fitness effects. First,  $\partial w_i / \partial z_{ip}$  is the effect of a change in trait  $p$  in the focal individual  $i$  on its own fitness (direct fitness effect). Second,  $\partial w_i / \partial z_{jp}$  is the effect of a change in trait  $p$  in a patch-neighbor (individual  $j \neq i$ ) on focal fitness (indirect fitness effect). This is weighted by the number  $(N-1)$  of such neighbors, and the pairwise relatedness coefficient under neutrality,  $r_2^\circ$ , which is the probability that a randomly sampled neighbor is identical-by-descent to the focal. Throughout, quantities with a superscript  $\circ$  are evaluated under neutrality, that is, in a population that is monomorphic for  $z$ . The quantities with a superscript  $\circ$  may thus depend on  $z$ , but we do not write such dependency to avoid notational clutter. The first two terms of equation (10) (labeled as “intragenerational effects”) thus correspond to the standard selection gradient in group-structured population, where traits have effects within generations only. This can be read as Hamilton’s rule in gradient form, that is, as  $-C + r_2^\circ B$ , where the cost is  $-C = \partial w_i / \partial z_{ip}$ , and the benefit is  $B = (N-1) \partial w_i / \partial z_{jp}$  (Rousset, 2004).

Directional selection on intergenerational effects is captured by the third term of equation (10) (labeled as “inter”). This consists of  $\partial w_i / \partial \epsilon$ , which is the fitness effect of an environmental change, weighted by  $E^\circ [\partial \epsilon / \partial z_p]$ , which is the expected effect of a change in trait  $p$  in all the local ancestors (i.e., from the same patch) of a focal individual on the environment experienced by this focal. Expectation here is taken over the neutral distribution of local genealogies of the focal (i.e., the distribution of the number of local ancestors of the focal at each past generation when the population is monomorphic, hence the superscript  $\circ$ ; equation B-4 in [Supplementary Appendix B](#) for definition of  $E^\circ[\cdot]$ ). What the last term of equation (10) tells us then is that selection favors a trait change when this change in a local lineage of individuals perturbs the local environment in a way such that on average, it increases the fitness of the members of that lineage (e.g., the production of a long-lasting common good that increases the fitness of downstream relatives, Lehmann, 2007). The intergenerational nature of these effects are revealed by expanding  $E^\circ [\partial \epsilon / \partial z_p]$  in terms of the environmental map  $F$  (equation 1) as,

$$E^\circ \left[ \frac{\partial \epsilon}{\partial z_p} \right] = \sum_{b=1}^{\infty} (N\bar{r}_{2,b}^\circ) \frac{\partial F}{\partial z_{ip}} \left( \frac{\partial F}{\partial \epsilon} \right)^{b-1} \tag{11}$$

([Supplementary Appendices B.3](#) and [B.4](#) for derivation—see also equation 16-20 in Mullon and Lehmann, 2018), where

$\partial F/\partial z_{ip}$  is the effect of a change in trait  $p$  in one focal individual (individual  $i$ ) on its local environment over one generation (from equation 1), and  $\bar{r}_{2,h}^\circ$  is the probability that an individual randomly sampled  $h \geq 1$  generations ago in the same patch to a focal individual is identical-by-descent to this focal (equation B-21 in Supplementary Appendix B for formal definition). Equation (11) can be understood as follows (Figure 1C for diagram). Consider the patch of the focal  $h$  generations ago. In this past generation, the focal individual has on average  $N\bar{r}_{2,h}^\circ$  ancestors in the patch. Each of these ancestors perturbs the environment by  $\partial F/\partial z_{ip}$  (solid green arrow in Figure 1C) due to a change in trait  $p$ . In turn, each perturbation persists through time via ecological inheritance, carried over each generation by a factor  $\partial F/\partial \epsilon$ . Thus a perturbation initiated  $h$  generations ago has decayed by a factor  $(\partial F/\partial \epsilon)^{h-1}$  by the time it reaches the focal (dashed green arrow in Figure 1C). Summing such effects from all past ancestors (so from  $h = 1$  to  $\infty$ ) obtains equation (11).

Overall, the last summand of equation (10) may be complicated, but it captures a simple biological notion: the intergenerational effects of a trait are shaped by directional selection to benefit downstream relatives (Lehmann, 2007). In our model, these benefits are transmitted through ecological inheritance of the state of the patch (according to  $\partial F/\partial \epsilon$ ) and affect the fitness of relatives when dispersal is limited (so that intergenerational relatedness is greater than zero  $\bar{r}_{2,h}^\circ > 0$ ).

The selection gradient  $s(z)$  (equation 10) characterizes directional selection and thus convergence stable trait values  $z^*$  toward which the population evolves when traits have intergenerational ecological effects. The selection gradient, however, cannot tell us whether such traits eventually become polymorphic. This requires an understanding of disruptive selection (Dercole & Rinaldi, 2008), which we describe next.

**Disruptive, stabilizing, and correlational selection**

Once the population expresses a convergence stable phenotype  $z^*$ , selection is either (a) stabilizing, in which case any mutant different from  $z^*$  is purged so that the population remains monomorphic for  $z^*$ , or (b) disruptive, favoring alternative phenotypes leading to polymorphism (Dercole & Rinaldi, 2008; Metz et al., 1995; Rousset, 2004). Whether selection is stabilizing or disruptive when  $n$  traits coevolve depends on the Hessian matrix (Leimar, 2009),

$$H(z^*) = \begin{pmatrix} h_{11}(z^*) & \dots & h_{1n}(z^*) \\ \vdots & \ddots & \vdots \\ h_{n1}(z^*) & \dots & h_{nn}(z^*) \end{pmatrix}, \tag{12}$$

whose  $(p, q)$ -entry is given by

$$h_{pq}(z^*) = \left. \frac{\partial^2 W(\zeta, z)}{\partial \zeta_p \partial \zeta_q} \right|_{\zeta = z = z^*}. \tag{13}$$

On its diagonal,  $H(z^*)$  indicates whether selection is disruptive on each trait (Lande & Arnold, 1983). Specifically, when  $h_{pp}(z^*) > 0$ , selection on trait  $p$  is disruptive when  $p$  evolves in isolation from the other traits (i.e., when all the other traits are fixed). Conversely, selection on trait  $p$  is stabilizing when  $h_{pp}(z^*) < 0$ . The off-diagonal elements of  $H(z^*)$ , meanwhile, give the correlational selection,  $h_{pq}(z^*)$ , on each pair of traits  $p$  and  $q$  (Lande & Arnold, 1983). These indicate the type of among-traits associations that selection favors within individuals: when  $h_{pq}(z^*) > 0$ , selection favors a

positive association (or correlation) among traits  $p$  and  $q$  and a negative association when  $h_{pq}(z^*) < 0$ . With  $n$  traits coevolving, selection in a population expressing a convergence stable phenotype  $z^*$  is stabilizing when the leading eigenvalue of  $H(z^*)$  is negative, and disruptive when the eigenvalue is positive (Débarre et al., 2014; Geritz et al., 2016; Leimar, 2009).

The Hessian  $H(z^*)$  in equation (13) is defined in terms of invasion fitness  $W(\zeta, z)$ . Our aim in this article is to characterize the Hessian matrix, and thus correlational and disruptive selection, in terms of individual fitness  $w_i$  (equation 4) and intergenerational effects through the environmental map  $F$  (equation 1), similarly to the selection gradient shown in section “Directional selection under ecological inheritance.” Our derivations can be found in Supplementary Appendix C. We summarize our results in the next section.

**Correlational selection under ecological inheritance**

We first show in Supplementary Appendix C.1 that correlational selection on traits  $p$  and  $q$  (or disruptive selection on trait  $p$  when  $p = q$ ) can be decomposed as the sum of two terms,

$$h_{pq}(z) = h_{g,pq}(z) + h_{e,pq}(z), \tag{14}$$

which we detail in sections “Intragenerational fitness effects” and “Intergenerational effects,” respectively.

**Intragenerational fitness effects**

The first term of equation (14),  $h_{g,pq}(z)$ , corresponds to correlational selection due to the intragenerational effects of traits on fitness (so ignoring intergenerational ecological effects on fitness and focusing on genetic effects on fitness only; hence, the  $g$  in the subscript of  $h_{g,pq}(z)$ ). We show in Supplementary Appendix C.2 that it can be expressed as

$$h_{g,pq}(z) = \frac{\partial^2 w_i}{\partial z_{ip} \partial z_{iq}} + (N-1)r_2^\circ \left( \frac{\partial^2 w_i}{\partial z_{ip} \partial z_{iq}} + \frac{\partial^2 w_i}{\partial z_{iq} \partial z_{ip}} + \frac{\partial^2 w_i}{\partial z_{ip} \partial z_{iq}} \right) + (N-1)(N-2)r_3^\circ \frac{\partial^2 w_i}{\partial z_{ip} \partial z_{hq}} + (N-1) \left( \frac{\partial w_i}{\partial z_{ip}} \frac{\partial r_2}{\partial z_q} + \frac{\partial w_i}{\partial z_{iq}} \frac{\partial r_2}{\partial z_p} \right), \tag{15}$$

which is equivalent to the coefficient of correlational selection derived in previous papers where traits have intragenerational effects only (equations 13a–c in Mullon et al. 2016, equations 7a–c in Mullon and Lehmann 2019; see also Ajar, 2003; Wakano & Lehmann, 2014 for the case where  $p = q$ ). We refer interested readers to these papers for a detailed interpretation of equation (15), but briefly this equation can be read as the sum of three terms. The first,  $\partial^2 w_i / (\partial z_{ip} \partial z_{iq})$ , is the effect of joint changes in traits  $p$  and  $q$  of the focal individual on its own fitness. This cross derivative quantifies the synergistic (or “multiplicative” or “interaction”) effects of traits on fitness: when positive, it tells us that fitness increases more when both traits  $p$  and  $q$  change in a similar way (i.e., both increase or both decrease, so that  $p$  and  $q$  have complementary effects on fitness); conversely when negative, fitness increases more when both traits  $p$  and  $q$  change in opposite ways (i.e., one increases and the other decreases, so that  $p$  and  $q$  have antagonistic effects on fitness). In a well-mixed population,

correlational selection depends only on such “direct” synergy (i.e., synergistic effects of focal traits on focal fitness, so that  $h_{pq}(z) = \partial^2 w_i / (\partial z_{ip} \partial z_{iq})$ , Lande, 1979; Phillips & Arnold, 1989; Leimar, 2009; Débarre et al., 2014).

