A mathematical framework for evo-devo dynamics

Mauricio González-Forero[*,1] **and Andy Gardner**[*]
[*]School of Biology, University of St Andrews, Dyers Brae, St Andrews KY16 9TH, UK

ABSTRACT Natural selection acts on phenotypes constructed over development, which raises the question of how development affects evolution. Existing mathematical theory has considered either evolutionary dynamics while neglecting developmental dynamics, or developmental dynamics while neglecting evolutionary dynamics by assuming evolutionary equilibrium. We formulate a mathematical framework that integrates explicit developmental dynamics into evolutionary dynamics. We consider two types of traits: genetic traits called control variables and developed traits called state variables. Developed traits are constructed over ontogeny according to a developmental map of ontogenetically prior traits and the social and non-social environment. We obtain general equations describing the evolutionary-developmental (evo-devo) dynamics. These equations can be arranged in a layered structure called the evo-devo process, where five elementary components generate all equations including those describing genetic covariation and the evo-devo dynamics. These equations recover Lande's equation as a special case and describe the evolution of Lande's $\mathbf{G}$-matrix from the evolution of the phenotype, environment, and mutational covariation. This shows that genetic variation is necessarily absent in some directions of phenotype space if at least one trait develops and enough traits are included in the analysis so as to guarantee dynamic sufficiency. Consequently, directional selection alone is generally insufficient to identify evolutionary equilibria. Instead, "total genetic selection" is sufficient to identify evolutionary equilibria if mutational variation exists in all directions of control space and exogenous plastic response vanishes. Developmental and environmental constraints influence the evolutionary equilibria and determine the admissible evolutionary trajectory. These results show that development has major evolutionary effects.

KEYWORDS Adaptation; Constraints; $\mathbf{G}$-matrix; Development; Life history; Trade-offs; Optimal control; Matrix population models; Adaptive dynamics; Quantitative genetics

Natural selection screens phenotypes produced over development, defined as the construction of the phenotype across the lifespan. Thus, a fundamental evolutionary question is how development affects evolution. Interest in this question is longstanding (Baldwin 1896, Waddington 1959 p. 399, and Gould and Lewontin 1979) and has steadily increased in recent decades.

A fundamental tool to understand how development affects evolution is Lande's (1979) equation. This equation states that evolutionary change in the multivariate mean phenotype $\bar{\mathbf{z}}$ is $\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}$, where the selection gradient $\boldsymbol{\beta}$ points in the direction of steepest fitness ascent in phenotype space and the additive genetic covariance matrix $\mathbf{G}$ describes the genetic covariation between the traits in phenotype space (Lande 1979; Walsh and Lynch 2018). From Lande's equation, it follows that genetic covariation may divert evolutionary change from the direction of steepest fitness ascent, and may prevent evolutionary change in some directions if genetic variation in those directions is absent (i.e., if $\mathbf{G}$ is singular). Thus, Lande's equation indicates that development affects evolution by inducing genetic covariation and hence via $\mathbf{G}$ (Charlesworth *et al.* 1982; Cheverud 1984; Maynard Smith *et al.* 1985).

Extensive efforts have been devoted to understand the structure of the $\mathbf{G}$-matrix. Most efforts have been empirical, but progress has been hampered by methodological difficulties (Blows and Hoffmann 2005; Mezey and Houle 2005; Hine and Blows 2006; Blows 2007; Meyer and Kirkpatrick 2008; Kirkpatrick 2009; Pavlicev *et al.* 2009; Walsh and Blows 2009). For instance: a strict estimation of the $\mathbf{G}$-matrix requires large sample sizes and that an arbitrarily large number of traits is analysed, which is impractical (Hill and Thompson 1978; Pavlicev *et al.* 2009); determining whether any eigenvalue of $\mathbf{G}$ is exactly zero, thus indicating that there is no genetic variation in some direction of phenotype space, is infeasible since one cannot sta-

---

doi: 10.1534/genetics.XXX.XXXXXX
Manuscript compiled: Monday 17th May, 2021

[1]Corresponding author. E-mail: mgf3@st-andrews.ac.uk.

tistically establish that a quantity is exactly zero (Kirkpatrick and Lofsvold 1992; Kirkpatrick 2009); and the structure of the **G**-matrix may change by many factors including time, so assessing its structure in a given generation offers little guarantee of its structure in the future (Kirkpatrick 2009; Björklund *et al.* 2013). Simulation and analytical work on the nature of the **G**-matrix has considered the effects of pleiotropy, selection, and drift (Jones *et al.* 2003, 2004, 2007, 2012; Chantepie and Chevin 2020; Engen and Sæther 2021). Yet, analytical work has been hindered by the mathematical complexity of the task (Arnold *et al.* 2008).

Interest in the evolutionary effects of development has increased with growing interest in the evolutionary effects of plasticity, niche construction, extra-genetic inheritance, and developmental bias (West-Eberhard 2003; Laland *et al.* 2015). Many studies have modeled the evolution of plasticity and its effects on the evolutionary process (Via and Lande 1985; Lande 2009, 2014; Michel *et al.* 2014; Lande 2019). Many others have modeled the evolutionary effects of niche construction (Laland *et al.* 1996, 1999, 2001; Lehmann 2007, 2008; Rendell *et al.* 2011; Creanza *et al.* 2012; Creanza and Feldman 2014; Kobayashi *et al.* 2019). There are also many models on the evolutionary effects of extra-genetic inheritance (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Day and Bonduriansky 2011; Mullon *et al.* 2021) and developmental bias (Salazar-Ciudad and Jernvall 2002; Salazar-Ciudad and Marín-Riera 2013; Milocco and Salazar-Ciudad 2020), although these have not always been verbally framed in such terms.

An important difficulty in understanding how development affects evolution is the existing lack of general mathematical frameworks that explicitly consider developmental and evolutionary dynamics. Lande's equation provides the insight of development as affecting genetic covariation, but Lande's equation has not been derived from an explicit account of development, which may hinder insight into the evolutionary effects of development. Lande's original derivation is based on the standard quantitative genetics approach of describing each individual's multivariate phenotype as breeding value plus uncorrelated error (Lande 1979). Breeding value is in turn the best linear prediction of the phenotype from gene content, using least-square regression (Fisher 1918; Crow and Kimura 1970; Falconer and Mackay 1996; Lynch and Walsh 1998; Walsh and Lynch 2018). This linear prediction can be carried out regardless of any mechanism by which the phenotype is constructed over ontogeny. Thus, details regarding evolutionary effects of development remain implicit in that approach. Consequently, while breeding values may depend on development as well as myriad other factors, information of how this dependence occurs is not made available by the linear regression of phenotype on gene content. This may have limited insight into how development affects the **G**-matrix.

There is a wide variety of mathematical frameworks that relate to the problem of understanding how development affects evolution, but there is a lack of synthesis of these frameworks to simultaneously consider developmental and evolutionary dynamics. First, the earliest frameworks of evolutionary dynamics considered non-overlapping generations without any class structure (Fisher 1922; Wright 1942; Lande 1979; Dieckmann and Law 1996) (Fig. 1A). These frameworks have been extended in various research lines that could be seen as incorporating different aspects of development. One line considers age structure, which allows individuals of different ages to coexist and to have age-specific survival and fertility rates (Lande 1982; Charlesworth 1993, 1994; Durinx *et al.* 2008; de Vries and Caswell 2018, 2019) (Fig. 1B). An important feature of age-structured models is that the forces of selection decline with age due to demography, in particular due to mortality and fewer remaining reproductive events as age advances (Medawar 1952; Hamilton 1966; Caswell 1978; Caswell and Shyu 2017). Such age-specific decline in the force of selection does not occur in unstructured models.

Second, age- or stage-structured models have been extended to traits that depend on a continuous variable (e.g., age), under the label of function-valued or infinite-dimensional traits (Kirkpatrick and Heckman 1989; Dieckmann *et al.* 2006; Coulson *et al.* 2010; Parvinen *et al.* 2013; Metz *et al.* 2016; Rees and Ellner 2016). The analogue of the **G**-matrix for infinite-dimensional traits (i.e., the genetic covariance function) is thought to be commonly singular since increasing the number traits in the analysis is likely to increase genetic correlations, as supported by empirical data (Wagner 1988; Kirkpatrick and Lofsvold 1992; Gomulkiewicz and Kirkpatrick 1992). While these models consider age-specific traits (Cheverud *et al.* 1983), these models have not considered explicit developmental constraints (but see Avila *et al.* 2021).

Third, another research line in life-history evolution has extended age-structured models to consider explicit developmental constraints, although this literature calls such constraints dynamic rather than developmental (Gadgil and Bossert 1970; Taylor *et al.* 1974; León 1976; Schaffer 1983; Houston *et al.* 1988; Houston and McNamara 1999; Sydsæter *et al.* 2008) (Fig. 1D). Such models consider two types of age-specific traits: control variables that are under genetic control, and state variables that are constructed over ontogeny according to developmental constraints. This explicit consideration of developmental constraints in an evolutionary context considers that the population is at an evolutionary equilibrium. Thus, this approach identifies evolutionarily stable (or uninvadable) controls and associated states using techniques from dynamic optimization such as optimal control and dynamic programming (Gadgil and Bossert 1970; Taylor *et al.* 1974; León 1976; Schaffer 1983; Houston *et al.* 1988; Houston and McNamara 1999). While the assumption of evolutionary equilibrium has enabled deep and numerous insights, it does not address the evolutionary dynamics which would provide a richer understanding. For instance, evolutionary equilibria might not be achieved in realistic evolutionary timescales, different equilibria might be achieved from different ancestral conditions, or equilibria might not be achieved at all (e.g., due to evolutionary cycles).

Fourth, another research line in quantitative genetics has considered unstructured models where a set of traits are functions of underlying traits such as gene expression or environmental variables (Wagner 1984, 1989; Hansen and Wagner 2001; Rice 2002; Martin 2014; Morrissey 2014, 2015) (Fig. 1C). This dependence of traits on other traits is used by this research line to describe the developmental map or the genotype-phenotype map, which is akin to the developmental constraints in life-history models. However, as this research line considers no explicit age progression, it considers implicit rather than explicit developmental (i.e., dynamic) constraints. Thus, this line has not considered the effect of age structure nor explicit developmental constraints (Wagner 1984, 1989; Hansen and Wagner 2001; Rice 2002; Martin 2014; Morrissey 2014, 2015). Overall, there has been a lack of integration of age structure, developmental constraints, and evolutionary dynamics into a single mathematical framework, which has yielded a fragmentary understanding of how

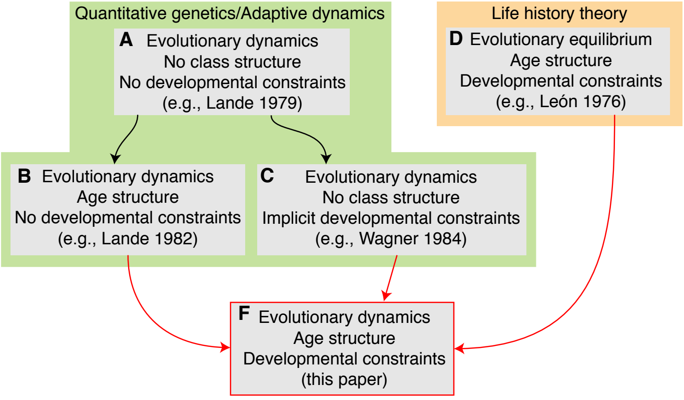

Figure 1 Previous mathematical frameworks on the question of how development affects evolution. Each box refers to a set of mathematical models considering the indicated assumptions. The arrows point to extensions to previous models.

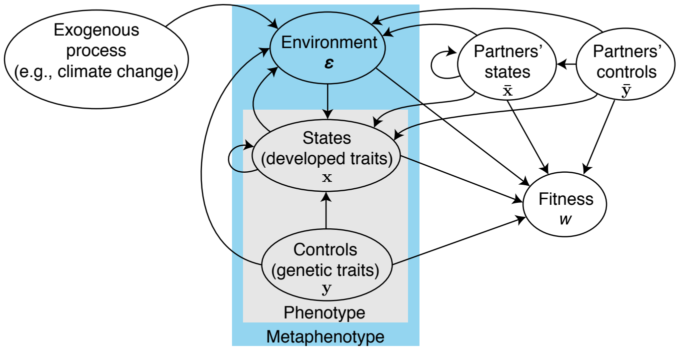

Figure 2 Causal diagram among the framework's components. Each arrow indicates the effect of a given variable on another one. States correspond to developed traits (e.g., body size) while controls correspond to genetic traits (e.g., gene expression). The phenotype consists of states and controls. The metaphenotype consists of states, controls, and environment. For simplicity, we assume that controls are open-loop, so the there is no arrow towards controls.

development—which unfolds as the individual ages—affects evolution.