The rest of equation (15) is due to limited dispersal and the interactions among contemporary relatives (i.e., living at the same generation) that result from such limitation. The remainder of the first line and the second line of equation (15) consists of what can be referred to as “indirect” synergistic effects (Mullon and Lehmann, 2019). These are effects of joint changes in traits  $p$  and  $q$  on focal fitness, where at least one of these changes occurs in a neighbor to the focal, weighted by relevant relatedness coefficients. Specifically,  $\partial^2 w_i / (\partial z_{ip} \partial z_{iq})$  is the effect on focal fitness of joint changes in trait  $p$  in the focal and in trait  $q$  in a neighbor (indexed  $j$ ), and  $\partial^2 w_i / (\partial z_{jp} \partial z_{jq})$ , of changes in traits  $p$  and  $q$  in the same neighbor  $j$ . Both are weighted by  $r_2^o$ . The second line of equation (15) features  $\partial^2 w_i / (\partial z_{jp} \partial z_{hq})$ , which is the effect on focal fitness of joint changes in different neighbors (indexed  $j$  and  $h$  with  $j \neq h$ ). This is weighted by  $r_3^o$ , which is the coefficient of three-way relatedness, that is, the probability that three individuals randomly sampled in a patch under neutrality are identical-by-descent. Finally, the third line of equation (15) consists of the product between the indirect fitness effect of one trait ( $\partial w_i / \partial z_{ip}$ ), and the effect of the other on pairwise relatedness ( $\partial r_2 / \partial z_q$ ), which quantifies the effect of a trait change on the probability that a rare mutant individual expressing this change interacts with another mutant in the same patch (equation C-15 for formal definition). This reveals in particular that selection favors an association among two traits when one trait improves the fitness of contemporary neighbors, and the other trait increases the probability that these contemporary neighbors are relatives (Mullon et al., 2016, 2018; Mullon and Lehmann, 2019).

### Intergenerational effects: three pathways for correlational selection via ecological inheritance

The second term of equation (14),  $h_{e,pq}(z)$ , is correlational selection due to the intergenerational ecological effects of traits on fitness (hence the  $e$  of  $h_{e,pq}(z)$ ) and thus constitutes the more novel part of our results. We find that this coefficient can be decomposed into three terms,

$$h_{e,pq}(z) = h_{exe,pq}(z) + h_{gxe,pq}(z) + h_{rxe,pq}(z), \quad (16)$$

corresponding to three pathways through which correlational selection can act owing to ecological inheritance (equation C-18 in Supplementary Appendix for decomposition).

### Environmentally mediated synergy

The first pathway,

$$h_{exe,pq}(z) = E^o \left[ \underbrace{\frac{\partial^2 \epsilon}{\partial z_p \partial z_q}}_{\text{synergy on } \epsilon} \right] \frac{\partial w_i}{\partial \epsilon} + E^o \left[ \underbrace{\frac{\partial \epsilon}{\partial z_p} \frac{\partial \epsilon}{\partial z_q}}_{\text{nonlinear fitness effects of } \epsilon} \right] \frac{\partial^2 w_i}{\partial \epsilon^2}, \quad (17)$$

can be thought of as the synergistic effects of traits on fitness via the environment (hence the  $exe$  subscript). Each of the two terms of equation (17) reveals one way such synergy can come about. The first, labeled “synergy on  $\epsilon$ ,” is the most intuitive. It consists of the product between (a)  $\partial w_i / \partial \epsilon$ , which is the fitness effect of an environmental change, and (b)  $E^o[\partial^2 \epsilon / (\partial z_p \partial z_q)]$ , which is the expected effect of a change in both traits  $p$  and  $q$  in all the local ancestors of a

focal individual on the environment experienced by this focal (where recall from section “Directional selection under ecological inheritance” that with  $E^o[\cdot]$ , expectation is taken over the neutral distribution of local genealogies of the focal, equation B-4 in Supplementary Appendix B for definition of  $E^o[\cdot]$ ). This expectation quantifies the intergenerational environmental modifications made by a lineage of individuals that express a joint change in traits  $p$  and  $q$ . The first term of equation (17) says that selection will associate two traits  $p$  and  $q$  when these have synergistic effects on the environment (according to  $E^o[\partial^2 \epsilon / (\partial z_p \partial z_q)]$ ) that in turn affects fitness (i.e.,  $\partial w_i / \partial \epsilon \neq 0$ ). As an example, consider a scenario where  $\epsilon$  is the amount of a common good that can be transferred between generations (e.g., pyoverdine in siderophore-producing bacteria), so that fitness increases with such an amount ( $\partial w_i / \partial \epsilon > 0$ ). Let trait  $p$  be the production of this common good and  $q$  its protection against degradation or expropriation (so that  $\epsilon$  depends on the product between both traits). Traits  $p$  and  $q$  would have complementary effects on  $\epsilon$  in this example ( $E^o[\partial^2 \epsilon / (\partial z_p \partial z_q)] > 0$ ). The first term of equation (17) tells us that in this case, selection favors a positive association between both traits, that is, that individuals who tend to participate more in the common good also tend to protect it more.

The second term of equation (17), labeled “nonlinear fitness effects of  $\epsilon$ ,” indicates that correlational selection can also associate traits that influence the environment independently of one another, according to  $E^o[\partial \epsilon / \partial z_p \times \partial \epsilon / \partial z_q]$ , which is the expectation of the product between the effect of a change in trait  $p$  in all the local ancestors of a focal individual on the environment experienced by this focal, and such an effect of a change in trait  $q$ . These independent ecological effects lead to correlational selection when the environment has non-linear effects on fitness (so  $\partial^2 w_i / \partial \epsilon^2 \neq 0$ ). In the common good example introduced in the previous paragraph for instance, selection for a positive association among production and protection would be strengthened where fitness accelerates with the amount of common good ( $\partial^2 w_i / \partial \epsilon^2 > 0$ ) and weakened where it decelerates ( $\partial^2 w_i / \partial \epsilon^2 < 0$ ). This is because such non-linearity in fitness creates synergy among traits via their ecological effects.

Correlational selection thus emerges when traits have synergistic effects on the environment or when traits influence the environment which in turn has nonlinear effects on fitness. The strength of these two effects depends on the inheritance of ecological effects from local ancestors, as quantified in equation (17) by  $E^o[\partial^2 \epsilon / (\partial z_p \partial z_q)]$  and  $E^o[\partial \epsilon / \partial z_p \times \partial \epsilon / \partial z_q]$ , respectively. We expand those in terms of the environmental  $F$  (equation 1) in Supplementary Appendix C.3.1. We show in particular that,

$$E^o \left[ \frac{\partial \epsilon}{\partial z_p} \frac{\partial \epsilon}{\partial z_q} \right] = \sum_{h=1}^{\infty} \sum_{h'=1}^{\infty} [N^2 \bar{r}_{3,b,h'}^o] \frac{\partial F}{\partial z_{ip}} \frac{\partial F}{\partial z_{iq}} \left( \frac{\partial F}{\partial \epsilon} \right)^{h-1} \left( \frac{\partial F}{\partial \epsilon} \right)^{h'-1}, \quad (18)$$

in which  $\bar{r}_{3,b,h'}^o$  is the intergenerational three-way coefficient of relatedness: The probability that a focal individual and two randomly sampled individuals from that same patch  $h > 0$  and  $h' > 0$  generations before the focal are all identical-by-descent under neutrality ( $h$  here is a dummy variable, not to be mixed up with correlational selection  $h_{pq}(z)$ , which we always write as a function of  $z$  to avoid confusion; see equation C-23 in Supplementary Appendix for formal definition of  $\bar{r}_{3,b,h'}^o$ ). We explain equation (18) graphically in

**Supplementary Figure S1.** The expression for the synergistic effects of traits on the environment,  $E^\circ[\partial^2\epsilon/(\partial z_p\partial z_q)]$ , is more complicated and more difficult to parse and we have therefore left it in **Supplementary Appendix C.3.1** (equation C-34).

**Gene–environment interactions**

The second pathway through which correlational selection can act owing to ecological inheritance (second term of **equation 16**) is given by

$$h_{g \times e, pq}(z) = \underbrace{\frac{\partial^2 w_i}{\partial z_{ip} \partial \epsilon} E^\circ \left[ \frac{\partial \epsilon}{\partial z_q} \right] + \frac{\partial^2 w_i}{\partial z_{iq} \partial \epsilon} E^\circ \left[ \frac{\partial \epsilon}{\partial z_p} \right]}_{\text{direct } g \times e \text{ interactions}} + (N-1) \underbrace{\left( \frac{\partial^2 w_i}{\partial z_{ip} \partial \epsilon} E^\circ \left[ R \frac{\partial \epsilon}{\partial z_q} \right] + \frac{\partial^2 w_i}{\partial z_{iq} \partial \epsilon} E^\circ \left[ R \frac{\partial \epsilon}{\partial z_p} \right] \right)}_{\text{indirect } g \times e \text{ interactions}}. \tag{19}$$

This pathway emerges when fitness is influenced by the interaction between the environment and traits (or the genes coding for these traits, hence the  $g \times e$  subscript). Specifically, the first term of **equation 19**, labeled “direct  $g \times e$  interactions,” consists of the interaction between the environment and the expression of one trait by the focal ( $\partial^2 w_i/(\partial z_{ip} \partial \epsilon)$ ), multiplied to the intergenerational ecological effects of the other trait ( $E^\circ[\partial \epsilon/\partial z_q]$ , which is the expected effect of a change in trait  $q$  in all the local ancestors of a focal individual on the environment experienced by this focal and is given by **equation 11**). To understand the implications of this, consider again a scenario where  $\epsilon$  is some intergenerational common good and one trait, say  $q$ , is the production or maintenance of this common good (so that  $E^\circ[\partial \epsilon/\partial z_q] > 0$ ). The other trait  $p$ , however, now is some costly competitive trait whose cost depends on environmental conditions (e.g., horn length in beetles; **Emlen, 1994**), so that individuals living in better patches (i.e., with greater  $\epsilon$ ) pay a lower expression cost (leading to  $\partial^2 w_i/(\partial z_{ip} \partial \epsilon) > 0$ ). The first term of **equation 19** in this example would be positive, indicating that it favors a positive association between traits  $p$  and  $q$ , i.e., individuals who participate more in the common good also express larger competitive traits. This is because individuals who contribute more to the common good also tend to live in better habitats (owing to limited dispersal and past relatives contributing to the environment, see **equation 11**). They can thus also afford to express larger competitive traits.

The second term of **equation 19**, labeled “indirect  $g \times e$  interactions,” consists of the interaction between the environment and the expression of one trait by a neighbor of the focal ( $\partial^2 w_i/(\partial z_{ip} \partial \epsilon)$ ), multiplied to  $E^\circ[R \times \partial \epsilon/\partial z_q]$ , which is the expected product between (a) the ecological effects of the other trait ( $\partial \epsilon/\partial z_q$ ) and (b) the frequency of relatives among the neighbors of the focal,  $R$ , which here should be seen as a random variable (with expectation  $E^\circ[.]$  taken as before over the distribution of local genealogies under neutrality so that  $E^\circ[R] = r_2^\circ$ ). This expected product  $E^\circ[R \times \partial \epsilon/\partial z_q]$  is indicative of the covariance between the genetic and ecological environments of the focal. When  $E^\circ[R \times \partial \epsilon/\partial z_q]$  is large, environmental transformations driven by trait  $q$  tend to have a large effect not only the focal individual but also on its contemporary patch relatives. If in turn, trait  $p$  of these relatives interacts with the environment to increase the fitness of the focal individual (according to  $\partial^2 w_i/(\partial z_{ip} \partial \epsilon)$ ), **equation 19** reveals

that correlational selection will associate these two traits. To see what indirect gene–environment interactions might entail, consider a situation where  $\epsilon$  is the state of the patch, trait  $q$  is some investment to maintain this state for future generations, and trait  $p$  is a trait that increases the fitness of neighbors living in the current generation such as helping. Assume further that the benefits of helping decrease with the patch state  $\epsilon$ , for instance because helping is mostly relevant when the environment is of low quality. Mathematically, this translates into negative indirect gene–environment interactions:  $\partial^2 w_i/(\partial z_{ip} \partial \epsilon) < 0$ . According to **equation 19**, this favors a negative correlation between investing into current members through helping (via  $p$ ) and investing into future patch members through patch maintenance (via  $q$ ), that is, individuals that invest more into future relatives invest less in present relatives and vice-versa.

The relevance of indirect gene–environment interactions for correlational selection depends on  $E^\circ[R \times \partial \epsilon/\partial z_q]$ , which we show is in terms of the environmental map  $F$  (**equation 1**) given by

$$E^\circ \left[ R \frac{\partial \epsilon}{\partial z_q} \right] = \sum_{b=1}^{\infty} [N r_{3,b}^\circ] \frac{\partial F}{\partial z_{iq}} \left( \frac{\partial F}{\partial \epsilon} \right)^{b-1}, \tag{20}$$

where  $r_{3,b}^\circ$  is the probability that two individuals living in the same generation, plus a third individual  $b$  generations ago, all randomly sampled from the same patch are identical-by-descent (equation C-39 for definition; **Supplementary Appendix C.3.2** for derivation of **equation 20**). This probability indicates the likelihood for an individual to influence the environment of at least two downstream relatives living  $b$  generations away in the same patch and thus directly interacting with one another. Accordingly, the greater  $r_{3,b}^\circ$ , the more influence a modification to the patch environment can have on social interactions, and thus the more relevant indirect gene–environment effects are to selection (**Supplementary Figure S2** for a graphical interpretation of **equation 20**).

**Biased ecological inheritance**

The third and final pathways for correlational selection ( $h_{r \times e, pq}(z)$  in **equation 16**) can be expressed as

$$h_{r \times e, pq}(z) = \left( E_q^{(1)} \left[ \frac{\partial \epsilon}{\partial z_p} \right] + E_p^{(1)} \left[ \frac{\partial \epsilon}{\partial z_q} \right] \right) \frac{\partial w_i}{\partial \epsilon}, \tag{21}$$

where  $E_q^{(1)}[\partial \epsilon/\partial z_p]$  is the expected effect of a change in trait  $p$  in all the local ancestors of a focal individual on the environment experienced by this focal, where expectation is taken over the perturbation of the distribution of local genealogies owing to a change in trait  $q$  (hence the superscript (1) and subscript  $q$  in  $E_q^{(1)}[.]$  to contrast with  $E^\circ[.]$ , which is expectation over the neutral distribution; equation C-6 for a formal definition of  $E_p^{(1)}[.]$ ). More intuitively perhaps,  $E_q^{(1)}[\partial \epsilon/\partial z_p]$  quantifies how trait  $q$  influences the way an environmental modification driven by a change in trait  $p$  is inherited. This can be seen more explicitly when we unroll  $E_q^{(1)}[\partial \epsilon/\partial z_p]$  over its intergenerational effects:

$$E_q^{(1)} \left[ \frac{\partial \epsilon}{\partial z_p} \right] = \sum_{b=1}^{\infty} \left[ N \frac{\partial \bar{r}_{2,b}}{\partial z_q} \right] \frac{\partial F}{\partial z_{ip}} \left( \frac{\partial F}{\partial \epsilon} \right)^{b-1} \tag{22}$$

(Supplementary Appendix C.3.3 for derivation). Here,  $\partial\bar{r}_{2,b}/\partial z_q$  is the effect of a change in trait  $q$  on the relatedness between individuals living in the same patch separated by  $b$  generations. To understand this effect better, consider a focal individual who expresses a change in trait  $q$  relative to a resident. This  $\partial\bar{r}_{2,b}/\partial z_q$  quantifies how such a trait change influences the probability that an individual randomly sampled in that same patch  $b$  generations ago is identical-by-descent to the focal, relative to the probability that two resident individuals separated by  $b$  generations are identical-by-descent under neutrality (i.e., relative to  $\bar{r}_{2,b}^0$ , Supplementary Appendix E.2 for details). So when for instance  $\partial\bar{r}_{2,b}/\partial z_q > 0$ , individuals that express greater values of trait  $q$  are more likely to transmit environmental modifications to their kin. What equation (22) substituted into (21) in turn says is that correlational selection will associate this trait  $q$  with another trait  $p$  when trait  $p$  leads to intergenerational environmental modifications that increase fitness (i.e., so that  $\partial F/\partial z_{ip} > 0$  in equation 22 and  $\partial w_i/\partial \epsilon > 0$  in equation 21; Supplementary Figure S3 for diagram). We explore the potential implications of such correlational selection in section "Joint evolution of dispersal with the attack rate on a local renewable resource" with a specific example.

**Summary**

To summarize our findings so far, we have identified three main pathways via which traits can be linked by correlational selection under ecological inheritance (equation 16). Each of these pathways can be expressed in terms of how a trait change in an individual causes an environmental modification that in turn influences the fitness of future relatives (equation 11, equation 18, equation 20, equation 22, and equation C-34 in Supplementary Appendix C.3.1). This perspective not only offers a clear view of correlational selection on intergenerational effects but also allows us to efficiently compute the Hessian matrix and thus investigate the conditions that lead to polymorphism in traits that influence the environment in the long term. In fact, what remains to be characterized for such computation are the various relevant relatedness coefficients (e.g.,  $\bar{r}_{3,b,b'}$ ) or their perturbation due to selection (e.g.,  $\partial\bar{r}_{2,b}/\partial z_q$ ). We do so in Supplementary Appendices D and E. Substituting for these into equation (11), equation (18), equation (20), equation (22), and equation (C-34) in Supplementary Appendix C.3.1, we obtain the expressions shown in Table 1. This Table 1, together with equation (10), equation (14), equation (15), equation (16), equation (17), equation (19), and equation (21), gives all that is necessary to investigate directional, correlational, and disruptive selection under the general model described in section "Life cycle, traits, and environmental dynamics." We illustrate such an approach in the next section.

**Joint evolution of dispersal with the attack rate on a local renewable resource**

We now go over a specific model that looks at the joint evolution of two ecologically relevant traits: (a) the rate of attack or consumption of a resource within patches and (b) dispersal between patches. The evolution of both traits has been investigated in isolation in multiple studies (for dispersal: Ajar, 2003; Gandon & Michalakis, 1999; Gandon & Rousset, 1999; Hamilton & May, 1977; Taylor & Frank, 1996;

for resource exploitation: Kylafis & Loreau, 2008; Lehmann, 2008; Messinger & Ostling, 2013; Pels et al., 2002; Rauch et al., 2002; Van Baalen & Sabelis, 1995), but none of those let both traits coevolve. Furthermore, studies so far have focused on the effects of directional selection, which is not sufficient to determine whether polymorphism emerges. Here we show that it readily does.

**A resource-consumer model in a patch-structured population**

We first specify a resource-consumer scenario and lay the building blocks of our analysis.

**Traits**

Each individual is characterized by two traits: (a) the rate  $z_1$  of attack on a local resource in a patch (during step (i) of the life cycle; see section "Life cycle, traits, and environmental dynamics") and (b) the probability  $z_2$  of juvenile dispersal, which we assume is costly with a probability  $c_d$  of dying during dispersal (step (iii) of the life).