Here we formulate a mathematical framework that integrates explicit developmental dynamics into evolutionary dynamics. To do this, we model some traits as being constructed over ontogeny, as is done in life-history models with dynamic constraints. We simultaneously consider age structure, developmental constraints, and evolutionary dynamics, and allow for environmentally-mediated phenotype construction, environmental constraints, population dynamics in a fast time scale, and environmental dynamics in a slow time scale. Environmentally-mediated phenotype construction allows for the developed phenotype to depend on (i) the non-social environment (i.e., plasticity) and (ii) the social environment, which can mechanistically describe extra-genetic inheritance and indirect genetic effects (Moore *et al.* 1997). Environmental constraints allow for the environment to depend on individuals' phenotypes, thus allowing for niche construction (though we do not consider ecological inheritance). Additionally, developmental constraints allow the phenotype to be "predisposed" to develop in certain ways, thus allowing for developmental bias. Our methods integrate tools from adaptive dynamics (Dieckmann and Law 1996), matrix population models (Caswell 2001; Otto and Day 2007), and optimal control (Sydsæter *et al.* 2008).

Materials and Methods

Overview

Here we provide an overview of our methods. First, we describe the framework's set-up, including its components and causal relationships as well as the three phases in which we divide an evolutionary time step. Second, we introduce notation to describe the phenotype, environment, and development. This gives an explicit description of the developmental dynamics. Third, we formally describe the three phases of an evolutionary time step. Fourth, we identify invasion fitness and use it to derive an equation describing the evolutionary dynamics of genetic traits (i.e., controls) under adaptive dynamics assumptions (Dieckmann and Law 1996). This equation depends on what we call the total selection gradient of controls. Thus, we obtain a description of explicit developmental and evolutionary dynamics. Fifth, we identify the selection gradient in age structured populations, which we use to calculate the total selection gradient of controls. Based on this setting, in Appendices 4-12, we derive equations describing the evolutionary dynamics of the various types of traits involved in our framework.

Set up

We base our framework on standard assumptions of adaptive dynamics (Dieckmann and Law 1996). We consider a large, age-structured, well mixed population of clonally reproducing individuals. The population is finite but, in a departure from Dieckmann and Law (1996), we let the population dynamics be deterministic rather than stochastic for simplicity (so there is no genetic drift). Thus, the only source of stochasticity in our framework is mutation. Each individual has a phenotype consisting of two types of traits: age-specific controls and age-specific states (Fig. 2; notation is summarised in Table 1). The values of controls at each age are genetically controlled by genetic loci, although the genetic details such as the number of loci need not be specified given our adaptive dynamics assumptions. States are constructed over development. We separate time scales, so developmental and population dynamics occur in a fast discrete ecological timescale t and evolutionary dynamics occur in a slow discrete evolutionary timescale τ. In addition to this standard separation of time scales used in adaptive dynamics, we add a phase to each evolutionary time step due to social development. Thus, for tractability, we partition a unit of evolutionary time in three phases: socio-developmental (socio-devo) stabilization dynamics, resident population dynamics, and resident-mutant population dynamics (Fig. 3).

At the start of the socio-devo stabilization phase of a given evolutionary time τ, the population consists of individuals all having the same resident genotype and phenotype. A new individual arises which has identical genotype and experiences the same environment as the resident, but develops a phenotype that may be different from that of the original resident due to social interactions. This developed phenotype is set as the new resident. This process is repeated until convergence to a socio-devo stable (SDS) resident or until divergence. If development is not social, the resident is trivially SDS so the socio-devo stabilization dynamics phase is unnecessary. If an SDS resident

Table 1 Notation summary

Symbol	Meaning
$\mathbf{x}$	States (developed traits)
$\mathbf{y}$	Controls (genetic traits)
$\mathbf{z}$	Phenotype (states and controls)
$\boldsymbol{\epsilon}$	Environment
$\mathbf{m}$	Metaphenotype (phenotype and environment)
N_a	Number of ages
N_s	Number of states
N_c	Number of controls
N_e	Number of environmental variables
$\mathbf{g}$	Developmental map
$\mathbf{h}$	Environmental map
$\mathbf{n}$	Population density
f	Fertility
p	Survival probability
ℓ	Survivorship
w	Fitness
λ	Invasion fitness
$\mathbf{u}$	Stable age distribution
$\mathbf{v}$	Reproductive value
ϕ	Force of selection on fertility
π	Force of selection on survival
t	Ecological time
τ	Evolutionary time
θ	Socio-devo stabilization time
T	Generation time
$\check{\mathbf{x}}$	Resident states in the context of mutant
$\hat{\mathbf{z}}$	Undeveloped phenotype
$\mathbf{a}_{\boldsymbol{\zeta}}$	Breeding value of $\boldsymbol{\zeta}$
$\mathbf{b}_{\boldsymbol{\zeta}}$	Stabilized breeding value of $\boldsymbol{\zeta}$
$\mathbf{G}_{\boldsymbol{\zeta}}$	Additive genetic covariance matrix of $\boldsymbol{\zeta}$
$\mathbf{H}_{\boldsymbol{\zeta}}$	Additive socio-genetic cross-covariance matrix of $\boldsymbol{\zeta}$
$\frac{\mathrm{s}\boldsymbol{\zeta}^\intercal}{\mathrm{s}\boldsymbol{\xi}}$	Stabilized effects of $\boldsymbol{\xi}$ on $\boldsymbol{\zeta}$
$\frac{\mathrm{d}\boldsymbol{\zeta}^\intercal}{\mathrm{d}\boldsymbol{\xi}}$	Total effects of $\boldsymbol{\xi}$ on $\boldsymbol{\zeta}$
$\frac{\delta\boldsymbol{\zeta}^\intercal}{\delta\boldsymbol{\xi}}$	Semi-total effects of $\boldsymbol{\xi}$ on $\boldsymbol{\zeta}$
$\frac{\partial\boldsymbol{\zeta}^\intercal}{\partial\boldsymbol{\xi}}$	Direct effects of $\boldsymbol{\xi}$ on $\boldsymbol{\zeta}$

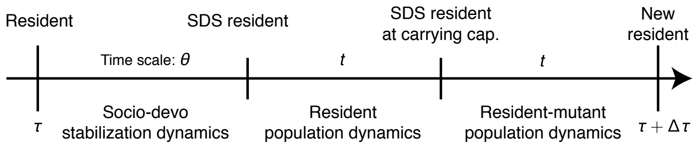

Figure 3 Phases of the evolutionary cycle. Evolutionary time is τ. SDS means socio-devo stable. The socio-devo stabilization dynamics phase is added to the standard separation of timescales in adaptive dynamics, which only consider the other two phases. The socio-devo stabilization dynamics phase is only needed if development is social (i.e., if the developmental map $\mathbf{g}$ depends on social partners' phenotype).

is achieved, the population moves to the next phase; if an SDS resident is not achieved, the analysis stops. We thus study the evolutionary dynamics of SDS phenotypes.

If an SDS resident is achieved, the population moves to the resident population dynamics phase. In this phase, the SDS resident undergoes density dependent population dynamics which we assume asymptotically converges to a carrying capacity.

Once an SDS resident has achieved carrying capacity, the population moves to the resident-mutant population dynamics phase. At the start of this phase, a random mutant control vector arises in a vanishingly small number of mutants. We assume that control mutation is unbiased and weak. Unbiased control mutation means that mutant controls are symmetrically distributed around the resident controls. Weak control mutation means that the variance of mutant controls around resident controls is marginally small. Weak mutation (Walsh and Lynch 2018, p. 1003) is also called δ-weak selection (Wild and Traulsen 2007). We assume that the mutant becomes either lost or fixed in the population (Priklopil and Lehmann 2020), establishing a new resident phenotype.

Repeating this evolutionary cycle generates long term evolutionary dynamics of an SDS phenotype.

Phenotype, environment, and development

We now introduce notation for the phenotype and environment, and describe the developmental dynamics. Each individual can live from age 1 to age $N_\mathrm{a} \in \mathbb{N}_+ = \{1, 2, 3, \ldots\}$. The phenotype is composed of $N_\mathrm{s} \in \mathbb{N}_+$ state variables and $N_\mathrm{c} \in \mathbb{N}_+$ control variables that have age specific values. Throughout, we denote resident variables with an "overbar" ($\bar{}$). Let $\bar{y}_{ia}$ be the i-th control variable of a resident individual of age a for $i \in \{1, \ldots, N_\mathrm{c}\}$ and $a \in \{1, \ldots, N_\mathrm{a}\}$ (e.g., a certain gene's expression level at a given age). Let $\bar{x}_{ia}$ be the i-th state variable of a resident individual of age a for $i \in \{1, \ldots, N_\mathrm{s}\}$ and $a \in \{1, \ldots, N_\mathrm{a}\}$ (e.g., a certain tissue's size at a given age). The controls of a resident of age a are given by $\bar{\mathbf{y}}_a = (\bar{y}_{1a}, \ldots, \bar{y}_{N_\mathrm{c}a})^\intercal$. The states of a resident of age a are given by $\bar{\mathbf{x}}_a = (\bar{x}_{1a}, \ldots, \bar{x}_{N_\mathrm{s}a})^\intercal$. The phenotype of a resident of age a is the vector $\bar{\mathbf{z}}_a = (\bar{\mathbf{x}}_a; \bar{\mathbf{y}}_a)$, where the semicolon indicates a "linebreak" so that the vector $\bar{\mathbf{x}}_a$ is placed on top of the vector $\bar{\mathbf{y}}_a$, that is, $\bar{\mathbf{z}}_a = (\bar{x}_{1a}, \ldots, \bar{x}_{N_\mathrm{s}a}, \bar{y}_{1a}, \ldots, \bar{y}_{N_\mathrm{c}a})^\intercal$. The controls of a resident across life are given by the vector $\bar{\mathbf{y}} = (\bar{\mathbf{y}}_1; \ldots; \bar{\mathbf{y}}_{N_\mathrm{a}})$. The states of a resident across life are given by the vector $\bar{\mathbf{x}} = (\bar{\mathbf{x}}_1; \ldots; \bar{\mathbf{x}}_{N_\mathrm{a}})$. The resident phenotype across life is the vector $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$. The notation for the mutant phenotype is analogous without the overbar (e.g., $\mathbf{z}$). We analogously denote the phenotype of a focal individual, either resident or mutant, with a bullet $\bullet$ subscript (e.g., $\mathbf{z}_\bullet$).

We now describe an individual's environment. We assume that an individual's environment can be described by $N_\mathrm{e} \in \mathbb{N}_+$ mutually independent environmental variables. Let $\epsilon_{ia\bullet}$ be the i-th environmental variable describing the focal individual's environment at age a for $i \in \{1, \ldots, N_\mathrm{e}\}$ and $a \in \{1, \ldots, N_\mathrm{a}\}$ (e.g., ambient temperature experienced by the focal individual at that age). The vector of environmental variables experienced by a focal individual at age a is $\boldsymbol{\epsilon}_{a\bullet} = (\epsilon_{1a\bullet}, \ldots, \epsilon_{N_\mathrm{e}a\bullet})^\intercal$. That the environmental variables are mutually independent means that changing one environmental variable at one age does not *directly* change any other environmental variable at any age (i.e., $\partial \epsilon_{kj\bullet} / \partial \epsilon_{ia\bullet} = 0$ if $i \neq k$ or $a \neq j$). We assume that environmental variables are mutually independent to be able to write each environmental variable as a function of variables that are not directly environment variables, which facilitates derivations. The environment experienced across life by the focal individual is $\boldsymbol{\epsilon}_\bullet = (\boldsymbol{\epsilon}_{1\bullet}; \ldots; \boldsymbol{\epsilon}_{N_\mathrm{a}\bullet})$. The notation for the environment of a resident is analogous without the bullet but with an overbar (e.g., $\bar{\boldsymbol{\epsilon}}$), and for a mutant without the bullet or the overbar (e.g., $\boldsymbol{\epsilon}$).