**Environment and its dynamics**

The environmental state  $\epsilon$  of a patch at a generation  $t$  is the abundance of the resource in that patch before consumption at that generation (so before step (i) of the life cycle). We derive the intergenerational dynamics of resource abundance (i.e., of  $\epsilon$  from  $t$  to  $t + 1$ ) from a model of consumer-resource dynamics that occur in continuous time within generations (Schmid et al., 2022). To specify these dynamics, let us denote intra-generational time by  $\tau$ , which runs from 0 to  $T$ , where  $T$  is the length in continuous time of a generation (i.e., a whole iteration of the life cycle). We let  $\epsilon_{t,\tau}$  be the resource abundance at time  $\tau$  within generation  $t$  in a focal patch. With this notation, the abundance  $\epsilon_{t,0}$  of the resource in that patch before consumption at generation  $t$  is given by  $\epsilon = \epsilon_{t,0} = \epsilon_{t-1,T}$ . To obtain  $\epsilon_{t+1}$ , we track  $\epsilon_{t,\tau}$  from  $\tau = 0$  to  $T$ . We assume that resource dynamics during that time period are decomposed into two phases: a consumption phase (for  $0 \leq \tau \leq \tau_1$ ) followed by a renewal phase (for  $\tau_1 < \tau \leq T$ ) so that  $\tau_1$  is the amount of time the resource is being consumed (and  $T - \tau_1$  the amount of time it renews itself).

*Consumption phase.*

First, each individual  $i \in \{1, \dots, N\}$  in the patch consumes the resource at a rate given by its trait  $z_{i1}$ . Specifically, the rate of change in the amount  $\rho_{i,\tau}$  of resources collected by individual  $i = 1, \dots, N$  at time  $\tau$  is

$$\frac{d\rho_{i,\tau}}{d\tau} = \epsilon_{t,\tau} z_{i1}, \tag{23}$$

while the rate of change in resource abundance in the patch is

$$\frac{d\epsilon_{t,\tau}}{d\tau} = -\epsilon_{t,\tau} \sum_{j=1}^N z_{j1} = -\epsilon_{t,\tau} N \bar{z}_1, \tag{24}$$

where  $\bar{z}_1 = \sum_{j=1}^N z_{j1}/N$  is the average attack rate in the patch. Solving equations (23) and (24) with initial conditions  $\rho_{i,0} = 0$  for each  $i \in \{1, \dots, N\}$ , we obtain that by the end of consumption, the resource abundance in the patch is

$$\epsilon_{t,\tau_1} = \epsilon_{t,0} e^{-\tau_1 N \bar{z}_1}, \tag{25}$$



**Table 1.** Weights on fitness effects relevant to directional, disruptive, and correlational selection under ecological inheritance. Recall that  $N$  is the (fixed) number of individuals per patch, and  $m$  is backward dispersal, that is, the probability that an individual randomly sampled in a patch under neutrality is an immigrant. This probability may be a fixed parameter or an evolving variable, in which case  $m$  depends on the resident trait  $\mathbf{z}$  (as, e.g., when traits that influence gene flow evolve, like in our example section “Joint evolution of dispersal with the attack rate on a local renewable resource”). The quantity  $w_{p,i}$  is the philopatric component of individual fitness, that is, the expected number of offspring of individual  $i$  that remain in their natal patch, which depends on the same parameter as total individual fitness equation (4) (equation 33 for an example).

Symbol	Value	equation <sup>a</sup>
$r_2^\circ$	$= \frac{(1-m)^2}{N-(N-1)(1-m)^2}$	(D-2)
$\bar{r}_2^\circ$	$= \frac{1}{N} + \frac{N-1}{N} r_2^\circ$	(D-3)
$r_3^\circ$	$= \frac{(1-m)^3(1+3(N-1)r_2^\circ)}{N^2-(N-1)(N-2)(1-m)^3}$	(D-5)
$\bar{r}_3^\circ$	$= \frac{1}{N^2} + \frac{3(N-1)}{N^2} r_2^\circ + \frac{(N-1)(N-2)}{N^2} r_3^\circ$	(D-6)
$E^\circ \left[ \frac{\partial \epsilon}{\partial z_p} \right]$	$= \frac{\partial F}{\partial z_{ip}} \frac{N(1-m)}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \bar{r}_2^\circ$	(B-25)
$E^\circ \left[ \frac{\partial \epsilon}{\partial z_p} \frac{\partial \epsilon}{\partial z_q} \right]$	$= \frac{\partial F}{\partial z_{ip}} \frac{\partial F}{\partial z_{iq}} \frac{N^2(1-m)}{1-\left(\frac{\partial F}{\partial \epsilon}\right)^2(1-m)} \left[ \bar{r}_3^\circ + 2 \frac{\partial F}{\partial \epsilon} C_\epsilon \right]$	(C-33)
$E^\circ \left[ \frac{\partial^2 \epsilon}{\partial z_p \partial z_q} \right]$	$= \frac{N(1-m)}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \left( \frac{\partial^2 F}{\partial z_{ip} \partial z_{iq}} \bar{r}_2^\circ + (N-1) \frac{\partial^2 F}{\partial z_{ip} \partial z_{iq}} \left[ \frac{2}{N} r_2^\circ + \frac{N-2}{N} r_3^\circ \right] \right)$ $+ \frac{\partial F}{\partial z_{ip}} \frac{\partial F}{\partial z_{iq}} \frac{\partial^2 F}{\partial \epsilon^2} \frac{N^2(1-m)^2}{\left(1-\frac{\partial F}{\partial \epsilon}(1-m)\right)\left(1-\left(\frac{\partial F}{\partial \epsilon}\right)^2(1-m)\right)} \left[ \bar{r}_3^\circ + 2 \frac{\partial F}{\partial \epsilon} C_\epsilon \right] + \frac{N^2(1-m)}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \left( \frac{\partial F}{\partial z_{ip}} \frac{\partial^2 F}{\partial z_{iq} \partial \epsilon} + \frac{\partial F}{\partial z_{iq}} \frac{\partial^2 F}{\partial z_{ip} \partial \epsilon} \right) C_\epsilon$	(C-35)
$E^\circ \left[ R \frac{\partial \epsilon}{\partial z_p} \right]$	$= \frac{\partial F}{\partial z_{ip}} \frac{N(1-m)^2}{N-\frac{\partial F}{\partial \epsilon}(1-m)^2(N-1)} \left( \frac{\partial F}{\partial \epsilon}(1-m) \bar{r}_2^\circ + N \bar{r}_3^\circ \right)$	(C-42)
$\frac{\partial r_2}{\partial z_p}$	$= \frac{2r_2^\circ}{1-m} \left[ \frac{\partial w_{p,i}}{\partial z_{ip}} [1+(N-1)r_2^\circ] + (N-1) \frac{\partial w_{p,i}}{\partial z_{ip}} [2r_2^\circ+(N-2)r_3^\circ] + N^2 \frac{\partial w_{p,i}}{\partial \epsilon} \frac{\partial F}{\partial z_{ip}} C_\epsilon \right]$	(E-22)
$E_p^{(1)} \left[ \frac{\partial \epsilon_i}{\partial z_q} \right]$	$= \frac{\partial r_2}{\partial z_p} \frac{\partial F}{\partial z_{iq}} \frac{N(1-m)}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \left( \frac{N-1}{N} + \frac{1}{2Nr_2^\circ} \right) + \frac{\frac{\partial F}{\partial \epsilon}}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \left( \frac{\partial w_{p,i}}{\partial z_{ip}} E^\circ \left[ \frac{\partial \epsilon}{\partial z_q} \right] + (N-1) \frac{\partial w_{p,i}}{\partial z_{ip}} E^\circ \left[ R \frac{\partial \epsilon}{\partial z_q} \right] \right)$ $+ \frac{\partial w_{p,i}}{\partial \epsilon} \frac{\partial F}{\partial z_{ip}} \frac{\partial F}{\partial z_{iq}} \frac{\frac{\partial F}{\partial \epsilon} N^2(1-m)}{\left(1-\frac{\partial F}{\partial \epsilon}(1-m)\right)\left(1-\left(\frac{\partial F}{\partial \epsilon}\right)^2(1-m)\right)} \left[ \bar{r}_3^\circ + 2 \frac{\partial F}{\partial \epsilon} C_\epsilon \right]$	(E-48)
$C_\epsilon$	$= \frac{(1-m)}{N-\frac{\partial F}{\partial \epsilon}(1-m)^2(N-1)} \left( (N-1)(1-m) \bar{r}_3^\circ + \frac{\bar{r}_2^\circ}{1-\frac{\partial F}{\partial \epsilon}(1-m)} \right)$	

Note. <sup>a</sup> Relevant equation in Supplementary Appendix where derivation can be found.

and that the amount of resources consumed by a focal individual  $i$  is,

$$\rho_{i,\tau_1} = \underbrace{\epsilon_{t,0} (1 - e^{-\tau_1 N \bar{z}_1})}_{\text{total consumed}} \underbrace{\frac{z_{i1}}{N \bar{z}_1}}_{i^{\text{th}} \text{ share}}. \tag{26}$$

As highlighted with the underbraces in equation (26), this amount can be separated between the total amount of resources consumed in the patch, and the share obtained by individual  $i$ . Equation (26) can thus be seen as a contest success function of the ratio type, which is commonly used to model competition for resources (Hirshleifer, 1989).

*Renewal phase.*

After consumption, we assume the resource renews itself growing logistically, according to

$$\frac{d\epsilon_{t,\tau}}{d\tau} = \gamma_0 \epsilon_{t,\tau} \left( 1 - \frac{\epsilon_{t,\tau}}{k} \right), \tag{27}$$

where  $\gamma_0$  is the per capita growth rate of the resource when at low abundance, and  $k$  the carrying capacity of a patch for the resource, which we set to  $k = 1$  for simplicity. Solving equation (27) for  $\tau_1 < \tau \leq T$  with initial condition given by equation (25), we obtain that by the end of generation  $t$  (so at the beginning of generation of  $t+1$ ), the resource abundance is

$$\epsilon_{t+1} = \epsilon_{t,T} = \frac{e^\gamma}{\epsilon(\gamma - 1) + e^{\tau_1 N \bar{z}_1}} \epsilon, \tag{28}$$

where  $\gamma = \gamma_0(T - \tau_1)$  is per-generation renewal rate (letting  $\gamma \rightarrow \infty$  then recovers the model of Schmid et al., 2022, in which resource abundance is fixed between generations). Using the notation of equation (1), the environmental map of our model then is,

$$\epsilon_{t+1} = F(\mathbf{z}_1, \mathbf{z}_2, \dots, \mathbf{z}_N, \epsilon) = \frac{e^\gamma}{\epsilon(\gamma - 1) + e^{\tau_1 N \bar{z}_1}} \epsilon, \tag{29}$$

where  $\epsilon = \epsilon_{t,0}$  is the resource abundance at the beginning of generation  $t$ . The environmental map equation (29)

is independent of dispersal (trait  $z_2$ ) as dispersal does not influence the way individuals consume resources.

**Resource equilibrium.**

Solving for equilibrium  $\hat{\epsilon} = F(z, z, \dots, z, \hat{\epsilon})$  (equation 2) and checking its stability (using equation 3), we find that in a monomorphic population where each individual expresses the same  $z = (z_1, z_2)$ , the resource abundance stabilizes for

$$\hat{\epsilon} = \frac{e^\gamma - e^{\tau_1 N z_1}}{e^\gamma - 1}, \tag{30}$$

which is positive as long as the renewal rate  $\gamma$  is large enough compared to consumption (specifically when  $\gamma > N z_1 \tau_1$ ). Otherwise, the resource goes extinct. We focus our attention on the case where the resource is maintained (so where  $\gamma > N z_1 \tau_1$ ).

**Fitness**

An individual uses the resources it has collected to produce offspring, favoring increased attack rate. Increasing one's attack rate may however also be costly, for instance due to lost opportunities or increased risk. To reflect these benefits and costs, we assume that the fecundity of a focal individual  $i$  with attack rate  $z_{i1}$  in a patch where its neighbors express rates  $z_{-i,1} = (z_{11}, z_{21}, \dots, z_{(i-1)1}, z_{(i+1)1}, \dots, z_{N1})$  and the resource abundance is  $\epsilon$ , is given by

$$f_i = \underbrace{\epsilon (1 - e^{-\tau_1 N z_1})}_{\text{resources consumed}} \frac{z_{i1}}{N \bar{z}_1} \times \underbrace{(1 - z_{i1})}_{\text{consumption cost}}. \tag{31}$$

This equation consists of the product between the amount of resources consumed by the focal individual (equation 26 with  $\epsilon_{i,0} = \epsilon$ ) and the individual cost of consumption. From equation (31), fecundity in a population monomorphic for  $z$  is

$$f^o = \hat{\epsilon} (1 - e^{-\tau_1 N z_1}) \frac{1}{N} (1 - z_1), \tag{32}$$

where the equilibrium amount of resources  $\hat{\epsilon}$  is given by equation (30). Under the island model of dispersal (e.g., equation 6.5 in Rousset, 2004), the fitness of a focal individual can then be written as

$$w_i = \underbrace{\frac{(1 - z_{i2}) f_i}{\sum_{j=1}^N (1 - z_{j2}) f_j / N + z_2 (1 - c_d) f^o}}_{=w_{p,i}, \text{ philopatric component}} + \underbrace{\frac{z_{i2} (1 - c_d) f_i}{(1 - z_2) f^o + z_2 (1 - c_d) f^o}}_{=w_{d,i}, \text{ dispersal component}}, \tag{33}$$

where the first term,  $w_{p,i}$ , is the philopatric component of fitness, i.e., the expected number of offspring that establish in their natal patch (consisting of the ratio of offspring of the focal that remain in their natal patch to the total number of offspring that enter competition in that patch); and the second,  $w_{d,i}$ , is the dispersal component, that is, the expected number of offspring that establish in non-natal patches (consisting of the ratio of offspring of the focal that leave their natal patch to the total number of offspring that enter competition in another patch).

**Relatedness**

In addition to the environmental map (equation 29) and fitness (equation 33), the analysis described in section

“Correlational selection under ecological inheritance” relies on several relatedness coefficients under neutrality and selection (Table 1). Those in turn depend on the backward probability of dispersal,  $m$  (i.e., the probability that in a monomorphic population, a randomly sampled individual is an immigrant). In this model where dispersal  $z_2$  is evolving, such probability is given by

$$m(z) = \frac{z_2 (1 - c_d)}{z_2 (1 - c_d) + (1 - z_2)}, \tag{34}$$

which consists of the ratio of the number of individuals dispersing into a patch to the total number of individuals that compete for breeding spots.

Equations (29)-(34) (together with Table 1) are all the ingredients necessary to perform the analysis of disruptive selection laid out in section “Correlational selection under ecological inheritance” (and section “Directional selection under ecological inheritance” for directional selection). Details on our analysis can be found in Supplementary Appendix A whose main results we summarize below, paying special attention on whether polymorphism emerges. All our derivations can also be followed from the accompanying Mathematica Notebook (Supplementary Files).

**Directional selection: convergence to intermediate dispersal and attack traits**

Substituting equations (29)-(33) into the selection gradient equation (10) and analyzing this gradient according to the approach described in section “Directional selection,” we find that the population first converges to a singular strategy  $z^* = (z_1^*, z_2^*)$  for both traits. In line with previous results (e.g., Ajar, 2003; Hamilton & May, 1977; Taylor, 1988), the singular value  $z_2^*$  for dispersal reads as,

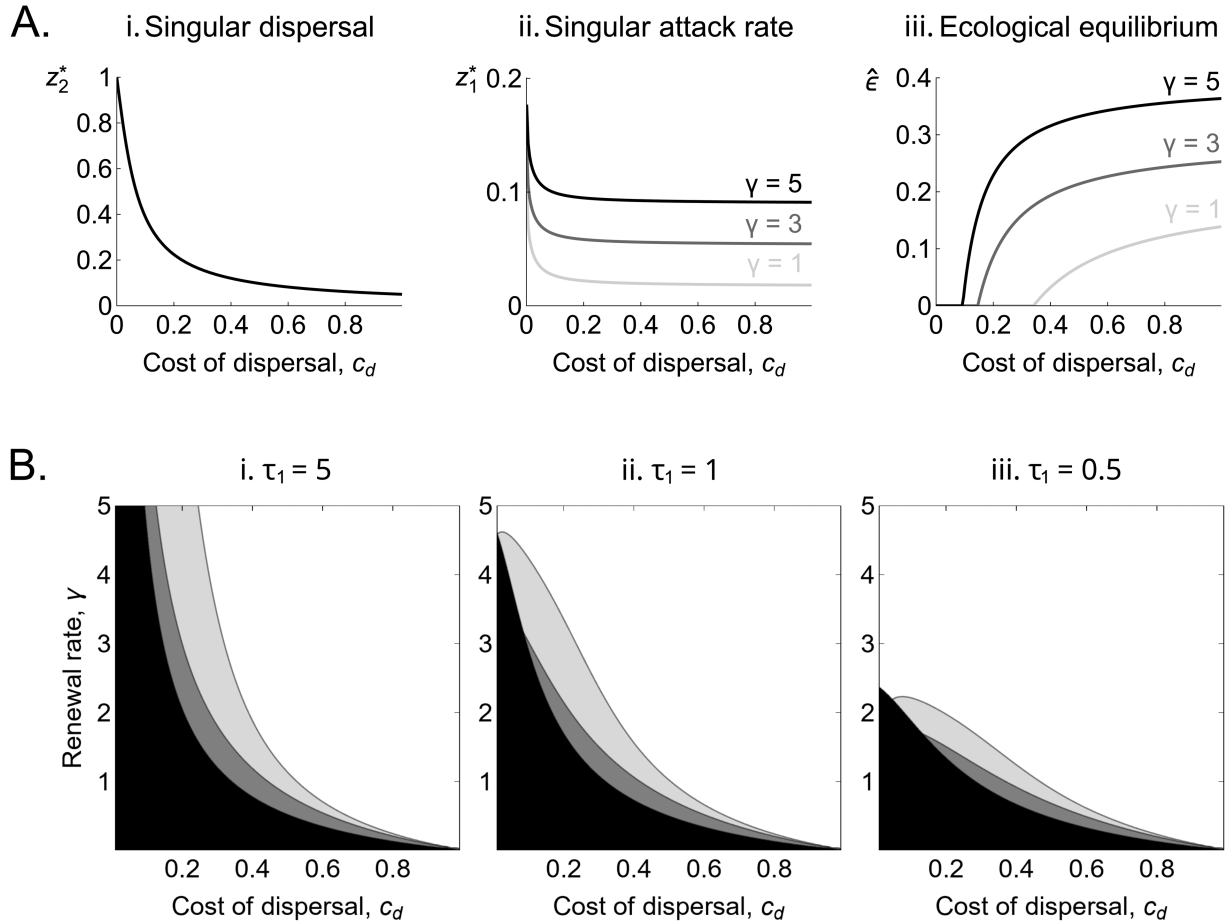
$$z_2^* = \frac{1 + 2Nc_d - \sqrt{1 + 4N(N-1)c_d^2}}{2Nc_d(1 + c_d)}, \tag{35}$$

which decreases with the cost  $c_d$  of dispersal and with the number  $N$  of individuals per patch (Figure 2Ai and Supplementary Figure S4Ai, Supplementary Appendix F.2.2 for details). The dispersal singular value  $z_2^*$  is independent of the attack rate. This is because the attack rate does not influence how fitness varies due to a marginal change in dispersal (as  $f_i = f^o$  for all  $i$  in equation 33 when the population is monomorphic for  $z_1$ ).