A focal individual's environment at age a satisfies the *environmental constraint* given by

$$\boldsymbol{\epsilon}_{a\bullet} = \mathbf{h}_a(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \tau), \tag{1}$$

for all $a \in \{1, \ldots, N_\mathrm{a}\}$. The function

$$\mathbf{h}_a(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \tau) = (h_{1a}(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \tau), \ldots, h_{N_\mathrm{e}a}(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \tau))^\intercal$$

is the *environmental map* at age a and it is a differentiable function of the individual's phenotype at that age (e.g., the individual's behaviour at age a may expose it to a particular environment), of the phenotype of social partners of any age (e.g., through social niche construction), and of evolutionary time due to slow exogenous environmental change (e.g., climate change). The environmental map $\mathbf{h}_a$ can also be a function of the population density of the resident ($\bar{\mathbf{n}}(t)$ defined below), but $\mathbf{h}_a$ is not a function of ecological time t in any other way. Consequently, the resident environment $\bar{\boldsymbol{\epsilon}}$ changes slowly: on the one hand, $\bar{\boldsymbol{\epsilon}}$ can change in ecological time through density dependence, but this dependence is evolutionarily immaterial in our analysis because, as is standard, we assume mutants arise when residents are at carrying capacity in which case the resident population density is at equilibrium; on the other hand, $\bar{\boldsymbol{\epsilon}}$ evolves over evolutionary time τ as it depends on τ indirectly through the resident phenotype and directly due to exogenous environmental change. We assume such limited environmental change to enable the resident population to reach carrying capacity to be able to use relatively simple techniques of evolutionary invasion analysis to derive selection gradients.

We call $\mathbf{m}_\bullet = (\mathbf{z}_\bullet; \boldsymbol{\epsilon}_\bullet)$ the metaphenotype (i.e., the aggregate of phenotype and environment) of a focal individual. Analogously, the metaphenotype of a resident is denoted without the bullet but with an overbar (e.g., $\bar{\mathbf{m}}$), and the metaphenotype of a mutant is denoted without the bullet or the overbar (e.g., $\mathbf{m}$).

We now describe the process of development. A focal individual's state variables at age $a+1$ satisfy the *developmental constraint* given by

$$\mathbf{x}_{a+1,\bullet} = \mathbf{g}_a(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{a\bullet}), \tag{2}$$

for all $a \in \{1, \ldots, N_\mathrm{a} - 1\}$ with initial condition $\mathbf{x}_{1\bullet} = \bar{\mathbf{x}}_1$ (provided that $N_\mathrm{a} > 1$). The function

$$\mathbf{g}_a(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{a\bullet}) = (g_{1a}(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{a\bullet}), \ldots, g_{N_\mathrm{s}a}(\mathbf{z}_{a\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{a\bullet}))^\intercal$$

is the *developmental map* (or genotype-phenotype map) at age a and it is a differentiable function of the individual's phenotype at that age, the phenotype of the individual's social partners which can be of any age, and the environment faced at that age (the term developmental function can be traced back to Gimelfarb 1982 through Wagner 1984; for the evolutionary implications of similar maps under non-overlapping generations see Mullon and Lehmann 2017, 2018). For simplicity, we assume that the state variables $\mathbf{x}_{1\bullet} = \bar{\mathbf{x}}_1$ at the initial age are constant, so they are not developmentally constrained and do not evolve. This assumption corresponds to the common assumption in life-history models that state variables at the initial age are given (Gadgil and Bossert 1970; Taylor *et al.* 1974; León 1976; Schaffer 1983; Sydsæter *et al.* 2008). A focal individual's developmental map across life is

$$\mathbf{g}(\mathbf{z}_\bullet, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_\bullet) = (\mathbf{g}_1(\mathbf{z}_{1\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{0\bullet}); \ldots; \mathbf{g}_{N_\mathrm{a}-1}(\mathbf{z}_{N_\mathrm{a}-1,\bullet}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{N_\mathrm{a}-1,\bullet})). \tag{3}$$

Then, the resident states can be written as $\bar{\mathbf{x}} = (\bar{\mathbf{x}}_1; \mathbf{g}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}))$.

Phases of the evolutionary cycle

We now formally describe the three phases in which we partition an evolutionary time step (Fig. 3). We start with the socio-devo stabilization dynamics phase, which yields the notions of socio-devo equilibrium and socio-devo stability.

Socio-devo stabilization dynamics occur as follows. For a resident phenotype $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$, new resident states $\mathbf{x}_\bullet$ are obtained from Eq. (2); the resulting $\mathbf{z}_\bullet$ is set as the new resident; and this is iterated. To write this formally, let θ denote time for the socio-devo stabilization dynamics. During the socio-devo stabilization phase, denote resident states at socio-devo time θ as $\bar{\mathbf{x}}(\theta)$. Then, writing $\bar{\mathbf{z}}$ in terms of its composing states and controls, the resident states at socio-devo time $\theta + 1$ are given by

$$\begin{aligned} &\bar{\mathbf{x}}_{a+1}(\theta+1) \\ &\quad = \mathbf{g}_a(\bar{\mathbf{x}}_a(\theta+1), \bar{\mathbf{y}}_a, \bar{\mathbf{x}}(\theta), \bar{\mathbf{y}}, \mathbf{h}_a(\bar{\mathbf{x}}_a(\theta+1), \bar{\mathbf{y}}_a, \bar{\mathbf{x}}(\theta), \bar{\mathbf{y}}, \tau)), \end{aligned} \tag{4}$$

for all $a \in \{1, \ldots, N_\mathrm{a} - 1\}$ and with given initial conditions $\bar{\mathbf{x}}(1)$ and $\bar{\mathbf{x}}_1(\theta+1) = \bar{\mathbf{x}}_1$. If $\lim_{\theta \to \infty} \bar{\mathbf{x}}(\theta)$ converges, this limit yields a socio-devo stable phenotype as defined below.

We say a phenotype $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$ is a socio-devo equilibrium if and only if $\bar{\mathbf{x}}$ is produced by development when everyone else in the population has that $\bar{\mathbf{z}}$ phenotype and everyone in the population experiences the same environment; specifically, a socio-devo equilibrium $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$ satisfies

$$\bar{\mathbf{x}}_{a+1} = \mathbf{g}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \mathbf{h}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \tau)), \tag{5}$$

for all $a \in \{1, \ldots, N_\mathrm{a} - 1\}$ with initial condition $\bar{\mathbf{x}}_1$. We assume that there is at least one socio-devo equilibrium for a given developmental map at evolutionary time τ.

It will be useful to note that if the resident phenotype is a socio-devo equilibrium, from Eqs. (1), (2), and (5), it follows that evaluation of the mutant controls at resident controls yields resident variables. That is, if $\bar{\mathbf{z}}$ is a socio-devo equilibrium, then

$$\begin{aligned} \mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}} &= \bar{\mathbf{x}} \\ \boldsymbol{\epsilon}|_{\mathbf{y}=\bar{\mathbf{y}}} &= \bar{\boldsymbol{\epsilon}} \\ \mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}} &= \bar{\mathbf{z}} \\ \mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}} &= \bar{\mathbf{m}}. \end{aligned}$$

Now, we say a phenotype $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$ is socio-devo stable (SDS) if and only if $\bar{\mathbf{z}}$ is a locally stable socio-devo equilibrium. A socio-devo equilibrium $\bar{\mathbf{z}} = (\bar{\mathbf{x}}; \bar{\mathbf{y}})$ is locally stable if and only if a marginally small deviation in the initial states $\bar{\mathbf{x}}(1)$ from the socio-devo equilibrium keeping the same controls leads the socio-devo stabilization dynamics to the same equilibrium. Thus, a socio-devo equilibrium $\bar{\mathbf{z}}$ is locally stable if all the eigenvalues of the matrix

$$\left.\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

have absolute value strictly less than one (Appendices 14 and 15). The requirement that this matrix has such eigenvalues arises naturally in the derivation of the evolutionary dynamics of states (Appendix 9). We assume that there is a unique SDS phenotype for a given developmental map at evolutionary time τ.

Once the SDS resident is reached in the socio-devo stabilization phase, we continue to the resident population dynamics phase (Fig. 3). Let the resident phenotype $\bar{\mathbf{z}}$ be SDS. Let $\bar{n}_a(t)$ denote the density of SDS resident individuals of age $a \in \{1, \dots, N_\mathrm{a}\}$ at ecological time t. The vector of resident density at t is $\bar{\mathbf{n}}(t) = (\bar{n}_1(t), \dots, \bar{n}_{N_\mathrm{a}}(t))^\intercal$. The life cycle is age-structured (Fig. 4). At age a, an SDS resident individual produces a number $A_{1a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ of offspring and survives to age $a+1$ with probability $A_{a+1,a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ (where we set $A_{N_\mathrm{a}+1,N_\mathrm{a}}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) = 0$ without loss of generality). The first argument of these two functions is the phenotype of the individual at that age, the second argument is the phenotype of the individual's social partners which can be of any age, and the third argument is density dependence. The SDS resident population thus has deterministic dynamics given by

$$\bar{\mathbf{n}}(t+1) = \mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))\bar{\mathbf{n}}(t), \tag{6}$$

where $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ is a density-dependent Leslie matrix whose entries $A_{ij}(\bar{\mathbf{z}}_j, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ give the age-specific survival probabilities and fertilities of SDS resident individuals; additionally, the first argument of $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ is the phenotype vector formed by the first argument of $A_{ij}(\bar{\mathbf{z}}_j, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ for all $i, j \in \{1, \dots, N_\mathrm{a}\}$. We assume that residents in the last age class reproduce (i.e., $A_{1N_\mathrm{a}}(\bar{\mathbf{z}}_{N_\mathrm{a}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) > 0$) and that residents can survive to the last age class with non-zero probability (i.e., $A_{a+1,a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) > 0$ for all $a \in \{1, \dots, N_\mathrm{a}-1\}$); this ensures that $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ is irreducible, with $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$ defined below (Sternberg 2010, section 9.4). We further assume that residents of at least two consecutive age classes have non-zero fertility (i.e., $A_{1a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) > 0$ and $A_{1,a+1}(\bar{\mathbf{z}}_{a+1}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) > 0$ for some $a \in \{1, \dots, N_\mathrm{a}-1\}$); this ensures that $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ is primitive (Sternberg 2010, section 9.4.1; i.e., raising $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ to a sufficiently high power yields a matrix whose entries are all positive). We assume that density dependence is such that the population dynamics of the SDS resident (Eq. 6) have a unique stable non-trivial equilibrium $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$ (a vector of non-negative entries some of which are positive), which solves

$$\bar{\mathbf{n}}^*(\bar{\mathbf{z}}) = \mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))\bar{\mathbf{n}}^*(\bar{\mathbf{z}}). \tag{7}$$

The sum of the entries of $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$ gives the carrying capacity, which depends on the SDS resident phenotype. From our assumptions rendering $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ irreducible and primitive and from the Perron-Frobenius theorem (Sternberg 2010, theorem 9.1.1), it follows that $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ has an eigenvalue $\bar{\lambda} = 1$ that is strictly greater than the absolute value of any other eigenvalue of the matrix. This $\bar{\lambda}$ describes the asymptotic growth rate of the resident population, as the resident population dynamics equilibrium $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$ is achieved.

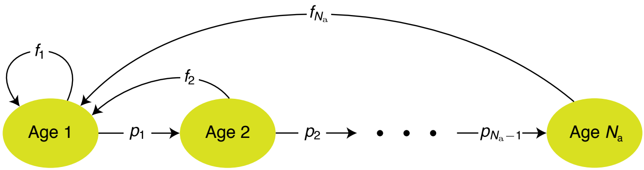

Figure 4 Age-structured life cycle. The vital rates shown are those of rare mutants: a mutant of age a produces f_a offspring and survives to age $a+1$ with probability p_a. See text for the vital rates of the resident.