The singular value  $z_1^*$  for the attack rate, meanwhile, satisfies the following equality,

$$\frac{1 - 2z_1^*}{(1 - z_1^*)z_1^*} = \left[ \frac{1 - z_1^* (1 + \lambda^2)}{(1 - z_1^*)z_1^*} + \left( \frac{1}{1 - e^{-N z_1^* \tau_1}} + \frac{\lambda e^{-N z_1^* \tau_1}}{e^\gamma - \lambda e^{-N z_1^* \tau_1}} \right) \times N \tau_1 (1 - \lambda^2) \right] \bar{r}_2^o, \tag{36}$$

where  $\lambda = 1 - m(z^*)$  is the probability that an individual is philopatric in a population monomorphic for  $z^*$ , which thus depends on the evolved dispersal strategy  $z_2^*$  (found by substituting equation 35 into equation 34). Solving equation (36) for  $z_1^*$  numerically, we find that when dispersal is costly (i.e.,  $c_d$  is large) the population evolves lower attack rate ( $z_1^*$  is small, Figure 2Aii). This is because when  $c_d$  is large, dispersal evolves to be limited (equation 35). As a result, intergenerational relatedness becomes large (i.e.,  $\bar{r}_{2,b}^o$  in equation (11) becomes large), which in turn favors the evolution of restraint so that



**Figure 2.** (A) Convergence stable (i) dispersal and (ii) attack rate, and (iii) associated resource abundance. Obtained from (a) equation (35); (b) solving equation (36) numerically for  $z_1^*$ ; and (c) from equation (30) with  $z_1^*$  (black:  $\gamma = 5$ ; dark gray:  $\gamma = 3$ ; light gray:  $\gamma = 1$ ). Note from Aiii that not all convergence stable attack rates plotted in Aii lead to the maintenance of the resource (i.e., lead to  $\hat{\epsilon} > 0$ ). When renewal rate is low for instance ( $\gamma = 1$ ), the cost of dispersal  $c_d$  must be greater than 0.35 for resource maintenance. Other parameters:  $\tau_1 = 5$ ,  $N = 10$ . See Supplementary Figure S4A for the effect of  $N$ . (B) Ecological and evolutionary outcomes. These graphs show the parameter regions where the joint evolution of attack rate and dispersal leads to resource extinction (in black); disruptive selection (in gray; dark gray for when the attack rate  $z_1$  evolves alone and dispersal is fixed for  $z_2^*$ ); and stabilizing selection (in white). In (a)  $\tau_1 = 0.5$ ; (b)  $\tau_1 = 1$ ; (c)  $\tau_1 = 5$ ; other parameters:  $N = 10$ , Supplementary Figure S4B for the effects of  $N$ . Supplementary Appendix F and Mathematica Notebook (Supplementary Files) for analysis.

individuals leave more resources to their downstream relatives (Lehmann, 2008). Conversely, when dispersal cost  $c_d$  is low, dispersal evolves to be large, which causes intergenerational relatedness to drop, and thus the evolution of high attack rates as consumption no longer affects relatives. In contrast, the attack rate decreases with patch size  $N$  (Supplementary Figure S4Aii). This is due to competition for resources being within patches such that the amount of resources collected by one individual is inversely proportional to  $N$  (equation 26). Consequently, the benefit from increased attack rate is smaller when patches are larger, favoring the evolution of lower attack rates. Another relevant parameter to the evolution of the attack rate is the rate  $\gamma$  of resource renewal. In particular, high renewal rate  $\gamma$  leads to more exploitative strategies (i.e., greater  $z_1^*$ , Figure 2Aii). This is because when  $\gamma$  is large, ecological inheritance is weak as the resource renews itself quickly after consumption. Individuals can thus consume more resources while incurring little cost to their descendants and the descendants of their relatives (i.e.,  $\partial F/\partial \epsilon$  is small in equation 11).

Plugging the singular strategy for attack rate  $z_1^*$  (given by equations 35–36) into the equilibrium resource abundance

(equation 30) allows us to understand the effect of evolutionary dynamics on the resource. As expected from the previous paragraph, high dispersal cost  $c_d$  leads to higher resource abundance as consumption evolves to be more restrained (Figure 2Aii). Conversely, low dispersal cost reduces resource abundance at evolutionary equilibrium. If in addition to low dispersal cost, the rate  $\gamma$  of renewal is also low, then the resource may in fact go extinct as it is unable to renew itself fast enough in the face of increased consumption (Figure 2.A.iii). We also find that the resource abundance at equilibrium decreases with patch size  $N$  (Supplementary Figure S4Aiii).

**Disruptive and correlational selection: the emergence of dispersive overconsumers and sessile scimpers**

To determine whether the population becomes polymorphic once it has converged to the singular phenotype  $z^* = (z_1^*, z_2^*)$  (given by equations 35–36), we substitute equations (29)–(33) into equation (14)–(21) and perform the analysis described in section “Disruptive, stabilizing, and correlational selection” (Supplementary Appendix F for details). As previously found

(Ajar, 2003), selection on dispersal is always stabilizing when dispersal evolves alone (equation F-12 here for our derivation). When the attack rate evolves but dispersal is fixed at its singular strategy, selection on the attack rate is typically stabilizing, except where dispersal cost  $c_d$  and renewal rate  $\gamma$  are low, close to their threshold values for resource maintenance (dark gray region in Fig 2B, Supplementary Appendix F.3.2 for details). When both traits coevolve, the range of values for  $c_d$  and  $\gamma$  for which selection is disruptive is wider (dark and light gray regions in Figure 2B). When  $c_d$  and  $\gamma$  are high, selection is always stabilizing (white region in Figure 2B). Unlike  $c_d$  and  $\gamma$ , patch size  $N$  has little effect on whether selection is stabilizing or disruptive (Supplementary Figure S4B).

In sum, the dynamics in our model lead to three outcomes depending mostly on the dispersal cost  $c_d$  and resource renewal rate  $\gamma$ : (a) when  $c_d$  and  $\gamma$  are both low, consumer evolution leads to resource extinction (so that if the consumer relies entirely on this resource, it would also go extinct); (b) when  $c_d$  and  $\gamma$  are high, the consumer remains monomorphic for dispersal and attack rate such that the resource is maintained; (c) when  $c_d$  and  $\gamma$  are intermediate, the consumer becomes polymorphic.

A closer look at correlational selection on dispersal and attack rate,  $h_{12}(z^*)$ , reveals two things about the nature of the polymorphism. The first is that since  $h_{12}(z^*)$  is always positive (Supplementary Appendix F.2.3), the polymorphism should be characterized by a positive association between the two traits. We thus expect two types to emerge: (a) one that consumes and disperses more (“dispersive overconsumers”) and (b) another that consumes and disperses less (“sessile scrimpers”). The second relevant aspect of this polymorphism that our analysis shows is that the term that mainly contributes to correlational selection is the one capturing biased ecological inheritance,  $h_{r \times e, 12}(z^*)$  (equation 21–22, Supplementary Appendix F.2.3 for details). More specifically, it is the combination of negative effects of dispersal on intergenerational relatedness,  $\partial \bar{r}_{2,b} / \partial z_2 < 0$ , and of consumption on the environment,  $\partial F / \partial z_{i1} < 0$ , that leads correlational selection to be positive (owing to equation 22). This indicates that polymorphism in our model is due to a positive association between dispersal and attack rate, leading scrimpers to preferentially inherit the patch they maintain from relatives, and overconsumers to preferentially inherit the patch they deplete from non-relatives.

### The rise and fall of overconsumption

To check our mathematical analyses, we ran individual-based stochastic simulations under conditions that lead to stabilizing and disruptive selection (Supplementary Appendix F.4 for simulation procedure and Supplementary Files for code). As predicted, the population gradually converges to the singular strategy for dispersal and consumption in both cases (Figure 3A and B). Concomitantly, the resource abundance goes to its equilibrium  $\hat{e}$  given by equation (30) (Figure 3C and D). Where selection is stabilizing, the population remains monomorphic for both traits (i.e., unimodally distributed around this strategy, Figure 3A), and the resource abundance within patches remains distributed around the ecological equilibrium  $\hat{e}$  (Figure 3C). In contrast, two morphs that correspond to dispersive overconsumers and sessile scrimpers emerge and become increasingly differentiated where selection is disruptive (Figure 3B). In this case, the distribution

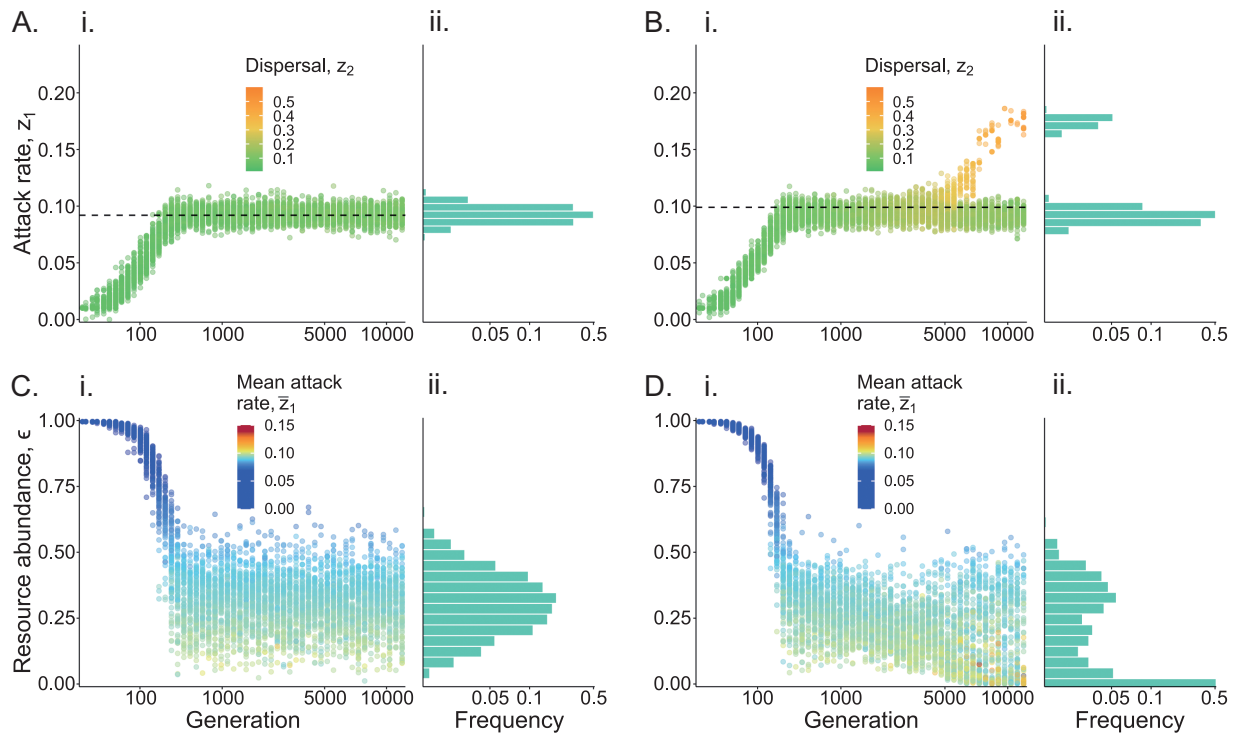
of resource densities becomes bimodal so that the population consists of patches of either low (i.e., with small  $\epsilon$ ) or high quality (i.e., with larger  $\epsilon$ , Figure 3D). This is due to variation in morph composition among patches such that patches with a greater frequency of overconsumers are typically of low quality (Supplementary Figure S5).

When two morphs coexist, our simulations reveal ecological and evolutionary cycles whereby the population alternates between generations during which scrimpers are common and resources are plentiful, and generations during which overconsumers are more abundant and resources are scarce (Figure 4A). With evolution favoring increasingly differentiated morphs, overconsumers have an increasingly detrimental effect on their patch so that the amplitude of these cycles increases (compare Figure 4A with Figure 4B, and red with blue in Figure 4C). In fact, there comes a time when overconsumers are so rare in periods of low abundance that they may stochastically go extinct (i.e., they become so rare in our simulations that by chance, none reproduce). The population is then monomorphic for the scrimper morph, which in the absence of the overconsumer morph is counterselected. The population thus converges once again to the singular strategy (given by equations 35 and 36), whereupon polymorphism emerges and collapses again and again (Figure 4D).

### Discussion

Here, we have extended current theory on the gradual evolution of traits under ecological inheritance to understand how phenotypic variation within populations is molded by disruptive and correlational selection. Our analyses indicate that ecological inheritance opens three pathways for correlational selection to shape polymorphism and create associations among traits (equation 16).

The first of these pathways associates traits that have synergistic effects on fitness via the environment ( $h_{e \times e, pq}(z)$ , equation 17). This is relevant to situations where several traits jointly contribute to the local environment which can be inherited by future generations of relatives. In a naked mole-rat colony for instance, a well-maintained burrow rests on multiple tasks, such as gnawing at the tunnel walls, digging, sweeping substrate, and bringing in material to build the nest. According to our model, the tendencies to perform these different tasks may become linked within individuals in two cases: (a) when traits have multiplicative effects on the environment (first term of equation 17) or (b) when the environment has nonlinear effects on fitness (second term of equation 17). In the absence of interference among characters, we may expect different traits with beneficial consequences for the environment, such as those contributing to a burrow, to have positive multiplicative effects. In this case, correlational selection favors a positive association between traits and within individuals (under case (a) above). Interestingly, such a positive association has been reported in the naked mole-rat among nest building and burrowing (Siegmann et al., 2021), so that rather than specializing in either of these two different tasks, individuals contribute either more or less to both within colonies. In fact, task specialization and labor division appear to be absent from many animal societies (controlling for sex- or condition-specific effects, Kitchen & Packer, 1999; e.g., in meerkat, Clutton-Brock et al., 2003, wild banded mongoose, Sanderson et al., 2015, and purple-crowned fairy-wren, Teunissen et al., 2020). According to equation 17 (second term),



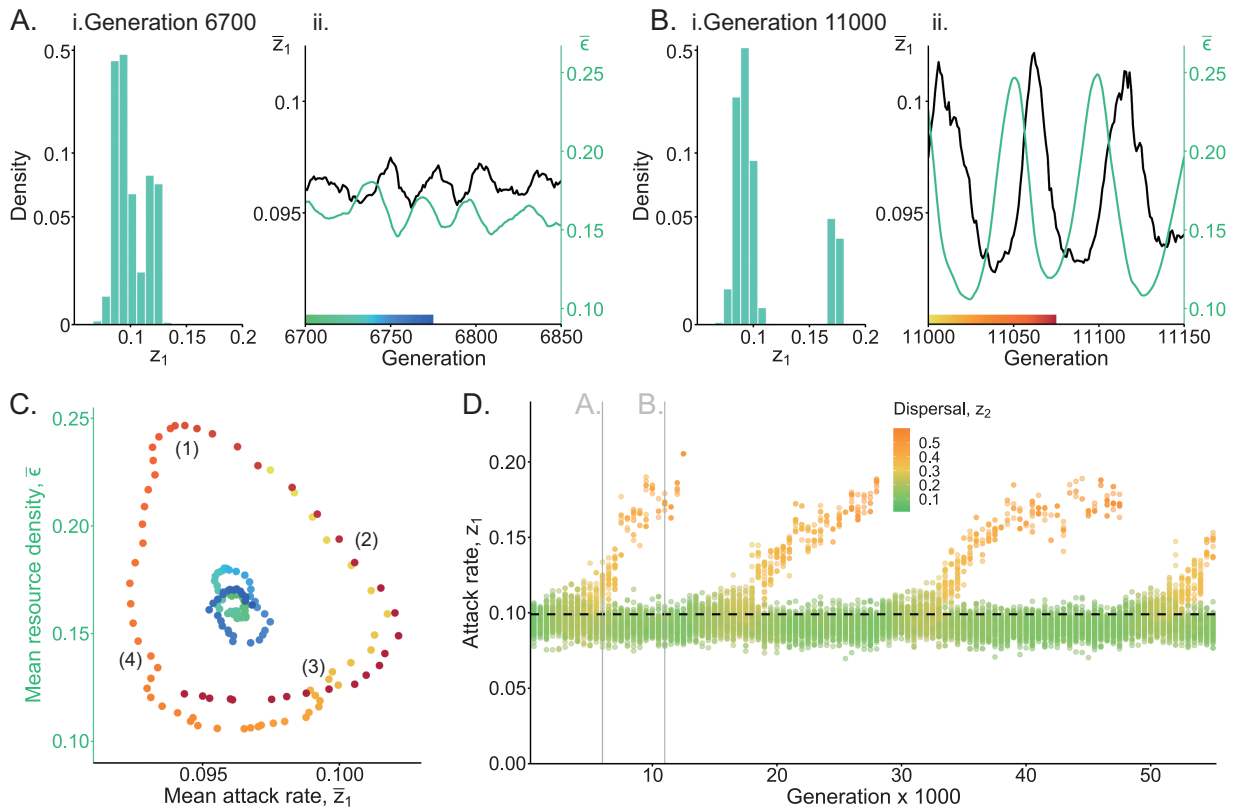
**Figure 3.** Coevolutionary dynamics of dispersal and attack rate, with concomitant resource abundance distribution. These graphs show the results of individual-based stochastic simulations for a population subdivided among  $N_p = 1,000$  patches (Supplementary Appendix F.4 for details), under stabilizing (A and C:  $c_d = 0.5$ ) and disruptive selection (B and D:  $c_d = 0.1$ ). Other parameters:  $\gamma = 5$ ,  $\tau_1 = 5$ ,  $N = 10$ . We chose  $N = 10$  for computational expediency. Similar dynamics are observed with larger patch sizes (Supplementary Figure S4C). (A–B) Attack rate and dispersal evolution. In (i) each point represents an individual, colored according to its dispersal probability (see figure for legends). (ii) Histogram of equilibrium of attack rates in the population. Dashed black line shows the convergence stable strategy (from equation 36). As expected, the population remains monomorphic under stabilizing selection in (A), and becomes polymorphic under disruptive selection in (B), where the polymorphism is characterized by a positive association between attack and dispersal. (C, D) Resource abundance distribution and association with attack rate. In (i) each point represents the resource abundance in that patch, colored according to the mean attack rate in the patch (see figure for legends). Patches where individuals on average express higher attack rates (warmer colors) tend to carry fewer resources. (ii) Histogram of resource abundance across patches.

one situation under which division of labor toward a heritable environmental factor may evolve (i.e., such that correlational selection is negative) is where traits have positive independent effects on the environment, but an improved environment results in diminishing returns on fitness (i.e., such that  $\partial^2 w_i / \partial \epsilon^2 < 0$ ). This would happen for instance when fitness saturates or plateaus with environmental quality, which is a natural assumption for most models (Foster, 2004 for a review on the diminishing returns of helping).

The two other pathways for correlational selection,  $h_{r_{x\epsilon}, p_{q}}(\mathbf{z})$  and  $h_{g_{x\epsilon}, p_{q}}(\mathbf{z})$ , favor the association between traits that lastingly modify the environment with traits that belong to two broad classes, respectively. One class consists of characters that influence the likelihood that environmental modifications are experienced by downstream relatives ( $h_{r_{x\epsilon}, p_{q}}(\mathbf{z})$ , equation 21). This should be especially relevant for traits that underlie gene flow as gene flow is the main driver of relatedness. We showed for instance in section “Joint evolution of dispersal with the attack rate on a local renewable resource” that selection readily links dispersal with the attack rate on a local resource, leading to the coexistence of two morphs: a dispersive morph that consumes more and depletes the local resource and a sessile morph that consumes less and maintains the resource. This positive association between dispersal and attack rate allows overconsumers to preferentially bequeath the patch they deplete to non-relatives, and more

frugal individuals to preferentially leave the patch they maintain to relatives. The polymorphism here differs from the social polymorphism described in Mullon et al. (2018) where the social trait has only immediate intragenerational effects, and not intergenerational effects like here. In fact, no polymorphism emerges in our illustrative example when there is no carry-over effects between generations (i.e., when the resource renewal rate  $\gamma$  is large such that resource abundance is the same at each generation). This highlights how the emergence of intraspecific trait variation in attack rate is driven by ecological inheritance rather than direct social interactions in our example.