Once the resident population has reached the equilibrium $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$, we move on to the resident-mutant population dynamics phase (Fig. 3). A rare mutant control $\mathbf{y}$ arises, where $\mathbf{y}$ is a realization of a multivariate random variable. A mutant has phenotype $\mathbf{z} = (\mathbf{x}; \mathbf{y})$ where the states $\mathbf{x}$ are given by the developmental constraint (Eq. 5); specifically, the states at age $a+1$ for an individual having the mutant control vector $\mathbf{y}$ are given by the developmental constraint

$$\mathbf{x}_{a+1} = \mathbf{g}_a(\mathbf{z}_a, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_a), \tag{8}$$

for all $a \in \{1, \dots, N_\mathrm{a}-1\}$ with initial condition $\mathbf{x}_1 = \bar{\mathbf{x}}_1$, where the mutant's environment is given by the environmental constraint

$$\boldsymbol{\epsilon}_a = \mathbf{h}_a(\mathbf{z}_a, \bar{\mathbf{z}}, \tau). \tag{9}$$

Let $n_a(t)$ denote the density of mutant individuals of age $a \in \{1, \dots, N_\mathrm{a}\}$ at ecological time t. The vector of mutant density at t is $\mathbf{n}(t) = (n_1(t), \dots, n_{N_\mathrm{a}}(t))^\intercal$. Given clonal reproduction, the population dynamics of the resident and rare mutant subpopulations are then given by the expanded system

$$\begin{pmatrix} \bar{\mathbf{n}}(t+1) \\ \mathbf{n}(t+1) \end{pmatrix} = \begin{pmatrix} \mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) & \mathbf{0} \\ \mathbf{0} & \mathbf{A}(\mathbf{z}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t)) \end{pmatrix} \begin{pmatrix} \bar{\mathbf{n}}(t) \\ \mathbf{n}(t) \end{pmatrix},$$

where the mutant projection matrix $\mathbf{A}(\mathbf{z}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ is given by evaluating the first argument of $\mathbf{A}(\bar{\mathbf{z}}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ at the mutant phenotype. Hence, $\mathbf{A}(\mathbf{z}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ is a density-dependent Leslie matrix whose ij-th entry is $A_{ij}(\mathbf{z}_j, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))$ that gives either the age-specific survival probability (for $i > 1$) or the age-specific fertility (for $i = 1$) of mutant individuals in the context of the resident. The rare mutant subpopulation thus has population dynamics given by $\mathbf{n}(t+1) = \mathbf{A}(\mathbf{z}, \bar{\mathbf{z}}, \bar{\mathbf{n}}(t))\mathbf{n}(t)$.

As mutants are rare, the mutant population dynamics around the resident equilibrium $\bar{\mathbf{n}}^*(\bar{\mathbf{z}})$ are to first order of approximation given by

$$\mathbf{n}(t+1) \approx \mathbf{J}\mathbf{n}(t), \tag{10}$$

where the local stability matrix for the mutant (Appendix 14) is

$$\mathbf{J} = \left.\frac{\partial \mathbf{A}(\mathbf{z}, \bar{\mathbf{z}}, \bar{\mathbf{n}})\mathbf{n}}{\partial \mathbf{n}^\intercal}\right|_{\mathbf{n}=\mathbf{n}^*} = \left(\frac{\partial}{\partial n_j} \sum_{k=1}^{N_\mathrm{a}} A_{ik}(\mathbf{z}_k, \bar{\mathbf{z}}, \bar{\mathbf{n}}) n_k \bigg|_{\bar{\mathbf{n}}=\bar{\mathbf{n}}^*} \right)$$
$$= \left(A_{ij}(\mathbf{z}_j, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}})) \right).$$

Explicitly,

$$\mathbf{J} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{N_\mathrm{a}-1} & f_{N_\mathrm{a}} \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & p_{N_\mathrm{a}-1} & 0 \end{pmatrix}, \tag{11}$$

where we denote the mutant's fertility at age a at the resident population dynamics equilibrium as

$$f_a = f_a(\mathbf{z}_a, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_a) = A_{1a}(\mathbf{z}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}})) \tag{12a}$$

and the mutant's survival probability from age a to $a+1$ as

$$p_a = p_a(\mathbf{z}_a, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_a) = A_{a+1,a}(\mathbf{z}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}})). \tag{12b}$$

We denote the fertility of a neutral mutant of age a as $f_a^\circ = f_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}_a) = A_{1a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$ and the survival probability of a neutral mutant from age a to $a+1$ as $p_a^\circ = p_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}_a) = A_{a+1,a}(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\mathbf{n}}^*(\bar{\mathbf{z}}))$, where the superscript $\circ$ denotes evaluation at $\mathbf{y} = \bar{\mathbf{y}}$ (so at $\mathbf{z} = \bar{\mathbf{z}}$ as the resident is a socio-devo equilibrium).

Evolutionary dynamics of controls

We can now identify invasion fitness and use it to obtain an equation describing the evolutionary dynamics of controls. Invasion fitness is the asymptotic growth rate of the mutant population and it enables the determination of whether the mutant invades the resident population (i.e., whether the mutation increases in frequency) (Otto and Day 2007). Because we assume that an individual's environment $\boldsymbol{\epsilon}_\bullet$ only depends on ecological time t through density dependence $\bar{\mathbf{n}}(t)$ and because $\mathbf{J}$ is evaluated at the resident equilibrium $\bar{\mathbf{n}}^*$, we have that $\mathbf{J}$ is constant with respect to t. Therefore, the asymptotic population dynamics of the mutant subpopulation around the resident equilibrium are given to first order of approximation by the eigenvalues and eigenvectors of $\mathbf{J}$. As for residents, we assume that mutants in the last age class reproduce ($f_{N_\mathrm{a}} > 0$) and that mutants can survive to the last age class with non-zero probability (i.e., $p_a > 0$ for all $a \in \{1, \dots, N_\mathrm{a} - 1\}$); so $\mathbf{J}$ is irreducible (Sternberg 2010, section 9.4). We similarly assume that mutants of at least two consecutive age classes have non-zero fertility (i.e., $f_a > 0$ and $f_{a+1} > 0$ for some $a \in \{1, \dots, N_\mathrm{a} - 1\}$); so $\mathbf{J}$ is primitive (Sternberg 2010, section 9.4.1; i.e., raising $\mathbf{J}$ to a sufficiently high power yields a matrix whose entries are all positive). Then, from the Perron-Frobenius theorem (Sternberg 2010, theorem 9.1.1), $\mathbf{J}$ has a real positive eigenvalue $\lambda = \lambda(\mathbf{y}, \bar{\mathbf{y}})$ whose magnitude is strictly larger than that of the other eigenvalues. Such leading eigenvalue λ is the asymptotic growth rate of the mutant population around the resident equilibrium, and thus gives the mutant's invasion fitness. Since the population dynamics of rare mutants are locally given by Eq. (10) where $\mathbf{J}$ projects the mutant population to the next ecological time step, the mutant population invades when invasion fitness satisfies $\lambda > 1$.

We consider the evolutionary change in controls from the evolutionary time τ, specifically the point at which the socio-devo stable resident is at carrying capacity as marked in Fig. 3, to the evolutionary time $\tau + \Delta\tau$ at which a new socio-devo stable resident is at carrying capacity. The vector $\mathbf{y}$ is a realization of a multivariate random variable $\mathbf{y}$ with probability density $M(\mathbf{y}, \bar{\mathbf{y}})$ called *the mutational distribution* (Dieckmann and Law 1996), with support in $\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}$ (abusing notation, we denote a random variable and its realization with the same symbol, as has been common practice—e.g., Lande 1979 and Lynch and Walsh 1998, p. 192). We assume that the mutational distribution is such that (i) the expected mutant control is the resident, $\mathrm{E}[\mathbf{y}] = \bar{\mathbf{y}}$; (ii) mutational variance is marginally small (i.e., selection is δ-weak) such that $0 < \mathrm{E}[||\mathbf{y} - \bar{\mathbf{y}}||^2] = \mathrm{tr}(\mathrm{cov}[\mathbf{y}, \mathbf{y}]) = \sum_{i=1}^{N_\mathrm{c}} \sum_{a=1}^{N_\mathrm{a}} \mathrm{E}[(y_{ia} - \bar{y}_{ia})^2] \ll 1$; and (iii) mutation is unbiased, that is, the mutational distribution is symmetric so skewness is $\mathrm{E}[(\mathbf{y} - \bar{\mathbf{y}})(\mathbf{y} - \bar{\mathbf{y}})^\intercal(\mathbf{y} - \bar{\mathbf{y}})] = \mathbf{0}$. Given small mutational variance, Taylor-expanding λ with respect to $\mathbf{y}$ around $\bar{\mathbf{y}}$, invasion fitness is to first order of approximation given by

$$\lambda = 1 + (\mathbf{y} - \bar{\mathbf{y}})^\intercal \left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} + O(||\mathbf{y} - \bar{\mathbf{y}}||^2), \tag{13}$$

where we use the fact that $\lambda|_{\mathbf{y}=\bar{\mathbf{y}}} = 1$ due to density dependence. A given entry of the operator $\mathrm{d}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$, say $\mathrm{d}/\mathrm{d}y_{ai}|_{\mathbf{y}=\bar{\mathbf{y}}}$, takes the total derivative with respect to y_{ia} while keeping all the other controls y_{jk} constant. Hence, we refer to $\mathrm{d}\lambda/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ as the *total selection gradient of controls* $\mathbf{y}$, which takes the total derivative considering both developmental constraints (Eq. 8) and environmental constraints (Eq. 9) (Appendix 16). Thus, the total selection gradient of controls can be interpreted as measuring *total genetic selection*. Since the mutant population invades when $\lambda > 1$ and mutational variances are marginally small (i.e., selection is δ-weak), the mutant population invades if and only if

$$(\mathbf{y} - \bar{\mathbf{y}})^\intercal \left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} > 0,$$

to first-order of approximation. The left-hand side of this inequality is the dot product of total selection on controls and the realized mutational effect on controls $(\mathbf{y} - \bar{\mathbf{y}})$. The dot product is positive if and only if the absolute value of the smallest angle between two non-zero vectors is smaller than 90 degrees. Hence, the mutant population invades if and only if total selection on controls has a vector component in the direction of the mutational effect on controls.

In Appendix 1, we show that the evolutionary dynamics of controls are given by a form of the canonical equation of adaptive dynamics:

$$\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \mathbf{G}_\mathbf{y} \left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{14a}$$

where

$$\mathbf{G}_\mathbf{y} = \mathrm{cov}[\mathbf{y}, \mathbf{y}] \tag{14b}$$

is equivalently the mutational covariance matrix (of controls) and the additive genetic covariance matrix of controls (cf. Eq. 6.1 of Dieckmann and Law 1996, Eq. 23 of Durinx *et al.* 2008, p. 332 of Fisher 1922, and Eq. 12 of Morrissey 2015). The canonical equation typically involves an additional scalar proportional to mutation rate and population size (cf. Eq. 6.1 of Dieckmann and Law 1996 and Eq. 23 of Durinx *et al.* 2008) but Eq. (14a) does not because of our assumption of deterministic population dynamics, consistently with previous results (e.g., Eqs. 6 and 25 of Wagner 1989).

From our definition of $\mathbf{y}$, $\mathbf{G}_\mathbf{y}$ is a block matrix whose aj-th block entry is the matrix $\mathbf{G}_{\mathbf{y}_a,\mathbf{y}_j} = \mathrm{cov}[\mathbf{y}_a, \mathbf{y}_j]$, which is the mutational or additive genetic cross-covariance matrix of the controls $\mathbf{y}_a$ at age a with the controls $\mathbf{y}_j$ at age j. In turn, the ik-th entry of $\mathbf{G}_{\mathbf{y}_a,\mathbf{y}_j}$ is $G_{y_{ia},y_{kj}} = \mathrm{cov}[y_{ia}, y_{kj}]$ which is the mutational or additive genetic covariance between the control y_{ia} and the control y_{kj}. Since $\mathbf{y} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times 1}$, then $\mathbf{G}_\mathbf{y} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}$.

Using a modification of the terminology of Houle (2001) and Klingenberg (2005, 2010), we say that there are no genetic constraints for a vector $\boldsymbol{\zeta}$ if and only if all the eigenvalues of its additive genetic covariance matrix $\mathbf{G}_{\boldsymbol{\zeta}}$ are equal and positive; that there are only relative genetic constraints if and only if $\mathbf{G}_{\boldsymbol{\zeta}}$ has different eigenvalues but all are positive; and that there are absolute genetic constraints if and only if $\mathbf{G}_{\boldsymbol{\zeta}}$ has at least one zero eigenvalue (i.e., $\mathbf{G}_\zeta$ is singular). If $\boldsymbol{\zeta} = \mathbf{y}$, we speak of mutational rather than genetic constraints. For example, we say there are absolute mutational constraints if and only if $\mathbf{G}_\mathbf{y}$ is singular, in which case there is no mutational variation in some directions of control space. Hence, if there are absolute mutational constraints (i.e., $\mathbf{G}_\mathbf{y}$ is singular), the evolutionary dynamics of controls can stop (i.e., $\Delta\bar{\mathbf{y}}/\Delta\tau = \mathbf{0}$) with a non-zero total selection gradient of controls (i.e., $\mathrm{d}\lambda/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$) (because a homogeneous system $\mathbf{A}\mathbf{x} = \mathbf{0}$ has non-zero solutions $\mathbf{x}$ with $\mathbf{A}$ singular if there is any solution to the system).

As the resident controls evolve, the resident state variables evolve. Specifically, at a given evolutionary time τ, from Eq. (8) resident states are given by the recurrence equation

$$\bar{\mathbf{x}}_{a+1} = \mathbf{g}_a^\circ = \mathbf{g}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}_a), \tag{14c}$$

for all $a \in \{1, \dots, N_\mathrm{a} - 1\}$ with $\bar{\mathbf{x}}_1$ constant and $\bar{\boldsymbol{\epsilon}}_a = \mathbf{h}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \tau)$. Intuitively, the evolutionary dynamics of states thus occur as an outgrowth of the evolutionary dynamics of controls and are modulated by the environmental dynamics.

Eq. (14a) describes the evolutionary dynamics of controls and Eq. (14c) describes the developmental dynamics of states, so together Eqs. (14) describe the evo-devo dynamics. To characterize the evo-devo process, we obtain general expressions for the total selection gradient of controls and for the evolutionary dynamics of the phenotype and the metaphenotype. To do this, we first derive the classical form of the selection gradient in age-structured populations, upon which we build our derivations.

Selection gradient in age-structured populations

To calculate the evo-devo dynamics given by Eqs. (14), we need to calculate the total selection gradient of controls $\mathrm{d}\lambda/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$. Since the life cycle is age structured (Eq. 11 and Fig. 4), the total selection gradient of controls has the form of the selection gradient in age structured populations, which is well-known but we re-derive it here for ease of reference.

We first use an eigenvalue perturbation theorem to write the selection gradient, which suggests a definition of relative fitness. Let $\bar{\zeta}$ and ζ respectively denote a resident and mutant trait value (or more specifically, $\bar{\zeta}$ is an entry of $\bar{\mathbf{m}}$ and ζ is an entry of $\mathbf{m}$). From a theorem on eigenvalue perturbation (Eq. 9 of Caswell 1978 or Eq. 9.10 of Caswell 2001), the selection gradient of ζ is

$$\begin{aligned}\left.\frac{\partial\lambda}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\mathbf{v}^{\circ\intercal}\left(\left.\frac{\partial\mathbf{J}}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right)\mathbf{u}^\circ \\ &= \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\sum_{i=1}^{N_\mathrm{a}}\sum_{j=1}^{N_\mathrm{a}} v_i^\circ\left(\left.\frac{\partial J_{ij}}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right)u_j^\circ,\end{aligned} \tag{15}$$

where $\mathbf{v}$ and $\mathbf{u}$ are respectively dominant left and right eigenvectors of $\mathbf{J}$ (Eq. 11). The vector $\mathbf{v}$ lists the mutant reproductive values and the vector $\mathbf{u}$ lists the mutant stable age distribution. In turn, $\mathbf{v}^\circ = \mathbf{v}|_{\mathbf{y}=\bar{\mathbf{y}}}$ lists the neutral (mutant) reproductive values and $\mathbf{u}^\circ = \mathbf{u}|_{\mathbf{y}=\bar{\mathbf{y}}}$ lists the neutral (mutant) stable age distribution. Substituting J_{ij} for the entries in Eq. (11) yields

$$\left.\frac{\partial\lambda}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\sum_{j=1}^{N_\mathrm{a}} u_j^\circ\left(v_1^\circ\left.\frac{\partial f_j}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} + v_{j+1}^\circ\left.\frac{\partial p_j}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right), \tag{16}$$

where we let $v_{N_\mathrm{a}+1} = 0$ without loss of generality. Eq. (15) motivates the definition of the relative fitness of a mutant individual per unit of generation time as

$$w = \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\mathbf{v}^{\circ\intercal}\mathbf{J}\mathbf{u}^\circ = \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\sum_{i=1}^{N_\mathrm{a}}\sum_{j=1}^{N_\mathrm{a}} v_i^\circ J_{ij} u_j^\circ \tag{17}$$

(cf. Lande 1982, his Eq. 12c) and of the relative fitness of a mutant individual of age j per unit of generation time as

$$w_j = \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}\sum_{i=1}^{N_\mathrm{a}} v_i^\circ J_{ij} u_j^\circ = \frac{1}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}u_j^\circ\left(v_1^\circ f_j + v_{j+1}^\circ p_j\right). \tag{18}$$

We now obtain that relative fitness depends on the so-called forces of selection, which decrease with age. Age-specific relative fitness (Eq. 18) depends on the neutral stable age distribution u_j° and the neutral reproductive value v_{j+1}°, which are well-known quantities but we re-derive them in Appendix 2 for ease of reference. We obtain that the neutral stable age distribution and neutral reproductive value are

$$u_j^\circ = \ell_j^\circ u_1^\circ \tag{19a}$$

$$v_j^\circ = \frac{1}{\ell_j^\circ}v_1^\circ\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ, \tag{19b}$$

for $j \in \{1, \dots, N_\mathrm{a}\}$ and where u_1° and v_1° can take any positive value. The quantity $\ell_j^\circ = \prod_{k=1}^{j-1} p_k^\circ$ is the survivorship of neutral mutants from age 1 to age j. Hence, the weights on fertility and survival in Eq. (18) are

$$\frac{u_j^\circ v_1^\circ}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ} = \frac{1}{T}\ell_j^\circ \tag{20a}$$

$$\frac{u_j^\circ v_{j+1}^\circ}{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ} = \frac{1}{T}\frac{1}{p_j^\circ}\sum_{k=j+1}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ, \tag{20b}$$

where generation time is

$$T = \sum_{j=1}^{N_\mathrm{a}} j\ell_j^\circ f_j^\circ \tag{21}$$

(Charlesworth 1994, Eq. 1.47c; Bulmer 1994, Eq. 25, Ch. 25; Bienvenu and Legendre 2015, Eqs. 5 and 12). Eqs. (19) and (20) recover classic equations (Hamilton 1966 and Caswell 1978, his Eqs. 11 and 12). We denote the forces of selection on fertility at age j as

$$\phi_j(\bar{\mathbf{z}}) = \ell_j^\circ \tag{22a}$$

and on survival at age j as

$$\pi_j(\bar{\mathbf{z}}) = \frac{1}{p_j^\circ}\sum_{k=j+1}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ, \tag{22b}$$

which are independent from the mutant trait value because they are evaluated at the resident trait value. It is easily checked that ϕ_j and π_j decrease with j (respectively, if $p_j^\circ < 1$ and $f_{j+1}^\circ > 0$ provided that p_j° changes smoothly with age).

We can then obtain a biologically informative expression for the selection gradient in terms relative fitness. Using Eqs. (18), (20), and (22), a mutant's relative fitness at age j is

$$w_j = \frac{1}{T}\left(\phi_j f_j + \pi_j p_j\right), \tag{23}$$

or with explicit arguments using Eq. (12),

$$w_j(\mathbf{z}_j, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_j) = \frac{1}{T}\left[\phi_j(\bar{\mathbf{z}})f_j(\mathbf{z}_j, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_j) + \pi_j(\bar{\mathbf{z}})p_j(\mathbf{z}_j, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_j)\right]. \tag{24}$$

Using Eqs. (17), (18), and (23), a mutant's relative fitness is

$$w = \sum_{j=1}^{N_\mathrm{a}} w_j = \frac{1}{T}\sum_{j=1}^{N_\mathrm{a}}\left(\phi_j f_j + \pi_j p_j\right), \tag{25}$$

or with explicit arguments,

$$w(\mathbf{z},\bar{\mathbf{z}},\boldsymbol{\epsilon}) = \sum_{j=1}^{N_{\mathrm{a}}} w_j(\mathbf{z}_j,\bar{\mathbf{z}},\boldsymbol{\epsilon}_j). \tag{26}$$

From Eqs. (15) and (17), the selection gradient entry for trait ζ is

$$\left.\frac{\partial\lambda}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\partial w}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_{\mathrm{a}}} \left.\frac{\partial w_j}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

The same procedure applies for total rather than partial derivatives, so the total selection gradient of ζ is

$$\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\mathrm{d}w}{\mathrm{d}\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_{\mathrm{a}}} \left.\frac{\mathrm{d}w_j}{\mathrm{d}\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{27}$$

It is often convenient to write selection gradients in terms of lifetime reproductive success if possible. In Appendix 3, we re-derive that the selection gradients can be expressed in terms of expected lifetime reproductive success, as previously known (Bulmer 1994; Caswell 2009), because of our assumption that mutants arise when residents are at carrying capacity (Mylius and Diekmann 1995). For our life cycle, a mutant's expected lifetime reproductive success is

$$R_0 = \sum_{j=1}^{N_{\mathrm{a}}} \ell_j f_j, \tag{28}$$

(Caswell 2001). In Appendix 3, we show that the selection gradient can be written as

$$\left.\frac{\partial\lambda}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{1}{T}\left.\frac{\partial R_0}{\partial\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{29a}$$

and that the total selection gradient can be written as

$$\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{1}{T}\left.\frac{\mathrm{d}R_0}{\mathrm{d}\zeta}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{29b}$$

which recover previous equations (Bulmer 1994, Eq. 25 of Ch. 5; and Caswell 2009, Eqs. 58-61).

Data Availability

All data necessary for confirming the conclusions of the article are present within the article, figures, tables, and appendices.

Results

We obtain a series of equations that describe the evolutionary dynamics of genetic and developed traits as well as the environment. Since developmental (Eq. 8) and environmental (Eq. 9) constraints are explicit, these equations provide formulas for genetic covariation and other high-level quantities from low-level mechanistic processes. We term the resulting set of equations the "evo-devo process". It is convenient to arrange the evo-devo process in a layered structure, where each layer is formed by components in layers below (Fig. 5). We thus present the evo-devo process starting from the lowest-level layer up to the highest. The derivations of all these equations are provided in the Appendices.

Layer 1: elementary components

All the components of the evo-devo process can be calculated from models or estimation of five elementary components. These elementary components are the mutational covariance matrix $\mathbf{G}_{\mathbf{y}}$, fertility $f_a(\mathbf{z}_a,\bar{\mathbf{z}},\boldsymbol{\epsilon}_a)$, survival probability $p_a(\mathbf{z}_a,\bar{\mathbf{z}},\boldsymbol{\epsilon}_a)$, developmental map $\mathbf{g}_a(\mathbf{z}_a,\bar{\mathbf{z}},\boldsymbol{\epsilon}_a)$, and environmental map $\mathbf{h}_a(\mathbf{z}_a,\bar{\mathbf{z}},\tau)$ for all ages a (Fig. 5, Layer 1).

Layer 2: direct effects

We now obtain the equations for the next layer, that of the direct-effect matrices which constitute nearly elementary components of the evo-devo process. Direct-effect matrices measure the effect that a variable has on another variable without considering any constraints. Direct-effect matrices capture various effects of age structure, including the declining forces of selection as age advances.