Other than the attack rate, variation in handling time or feeding efficiency can also affect resource abundance (Holling, 1959; Rueffler et al., 2006) and may thus also become linked with dispersal. The expectation from our model is that individuals that have a more negative impact on resource abundance, such as with shorter handling time or greater feeding efficiency, evolve to disperse more readily. In addition to resources, individuals can modify many other environmental factors that are relevant to fitness (Estrela et al., 2019 for review). For example, *Drosophila* larvae metabolically release nitrogenous waste thereby deteriorating the rearing environment of future larvae (Borash et al., 1998). Microbes can modify the pH of their environment which feeds back on their growth and survival (Ratzke & Gore, 2018). Others



**Figure 4.** Ecological and evolutionary cycles when the attack rate coevolves with dispersal. Our simulations under disruptive selection are characterized by cycles that occur at different time scales (all plots here are with the same parameters as in ). (A-C) fluctuations on short ecological time scales (in the order of tens of generations) and (D) on long evolutionary times scales (in the order of thousands of generations). At the onset of polymorphism when both morphs are weakly diverged (e.g., at generation 6,700, Ai for trait distribution in the population), the population fluctuates between periods with more and fewer overconsumers (in black in Aii), and of lower and higher abundance (in green in Aii). When later on the divergence among morphs is greater (e.g., at generation 11,000, Bi for trait distribution in the population), the amplitude of these fluctuations also increases (Bii). The joint fluctuations in population average attack rate and resource abundance shown in A and B can be mapped onto a phase plot, which is shown in (C) (blue tones for fluctuations seen Aii, and red tones for fluctuations seen Bii; see x-axes of Aii and Bii for color legend of time points). This phase plot C shows four phases: (1) when the resource is abundant and consumption is low, it favors an increase in overconsumers; (2) as overconsumers become more frequent, resource abundance falls; (3) when the resource is scarce, overconsumers are counterselected; (4) once overconsumers are rare, resource abundance increases. As the morphs become increasingly differentiated due to disruptive selection, the overconsumer morph becomes increasingly rare, leading to its stochastic extinction in times of low abundance, until it re-appears through disruptive selection whereupon the evolutionary cycles starts again (these evolutionary cycles are shown in (D), where each point represents an individual, colored according to its dispersal probability—see figure for legends).

can reduce the concentration of toxic metals or antibiotics, improving their substrate (Frost et al., 2018; O’Brien et al., 2014; Yurtsev et al., 2016). The traits that underlie such modifications may thus also become linked to dispersal, leading to kin-biased ecological inheritance. A broad-brush conclusion from our model is therefore that under ecological inheritance, correlational selection may associate dispersal with multiple traits that have environmental effects, leading to the emergence of dispersal syndromes (Ronce & Clobert, 2012). Such syndromes, which have been observed across a wide range of taxa (fish, Cote et al., 2010b; Fraser et al., 2001; mammals, Haughland & Larsen, 2004; lizards, Cote & Clobert, 2007; for reviews: Cote et al., 2010a; Spiegel et al., 2017), are ecologically and evolutionarily significant as they influence the demographic and genetic consequences of movement (Edelaar & Bolnick, 2012; Raffard et al., 2021; Ronce & Clobert, 2012). In the model presented in section “Joint evolution of dispersal with the attack rate on a local renewable resource” for instance, the association between dispersal and attack rate on a resource led to complex dynamics, with cycles occurring both on ecological and evolutionary timescales (Figure 4).

The second class of traits that selection associates with characters that modify the environment consists of traits whose effects on fitness depend on that environment, that is, due to “gene-environment” interactions ( $h_{g \times e, pq}(z)$ , equation 19). Such context- or environment-dependent effects are not uncommon. Traits that are useful during competitive interactions, like conspicuous traits to attract mates (Dougherty, 2021; Mappes et al., 1996; Woods et al., 2007) or fighting appendages like antlers or horns (Emlen, 2008; Miller, 2013), are costly to produce, but expression costs likely depend on the environment, at least partly. Indeed, individuals that grow in better conditions or are better provisioned often show more extravagant traits without suffering a greater cost of expression (Mappes et al., 1996; Vehrenkamp et al., 1989). The suggestion from our analysis is that context-dependent traits of the sort should become linked to characters that improve the environment when this environment is bequeathed to relatives. This is because such combination of linkage and ecological inheritance allows genes that are good in certain environments to be expressed more often in those environments. This reasoning extends to traits that have

indirect context-dependent fitness effects (“indirect  $g \times e$  interactions” term in [equation 19](#)), for instance favoring the association of helping with traits that deteriorate the environment when the fitness effects of helping increase as the environment decreases in quality (as observed, e.g., for cooperative breeding in birds [Emlen, 1982](#)). The above considerations should be especially relevant to plastic phenotypes through reaction norms ([Stearns, 1989](#); [West-Eberhard, 1989](#)), where one of the evolving trait is the response to the environment and another is modification to this environment. Our model can in fact readily be used to investigate how correlational selection associates environmental response with environmental modification within individuals, and thus help understand the maintenance of variation in plasticity and reaction norms ([Pigliucci, 2005](#)).

The gene-environment interactions of our model can also be connected to the so-called process of niche construction, which is “the process whereby organisms actively modify their own and each other’s evolutionary niches” ([Laland et al., 2016](#)). This definition is made more explicit by considering the formal models developed by the authors that use it. The typical set-up is a population genetics model with two loci, E and A, at each of which two alleles segregate ([Laland et al., 1996, 1999](#); [Odling-Smee et al., 2003](#); [Silver & Di Paolo, 2006](#)). The current and past allele frequency in the population at locus E determines an environmental variable, which in turn determines whether carrying allele  $a$  or  $A$  at locus A is more beneficial. Such fitness epistasis via the environment is precisely captured by the direct gene-environment interactions in [equation \(19\)](#) (specifically by the first term where trait  $p$  is the allelic frequency within individuals at locus A and trait  $q$  at locus E). Our approach thus encompasses these models. But whereas population genetics models focus on short-term evolution through changes in frequency of alleles with potentially large effects, the approach we take here investigates phenotypic evolution in the long term under the constant input of mutations with weak effects. One of the main contributions of this approach is to provide a way to determine whether gradual evolution in a dispersal-limited population leads to polymorphism in “niche construction” traits owing to disruptive selection and frequency-dependent interactions. The polymorphism here contrasts in two ways with the genetic polymorphism reported in the population genetics models of niche construction ([Laland et al., 1996, 1999](#); [Odling-Smee et al., 2003](#)). First, the genetic polymorphism in these previous models is due to specific assumptions about fitness and genetic constraints that create overdominance rather than because of disruptive selection on traits like in our model. Second, while we allow for limited dispersal and local environmental effects, these population genetics models assume that the population is well mixed and that the same environment is experienced by all individuals in the population (though see [Silver & Di Paolo, 2006](#) for simulations). This entails that a trait cannot be statistically associated with its environmental effect and as a result, there cannot be any selection on a trait’s intergenerational effects (to see this, one can put all relatedness coefficients and their perturbations to zero in our equations; [Brodie, 2005](#); [Dawkins, 1982, 2004](#); [Lehmann, 2007, 2008](#)). The intergenerational environmental effects of traits that evolve in those population genetics models are thus a complete by-product of evolution rather than an adaptation.

Like all formal models, ours relies on many assumptions that are relaxed in nature. One is that individuals are haploid

and reproduce asexually. Provided genes have additive effects on traits, diploidy and sexual reproduction do not influence evolutionary dynamics under directional selection ([Geritz & Kisdi, 2000](#); [Rousset, 2004](#)). The emergence of polymorphism due to correlational selection may however depend on the genetic architecture of traits. Where different traits are encoded by separate loci, meiotic recombination breaks the positive genetic linkage favored by correlational selection. But if the genetic architecture is allowed to evolve (through, e.g., recombination modifiers or pleiotropic loci), then correlational selection favors an architecture that allows associations among traits to be heritable ([Sinervo & Svensson, 2002](#)), which in turn leads to polymorphism ([Mullon et al., 2018](#)). Another useful simplifying assumption we have made is that individuals disperse uniformly among patches, so that there is no isolation-by-distance. While isolation-by-distance does not lead to fundamental changes in how selection shapes traits with lasting ecological effects (as shown by analyses of directional selection, [Lehmann, 2008](#)), it introduces interesting effects whereby selection depends not only on temporal but also on spatial environmental effects of traits. Finally, we have assumed that patches are of constant size and that traits influence a single environmental variable. We extended our example (section “Joint evolution of dispersal with the attack rate on a local renewable resource”) using individual-based simulations to consider changing local population size in response to trait evolution ([Supplementary Figure S6](#) and [Supplementary Files](#) for code). Our simulations show similar evolutionary dynamics as those found in the baseline model ([Supplementary Figure S6](#)), which suggests that incorporating explicit demography does not necessarily affect disruptive selection and the nature of polymorphism in this example. But as analyses of directional selection have demonstrated ([Lehmann & Rousset, 2010](#); [Lion, 2016](#), for reviews), demographic structure can in some cases influence qualitatively the evolution of social traits in spatially structured populations. It may thus be interesting, albeit challenging, to extend our analysis of disruptive selection to include demographic fluctuations owing to trait evolution and multiple environmental variables (extending, e.g., [Ohtsuki et al., 2020](#) to consider intergenerational effects on patch state). This would be useful to investigate whether the evolution of environmental degradation, such as through resource depletion or release of pollutants, can lead to population extinction ([Gyllenberg & Parvinen, 2001](#); [Ferriere & Legendre, 2013](#); [Matsuda & Abrams, 1994](#)).

To sum up, we have investigated the coevolution of multiple traits in a group-structured population when these traits affect the group environment, which is then bequeathed to future generations. We found that such bequeathal provides ground for different types of traits to become linked by selection, with implications for a wide range of traits involved in niche construction, division of labor, dispersal syndromes, condition dependence, and phenotypic plasticity. Our results broadly suggest that ecological inheritance can contribute to phenotypic diversity within populations, and potentially lead to complex polymorphism involving multiple traits with long-lasting effects on the environment.

## Supplementary material

Supplementary material is available online at *Evolution*.

## Data availability

All used C++ scripts and Mathematica Notebooks are deposited on Github: [https://github.com/iris-prigent/Supplementary\\_Evolution](https://github.com/iris-prigent/Supplementary_Evolution).

## Author contributions

I.P. and C.M. conceived the study and performed the analyses. I.P. wrote the first draft of the manuscript, and both authors contributed to the final version.

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