Direct-effect matrices include Lande's (1979) selection gradients, which have the following structure due to age-structure. The *selection gradient of states* or, equivalently, the block column vector of *direct effects of a mutant's states on fitness* is

$$\begin{aligned}\left.\frac{\partial w}{\partial \mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\left(\frac{\partial w}{\partial \mathbf{x}_1};\cdots;\frac{\partial w}{\partial \mathbf{x}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\partial w_1}{\partial \mathbf{x}_1};\cdots;\frac{\partial w_{N_{\mathrm{a}}}}{\partial \mathbf{x}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{a}}N_{\mathrm{s}}\times 1},\end{aligned} \tag{30}$$

which measures directional selection on developed traits (Lande 1979). Note that the second line in Eq. (30) takes the derivative of fitness at each age, which from Eq. (24) contains weighted fertility and survival effects of states at each age. Similarly, the *selection gradient of controls* or, equivalently, the block column vector of *direct effects of a mutant's controls on fitness* is

$$\begin{aligned}\left.\frac{\partial w}{\partial \mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\left(\frac{\partial w}{\partial \mathbf{y}_1};\cdots;\frac{\partial w}{\partial \mathbf{y}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\partial w_1}{\partial \mathbf{y}_1};\cdots;\frac{\partial w_{N_{\mathrm{a}}}}{\partial \mathbf{y}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{a}}N_{\mathrm{c}}\times 1},\end{aligned} \tag{31}$$

which measures directional selection on controls (Lande 1979). The *selection gradient of the environment* or, equivalently, the block column vector of *direct effects of a mutant's environment on fitness* is

$$\begin{aligned}\left.\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\left(\frac{\partial w}{\partial \boldsymbol{\epsilon}_1};\cdots;\frac{\partial w}{\partial \boldsymbol{\epsilon}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\partial w_1}{\partial \boldsymbol{\epsilon}_1};\cdots;\frac{\partial w_{N_{\mathrm{a}}}}{\partial \boldsymbol{\epsilon}_{N_{\mathrm{a}}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{a}}N_{\mathrm{e}}\times 1},\end{aligned} \tag{32}$$

which measures the environmental sensitivity of selection (Chevin *et al.* 2010). The selection gradients in Eqs. (30)–(32) capture the declining forces of selection in that increasingly rightward block entries have smaller magnitude if survival and fertility effects are of the same magnitude as age increases.

We use the above definitions to form the selection gradients of the phenotype and metaphenotype. The *selection gradient of the phenotype* is

$$\left.\frac{\partial w}{\partial \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial w}{\partial \mathbf{x}};\frac{\partial w}{\partial \mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{a}}(N_{\mathrm{s}}+N_{\mathrm{c}})\times 1},$$

and the *selection gradient of the metaphenotype* is

$$\left.\frac{\partial w}{\partial \mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial w}{\partial \mathbf{x}};\frac{\partial w}{\partial \mathbf{y}};\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{a}}(N_{\mathrm{s}}+N_{\mathrm{c}}+N_{\mathrm{e}})\times 1}.$$

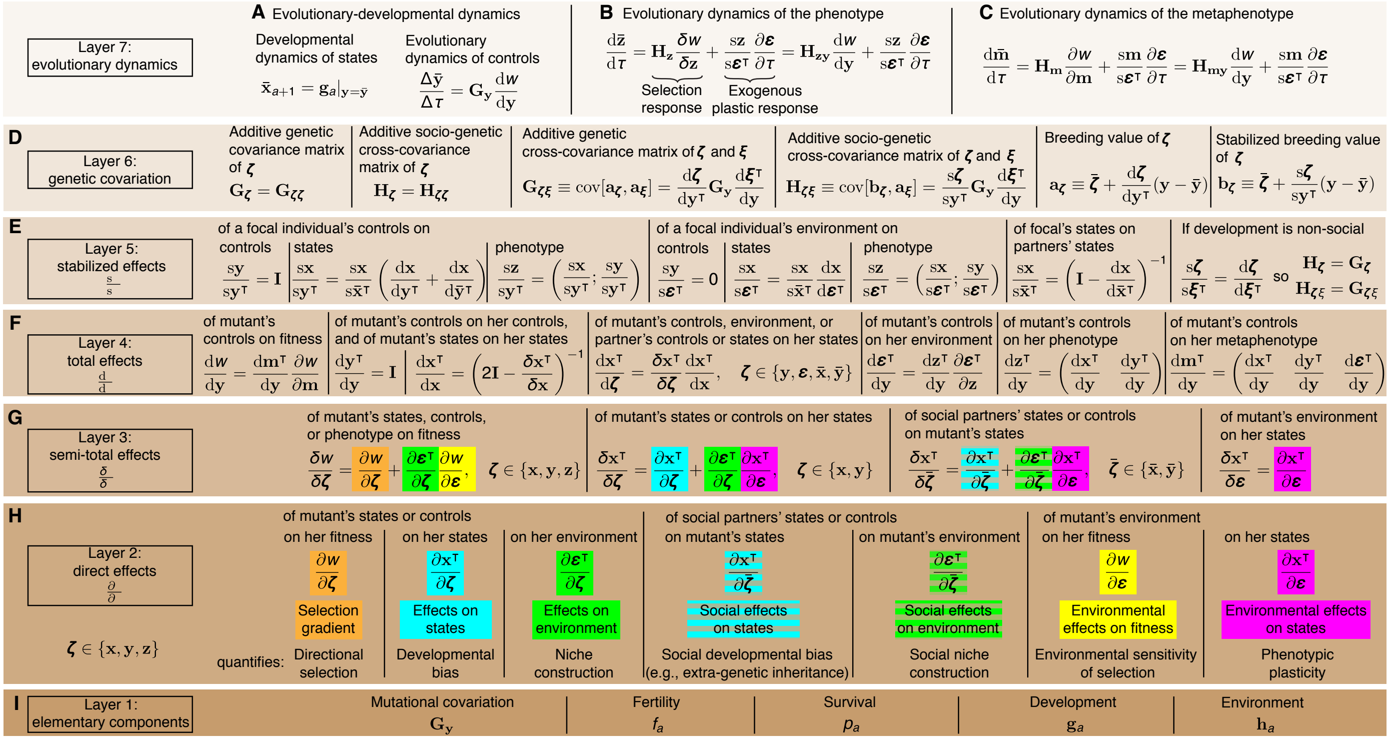

Figure 5 The evo-devo process and its layered structure. Here we summarize the equations composing the evo-devo process arranged in a layered structure. Each layer is formed by components in layers below. Layer 7 describes the evolutionary dynamics equivalently as (A) evo-devo dynamics, as (B) evolutionary dynamics of the phenotype, or as (C) evolutionary dynamics of the metaphenotype. (D) Layer 6 describes genetic covariation. (E) Layer 5 describes stabilized effects (total derivatives after socio-devo stabilization, denoted by s/s). (F) Layer 4 describes total effects (total derivatives before socio-devo stabilization, denoted by d/d, which consider both developmental and environmental constraints). (G) Layer 3 describes semi-total effects (semi-total derivatives, denoted by δ/δ, that is, total derivatives considering environmental but not developmental constraints). (H) Layer 2 describes direct effects (partial derivatives, denoted by ∂/∂, which do not consider any constraints). (I) Layer 1 comprises the elementary components of the evo-devo process that generate all layers above. All derivatives are evaluated at $\mathbf{y} = \bar{\mathbf{y}}$. See text for the equations of direct-effect matrices, which have structure due to age structure. See Fig. 2 and Table 1 for the meaning of symbols.

Direct-effect matrices also include matrices that measure developmental bias. These matrices have specific, sparse structure due to *the arrow of developmental time*: changing a trait at a given age cannot have effects on the developmental past of the individual and only directly affects the developmental present or immediate future. The block matrix of *direct effects of a mutant's states on her states* is

$$\left.\frac{\partial \mathbf{x}^\intercal}{\partial \mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial \mathbf{x}_1^\intercal}{\partial \mathbf{x}_1} & \cdots & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{x}_1}\\ \vdots & \ddots & \vdots \\ \frac{\partial \mathbf{x}_1^\intercal}{\partial \mathbf{x}_{N_a}} & \cdots & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{x}_{N_a}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \mathbf{I} & \frac{\partial \mathbf{x}_2^\intercal}{\partial \mathbf{x}_1} & \cdots & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I} & \cdots & \mathbf{0} & \mathbf{0}\\ \vdots & \vdots & \ddots & \vdots & \vdots\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{I} & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{x}_{N_a-1}}\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{I}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_a N_s \times N_a N_s}, \tag{33a}$$

which can be understood as measuring developmental bias from states. The equality (33a) follows because the direct effects of a mutant's states on her states are only non-zero at the next age (from the developmental constraint in Eq. 8) or when states are differentiated with respect to themselves. Analogously, the block matrix of *direct effects of a mutant's controls on her states* is

$$\left.\frac{\partial \mathbf{x}^\intercal}{\partial \mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial \mathbf{x}_1^\intercal}{\partial \mathbf{y}_1} & \cdots & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{y}_1}\\ \vdots & \ddots & \vdots \\ \frac{\partial \mathbf{x}_1^\intercal}{\partial \mathbf{y}_{N_a}} & \cdots & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{y}_{N_a}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \mathbf{0} & \frac{\partial \mathbf{x}_2^\intercal}{\partial \mathbf{y}_1} & \cdots & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0}\\ \vdots & \vdots & \ddots & \vdots & \vdots\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\partial \mathbf{x}_{N_a}^\intercal}{\partial \mathbf{y}_{N_a-1}}\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_a N_c \times N_a N_s}, \tag{33b}$$

which can be understood as measuring developmental bias from controls. Note that the main block diagonal is zero.

Direct-effect matrices also include a matrix measuring plasticity. Indeed, the block matrix of *direct effects of a mutant's environment on her states* is

$$\begin{aligned}\left.\frac{\partial \mathbf{x}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\partial \mathbf{x}_1^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\partial \mathbf{x}_1^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{0} & \frac{\partial \mathbf{x}_2^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad \text{(33c)} \\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e} \times N_\mathrm{a}N_\mathrm{s}},\end{aligned}$$

which can be understood as measuring plasticity (Noble *et al.* 2019).

In turn, direct-effect matrices include matrices describing niche construction. The block matrix of *direct effects of a mutant's states or controls on her environment* is

$$\begin{aligned}\left.\frac{\partial \boldsymbol{\epsilon}^{\mathsf{T}}}{\partial \boldsymbol{\zeta}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_1} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_1} \\ \vdots & \ddots & \vdots \\ \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_{N_\mathrm{a}}} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_1} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}_2^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_2} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}-1}^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_{N_\mathrm{a}-1}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\zeta}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad \text{(33d)}\end{aligned}$$

for $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}\}$, which can be understood as measuring niche construction by states or controls. The equality (33d) follows from the environmental constraint in Eq. (9) since the environment faced by a mutant at a given age is directly affected by mutant states or controls at the same age only (i.e., $\partial \boldsymbol{\epsilon}_j^{\mathsf{T}} / \partial \boldsymbol{\zeta}_a = \mathbf{0}$ for $a \neq j$).

Direct-effect matrices also include matrices describing mutual environmental dependence. The block matrix of *direct effects of a mutant's environment on itself* is

$$\begin{aligned}\left.\frac{\partial \boldsymbol{\epsilon}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_1} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}_2^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_2} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}-1}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}-1}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \mathbf{I} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e} \times N_\mathrm{a}N_\mathrm{e}}, \qquad \text{(34)}\end{aligned}$$

which measures mutual environmental dependence. The second-to-last equality follows from the environmental constraint (Eq. 9) and the last equality follows from our assumption that environmental variables are mutually independent, so $\partial \boldsymbol{\epsilon}_a^{\mathsf{T}} / \partial \boldsymbol{\epsilon}_a |_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{I}$ for all $a \in \{1, \ldots, N_\mathrm{a}\}$. It is conceptually useful to write $\partial \boldsymbol{\epsilon}^{\mathsf{T}} / \partial \boldsymbol{\epsilon} |_{\mathbf{y}=\bar{\mathbf{y}}}$ rather than only $\mathbf{I}$, and we do so throughout.

Additionally, direct-effect matrices include matrices describing social developmental bias, which capture effects of extra-genetic inheritance and indirect genetic effects. The block matrix of *direct effects of social partners' states or controls on a mutant's states* is

$$\begin{aligned}\left.\frac{\partial \mathbf{x}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\partial \mathbf{x}_1^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} \\ \vdots & \ddots & \vdots \\ \frac{\partial \mathbf{x}_1^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{0} & \frac{\partial \mathbf{x}_2^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} \\ \mathbf{0} & \frac{\partial \mathbf{x}_2^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_2} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_2} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \frac{\partial \mathbf{x}_2^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} & \cdots & \frac{\partial \mathbf{x}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad \text{(35)}\end{aligned}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$, where the equality follows because states $\mathbf{x}_1$ at the initial age are constant. The matrix in Eq. (35) can be understood as measuring social developmental bias from either states or controls, including extra-genetic inheritance and indirect genetic effects. This matrix can be less sparse than previous direct-effect matrices because the mutant's states can be affected by the states or controls of social partners of *any* age.

Direct-effect matrices also include matrices describing social niche construction. The block matrix of *direct effects of social partners' states or controls on a mutant's environment* is

$$\left.\frac{\partial \boldsymbol{\epsilon}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_1} \\ \vdots & \ddots & \vdots \\ \frac{\partial \boldsymbol{\epsilon}_1^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} & \cdots & \frac{\partial \boldsymbol{\epsilon}_{N_\mathrm{a}}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad \text{(36)}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$, which can be understood as measuring social niche construction by either states or controls. This matrix does not contain any zero entries in general because the mutant's environment at any age can be affected by the states or controls of social partners of any age.

We use the above definitions to form direct-effect matrices measuring niche construction by the phenotype and social niche construction by partners' phenotypes. The block matrix of *direct effects of a mutant's phenotype on her environment* is

$$\left.\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \mathbf{x}}; \frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{e}}, \tag{37}$$

which measures niche construction by the phenotype. The block matrix of *direct effects of social partners' phenotypes on a mutant's environment* is

$$\left.\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \bar{\mathbf{z}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \bar{\mathbf{x}}}; \frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \bar{\mathbf{y}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{e}}, \tag{38}$$

which measures social niche construction by partners' phenotypes.

We will see that the evolutionary dynamics of the environment depends on a matrix measuring "inclusive" niche construction. This matrix is the transpose of the matrix of *direct social effects of a focal individual's phenotype on hers and a partner's environment*

$$\left.\frac{\partial (\boldsymbol{\epsilon}+\check{\boldsymbol{\epsilon}})}{\partial \mathbf{z}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{z}^{\intercal}} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{z}}^{\intercal}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}, \tag{39}$$

where we denote by $\check{\boldsymbol{\epsilon}}$ the environment a resident experiences when she develops in the context of mutants (a donor perspective for the mutant). Thus, this matrix can be interpreted as inclusive niche construction by the phenotype. Note that the second term on the right-hand side of Eq. (39) is the direct effects of social partners' phenotypes on a focal mutant (a recipient perspective for the mutant). Thus, inclusive niche construction by the phenotype can be equivalently interpreted either from a donor or a recipient perspective.

Layer 3: semi-total effects

We now proceed to obtain the equations of the next layer of the evo-devo process, that of semi-total effects. Semi-total-effect matrices measure the total effects that a variable has on another variable considering environmental constraints, without considering developmental constraints (Appendix 16).

Semi-total-effect matrices include semi-total selection gradients, which capture some of the effects of niche construction. The *semi-total selection gradient* of vector $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}\}$ is

$$\left.\frac{\delta w}{\delta \boldsymbol{\zeta}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial w}{\partial \boldsymbol{\zeta}} + \frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \boldsymbol{\zeta}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{40}$$

Thus, the semi-total selection gradient of $\boldsymbol{\zeta}$ depends on directional selection on $\boldsymbol{\zeta}$, niche construction by $\boldsymbol{\zeta}$, and environmental sensitivity of selection, without considering developmental constraints. Consequently, semi-total selection gradients measure semi-total selection, which is directional selection in the fitness landscape modified by the interaction of niche construction and environmental sensitivity of selection.

Semi-total selection on the environment equals directional selection on the environment because we assume environmental variables are mutually independent. The *semi-total selection gradient of the environment* is

$$\left.\frac{\delta w}{\delta \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \boldsymbol{\epsilon}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times 1}. \tag{41}$$

Given our assumption that environmental variables are mutually independent, the matrix of direct effects of the environment on itself is the identity matrix. Thus, the semi-total selection gradient of the environment equals the selection gradient of the environment.

Semi-total-effect matrices also include matrices describing semi-total developmental bias, which capture additional effects of niche construction. The block matrix of *semi-total effects of* $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \bar{\mathbf{x}}, \bar{\mathbf{y}}\}$ *on a mutant's states* is

$$\left.\frac{\delta \mathbf{x}^{\intercal}}{\delta \boldsymbol{\zeta}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial \mathbf{x}^{\intercal}}{\partial \boldsymbol{\zeta}} + \frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \boldsymbol{\zeta}}\frac{\partial \mathbf{x}^{\intercal}}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{42}$$

Thus, the semi-total effects of $\boldsymbol{\zeta}$ on states depend on the developmental bias from $\boldsymbol{\zeta}$, niche construction by $\boldsymbol{\zeta}$, and plasticity, without considering developmental constraints. Consequently, semi-total effects on states can be interpreted as measuring semi-total developmental bias, which measures developmental bias in the developmental process modified by the interaction of niche construction and plasticity.

Finally, semi-total-effect matrices include matrices describing semi-total plasticity, which equals plasticity because environmental variables are mutually independent. The block matrix of *semi-total effects of a mutant's environment on her states* is

$$\left.\frac{\delta \mathbf{x}^{\intercal}}{\delta \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \boldsymbol{\epsilon}}\frac{\partial \mathbf{x}^{\intercal}}{\partial \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{s}}. \tag{43}$$

Given our assumption that environmental variables are mutually independent, the matrix of direct effects of the environment on itself is the identity matrix. Thus, the semi-total effects of the environment on the states, or semi-total plasticity, equal the direct effects of the environment on states, that is, plasticity.

Layer 4: total effects

We now move to obtain equations for the next layer of the evo-devo process, that of total-effect matrices. Total-effect matrices measure the total effects of a variable on another one considering both developmental and environmental constraints, but before the effects of social development have stabilized in the population.

The total effects of states on themselves describe developmental feedback. The block matrix of *total effects of a mutant's states on her states* is

$$\left.\frac{\mathrm{d}\mathbf{x}^{\intercal}}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(2\mathbf{I} - \frac{\delta \mathbf{x}^{\intercal}}{\delta \mathbf{x}}\right)^{-1}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{a=1}^{N_\mathrm{a}}\left(\frac{\delta \mathbf{x}^{\intercal}}{\delta \mathbf{x}} - \mathbf{I}\right)^{a-1} \tag{44}$$
$$\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}},$$

which we prove is always invertible (Appendix 4, Eq. A32). This matrix can be interpreted as a lifetime collection of developmentally immediate pulses of semi-total effects of states on themselves. Thus, total effects of states on themselves describe total developmental bias from states, or *developmental feedback* which may cause major phenotypic effects at subsequent ages. By depending on semi-total developmental bias from states, developmental feedback depends on developmental bias from states, niche-construction by states, and plasticity (Eq. 42). Eq. (44) has the same form of an equation provided by Morrissey (2014) for his total-effect matrix of traits on themselves (his Eq. 2) if there is no plasticity or niche construction by states.

The total effects of controls on states correspond to Wagner's developmental matrix. The block matrix of *total effects of a mutant's controls on her states* is given by

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{y}}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{s}}, \tag{45}$$

which is singular because initial states are not affected by any control and final controls do not affect any state (so $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has rows and columns that are zero; Appendix 5, Eq. A54). From Eq. (45), this matrix can be interpreted as involving a developmentally immediate pulse caused by a change in controls followed by the developmental feedback triggered among states. The matrix of total effects of controls on states measures total developmental bias from controls and corresponds to Wagner's (1984, 1989) developmental matrix (his $\mathbf{B}$) (see also Martin 2014).

The total effects of the environment on states measure total plasticity. The block matrix of *total effects of a mutant's environment on her states* is

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\delta\mathbf{x}^\intercal}{\delta\boldsymbol{\epsilon}}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{s}}, \tag{46}$$

which measures total plasticity, considering both environmental and developmental constraints. Thus, total plasticity can be interpreted as a developmentally immediate pulse of plastic change followed by the developmental feedback triggered among states.

The total effects of social partners' controls or states on states measure total social developmental bias. The block matrix of *total effects of social partners' states or controls on a mutant's states* is

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\bar{\boldsymbol{\zeta}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\delta\mathbf{x}^\intercal}{\delta\bar{\boldsymbol{\zeta}}}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{47}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$. This matrix can be interpreted as measuring total social developmental bias from states or controls, as well as total effects on states of extra-genetic inheritance, and total indirect genetic effects. From Eq. (47), total social developmental bias can be interpreted as a developmentally immediate pulse caused by a change in social partners' traits followed by the developmental feedback triggered among the mutant's states.

Total effects on controls are simple since controls are open-loop. The block matrix of *total effects of a mutant's controls on themselves* is

$$\left.\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{I} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}, \tag{48}$$

and the block matrix of *total effects of a vector* $\boldsymbol{\zeta} \in \{\mathbf{x}, \boldsymbol{\epsilon}, \bar{\mathbf{x}}, \bar{\mathbf{y}}, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}, \bar{\mathbf{m}}\}$ *on a mutant's controls* is

$$\left.\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\boldsymbol{\zeta}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}.$$

These two equations follow because controls are open-loop (Appendix 5, Eq. A51).

Total effects of states and controls on the environment quantify total niche construction. Total niche construction by states is quantified by the block matrix of *total effects of a mutant's states on her environment*

$$\begin{aligned}\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{e}},\end{aligned} \tag{49}$$

which can be interpreted as showing that developmental feedback of states occurs first and then direct niche-constructing effects by states follow. Similarly, total niche construction by controls is quantified by the block matrix of *total effects of a mutant's controls on her environment*

$$\begin{aligned}\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}} + \frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{e}},\end{aligned} \tag{50}$$

which depends on niche construction by controls and on total developmental bias from controls followed by niche construction by states. The analogous relationship holds for total niche construction by the phenotype, quantified by the block matrix of *total effects of a mutant's phenotype on her environment*

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{e}}, \tag{51}$$

which depends on developmental feedback across the phenotype and niche construction by the phenotype.

Total effects of the environment on itself quantify environmental feedback. The block matrix of *total effects of a mutant's environment on her environment* is

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\boldsymbol{\epsilon}} + \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{e}}, \tag{52}$$

measuring *environmental feedback*, which includes mutual environmental dependence plus total plasticity followed by niche construction by states.

We can use some of the previous total-effect matrices to construct the following total-effect matrices. The block matrix of *total effects of a mutant's states on her phenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{x}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})},\end{aligned} \tag{53}$$

measuring total developmental bias from states on the phenotype. The block matrix of *total effects of controls on her phenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})},\end{aligned} \tag{54}$$

measuring total developmental bias from controls on the phenotype. When we later consider additive genetic covariances, it will be important that this matrix $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{y}$ is singular since it has fewer rows than columns (Horn and Johnson 2013, p. 14).

The block matrix of *total effects of a mutant's phenotype on her phenotype* is

$$\left.\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{x}}\\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0}\\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{55}$$

$$\in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})},$$

which can be interpreted as measuring developmental feedback across the phenotype. Since $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is square and block lower triangular, and since $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular (Appendix 4, Eq. A32), we have that $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular.

The block matrix of *total effects of a mutant's states on her metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{x}} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (56)\\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned}$$

measuring total developmental bias from states on the metaphenotype. The block matrix of *total effects of a mutant's controls on her metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (57)\\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned}$$

measuring total developmental bias from controls on the metaphenotype, and which is singular because it has fewer rows than columns.

The block matrix of *total effects of a mutant's environment on her metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (58)\\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned}$$

measuring total plasticity of the metaphenotype. The block matrix of *total effects of a mutant's phenotype on her metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{x}} \\ \frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (59)\\ &\in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned}$$

measuring total developmental bias from the phenotype on the metaphenotype. The block matrix of *total effects of a mutant's metaphenotype on her metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{x}} \\ \frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{y}} \\ \frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (60)\\ &\in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned}$$

measuring developmental feedback across the metaphenotype, and which we show is non-singular (Appendix 12).

We will see that the evolutionary dynamics of developed traits depends on a matrix measuring "inclusive" total developmental bias. This matrix is the transpose of the matrix of *total social effects of a focal individual's controls or states on hers and a partner's states*

$$\left.\frac{\mathrm{d}(\mathbf{x}+\check{\mathbf{x}})}{\mathrm{d}\boldsymbol{\zeta}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\zeta}^\intercal} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\boldsymbol{\zeta}}^\intercal}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad (61)$$

for $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}\}$ where we denote by $\check{\mathbf{x}}$ the states that a resident develops in the context of mutants (a donor perspective for the mutant). Thus, this matrix can be interpreted as measuring inclusive total developmental bias. Note that the second term on the right-hand side of Eq. (61) is the total effects of social partners' states or controls on a focal mutant (a recipient perspective for the mutant). Thus, inclusive total developmental bias can be equivalently interpreted either from a donor or a recipient perspective.

Having written expressions for the above total-effect matrices, we can now write the total selection gradients, which measure directional selection considering both developmental and environmental constraints. In Appendices 4-8, we show that the total selection gradient of vector $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}, \boldsymbol{\epsilon}, \mathbf{m}\}$ is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\boldsymbol{\zeta}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\boldsymbol{\zeta}}\frac{\partial w}{\partial \mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad (62)$$

which has the form of the chain rule in matrix notation. Hence, the total selection gradient of $\boldsymbol{\zeta}$ depends on directional selection on the metaphenotype and the total effects of $\boldsymbol{\zeta}$ on the metaphenotype. Consequently, the total selection gradient of $\boldsymbol{\zeta}$ measures total selection on $\boldsymbol{\zeta}$, which is directional selection on the metaphenotype transformed by the total effects of $\boldsymbol{\zeta}$ on the metaphenotype considering developmental and environmental constraints. Total selection gradients closely correspond to Morrissey's (2014, 2015) notion of extended selection gradient (denoted by him as $\boldsymbol{\eta}$). Total selection gradients take the following particular forms.

The total selection gradient of states is

$$\begin{aligned}\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial w}{\partial \mathbf{x}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (63)\\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\delta w}{\delta \mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\delta w}{\delta \mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial w}{\partial \mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

This gradient depends on directional selection on states (Eq. 30) and directional selection on the environment (Eq. 32). It also depends on developmental feedback (Eq. 44) and total niche construction by states, which also depends on developmental feedback (Eq. 49). Consequently, the total selection gradient of states can be interpreted as measuring total selection on developed traits in the fitness landscape modified by developmental feedback and by the interaction of total niche construction and environmental sensitivity of selection.

The total selection gradient of controls is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\partial w}{\partial \mathbf{x}} + \frac{\partial w}{\partial \mathbf{y}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (64)$$

$$\begin{aligned}
&= \left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} \frac{\delta w}{\delta \mathbf{x}} + \frac{\delta w}{\delta \mathbf{y}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}} \frac{\delta w}{\delta \mathbf{z}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{y}} \frac{\partial w}{\partial \mathbf{m}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{y}} \frac{\mathrm{d} w}{\mathrm{d} \mathbf{x}} + \frac{\delta w}{\delta \mathbf{y}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .
\end{aligned}$$

This gradient not only depends on directional selection on states and the environment, but also on directional selection on controls (Eq. 31). It also depends on Wagner's (1984, 1989) developmental matrix (Eq. 45) and on total niche construction by controls, which also depends on the developmental matrix (Eq. 50). Consequently, the total selection gradient of controls can be interpreted as measuring total genetic selection in a fitness landscape modified by the interaction of total developmental bias from controls and directional selection on developed traits and by the interaction of total niche construction by controls and environmental sensitivity of selection.

To derive equations describing the evolutionary dynamics of the metaphenotype, we make use of the total selection gradient of the environment, although such gradient is not necessary to obtain equations describing the evolutionary dynamics of the phenotype. The total selection gradient of the environment is

$$\begin{aligned}
\frac{\mathrm{d}w}{\mathrm{d}\boldsymbol{\epsilon}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\partial w}{\partial \mathbf{x}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\partial w}{\partial \boldsymbol{\epsilon}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (65) \\
&= \left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\delta w}{\delta \mathbf{x}} + \frac{\delta w}{\delta \boldsymbol{\epsilon}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\partial w}{\partial \mathbf{m}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\delta\mathbf{x}^\intercal}{\delta\boldsymbol{\epsilon}} \frac{\mathrm{d} w}{\mathrm{d} \mathbf{x}} + \frac{\delta w}{\delta \boldsymbol{\epsilon}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .
\end{aligned}$$

This gradient depends on total plasticity and on environmental feedback, which in turn depends on total plasticity and niche construction by states (Eq. 52). Consequently, the total selection gradient of the environment can be understood as measuring total selection on the environment in a fitness landscape modified by environmental feedback and by the interaction of total plasticity and directional selection on developed traits.

We can combine our expressions for the total selection gradients of states ($\mathbf{x}$) and controls ($\mathbf{y}$) into the total selection gradient of the phenotype ($\mathbf{z} = (\mathbf{x};\mathbf{y})$). The total selection gradient of the phenotype is

$$\begin{aligned}
\frac{\mathrm{d}w}{\mathrm{d}\mathbf{z}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}} \frac{\partial w}{\partial \mathbf{z}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{z}} \frac{\partial w}{\partial \boldsymbol{\epsilon}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \qquad (66) \\
&= \left(\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}} \frac{\delta w}{\delta \mathbf{z}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{z}} \frac{\partial w}{\partial \mathbf{m}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .
\end{aligned}$$

Thus, the total selection gradient of the phenotype can be interpreted as measuring total phenotypic selection in a fitness landscape modified by developmental feedback across the phenotype and by the interaction of total niche construction by the phenotype and environmental sensitivity of selection. In turn, the total selection gradient of the metaphenotype is

$$\frac{\mathrm{d}w}{\mathrm{d}\mathbf{m}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{m}} \frac{\partial w}{\partial \mathbf{m}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad (67)$$

which can be interpreted as measuring total metaphenotypic selection in a fitness landscape modified by developmental feedback across the metaphenotype.

Layer 5: stabilized effects

We now move on to obtain equations for the next layer of the evo-devo process, that of stabilized-effect matrices. Stabilized-effect matrices measure the total effects of a variable on another one considering both developmental and environmental constraints, now after the effects of social development have stabilized in the population. Stabilized-effect matrices arise in the derivation of the evolutionary dynamics of states and environment as a result of social development. If development is not social (i.e., $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$), then all stabilized-effect matrices ($\mathrm{s}\boldsymbol{\zeta}^\intercal/\mathrm{s}\boldsymbol{\xi}|_{\mathbf{y}=\bar{\mathbf{y}}}$) except one ($\mathrm{s}\mathbf{x}^\intercal/\mathrm{s}\bar{\mathbf{x}}|_{\mathbf{y}=\bar{\mathbf{y}}}$) reduce to corresponding total-effect matrices ($\mathrm{d}\boldsymbol{\zeta}^\intercal/\mathrm{d}\boldsymbol{\xi}|_{\mathbf{y}=\bar{\mathbf{y}}}$).

The stabilized effects of a focal individual's states on social partners' states measure social feedback. The transpose of the matrix of *stabilized effects of a focal individual's states on social partners' states* is

$$\begin{aligned}
\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\mathbf{I} - \frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \right)^{-1} = \left(\mathbf{I} - \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \right)^{-1} \\
&= \sum_{\theta=1}^{\infty} \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal} \right)^{\theta-1}\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}}, \qquad (68)
\end{aligned}$$

where the last equality follows by the geometric series of matrices. The matrix $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is invertible by our assumption that all eigenvalues of $\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ have absolute value strictly less than one, to guarantee that the resident is socio-devo stable. The matrix $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ can be interpreted as as a collection of total effects of a focal individual's states on social partners' states over socio-devo stabilization (Eq. 4); or vice versa, of social partners' states on a focal individual's states. Thus, the matrix $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ describes *social feedback* arising from social development. This matrix closely corresponds to an analogous matrix found in the indirect genetic effects literature (Moore *et al.* 1997, Eq. 19b and subsequent text). If development is not social from states (i.e., $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\bar{\mathbf{x}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$), then the matrix $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is the identity matrix. This is the only stabilized-effect matrix that does not reduce to the corresponding total-effect matrix when development is not social.

The stabilized effects of a focal individual's states or controls on her states measure stabilized developmental bias. We define the transpose of the matrix of *stabilized effects of a focal individual's states or controls on states* as

$$\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\zeta}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}(\mathbf{x}+\check{\mathbf{x}})}{\mathrm{d}\boldsymbol{\zeta}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \qquad (69a)$$

for $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}\}$. This matrix can be interpreted as measuring stabilized developmental bias from $\boldsymbol{\zeta}$, where a focal individual's controls or states first affect the development of her own and social partners' states which then feedback to affect the individual's states. Stabilized developmental bias is "inclusive" in that it includes both the effects of the focal individual on herself and on social partners. Note that if development is not social (i.e., $\mathrm{d}\mathbf{x}^\top/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$), then a stabilized developmental bias matrix ($\mathrm{s}\mathbf{x}/\mathrm{s}\boldsymbol{\zeta}^\top|_{\mathbf{y}=\bar{\mathbf{y}}}$) reduces to the corresponding total developmental bias matrix ($\mathrm{d}\mathbf{x}/\mathrm{d}\boldsymbol{\zeta}^\top|_{\mathbf{y}=\bar{\mathbf{y}}}$).

The stabilized effects of the environment on states measure stabilized plasticity. The transpose of the matrix of *stabilized effects of a focal individual's environment on states* is

$$\left.\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\top}\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\epsilon}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{e}}. \tag{69b}$$

This matrix can be interpreted as measuring stabilized plasticity, where the environment first causes total plasticity in a focal individual and then the focal individual causes stabilized social effects on social partners. Stabilized plasticity does not consider inclusive effects of the environment. If development is not social (i.e., $\mathrm{d}\mathbf{x}^\top/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$), then stabilized plasticity reduces to total plasticity.

The stabilized effects on controls are simple since controls are open-loop. The transpose of the matrix of *stabilized effects of a focal individual's states or environment on controls* is

$$\left.\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\zeta}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}\boldsymbol{\zeta}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}, \tag{70a}$$

for $\boldsymbol{\zeta} \in \{\mathbf{x}, \boldsymbol{\epsilon}\}$ and the transpose of the matrix of *stabilized effects of a focal individual's controls on controls* is

$$\left.\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}\mathbf{y}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{I} \quad \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}. \tag{70b}$$

These two equations follow because controls are open-loop.

The stabilized effects of states or controls on the environment measure stabilized niche construction. Although the matrix

$$\left.\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{x}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

appears in some of the matrices we construct, it is irrelevant as it disappears in the matrix products we encounter. The following matrix does not disappear. The transpose of the matrix of *stabilized effects of a focal individual's controls on the environment* is

$$\left.\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial(\boldsymbol{\epsilon}+\check{\boldsymbol{\epsilon}})}{\partial\mathbf{z}^\top}\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{c}}, \tag{71a}$$

which is formed by stabilized developmental bias from controls on the phenotype followed by inclusive niche construction by the phenotype. This matrix can be interpreted as measuring stabilized niche construction by controls. Note that if development is not social (i.e., $\mathrm{d}\mathbf{x}^\top/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$), then stabilized niche construction by controls reduces to total niche construction by controls (see Eqs. 50 and 39).

The stabilized effects of the environment on itself measure stabilized environmental feedback. The transpose of the matrix of *stabilized effects of a focal individual's environment on the environment* is

$$\left.\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial(\boldsymbol{\epsilon}+\check{\boldsymbol{\epsilon}})}{\partial\mathbf{z}^\top}\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\top}+\frac{\partial\boldsymbol{\epsilon}}{\partial\boldsymbol{\epsilon}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{e}}, \tag{71b}$$

which is formed by stabilized plasticity of the phenotype, followed by inclusive niche construction by the phenotype, plus mutual environmental dependence.

The following stabilized-effect matrices are simply collections of already defined stabilized-effect matrices. The transpose of the matrix of *stabilized effects of a focal individual's controls on the phenotype* is

$$\left.\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top};\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{c}}, \tag{72a}$$

measuring stabilized developmental bias from controls on the phenotype. The transpose of the matrix of *stabilized effects of a focal individual's environment on the phenotype* is

$$\left.\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\top};\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{e}}, \tag{72b}$$

measuring stabilized plasticity of the phenotype. The transpose of the matrix of *stabilized effects of a focal individual's phenotype on the phenotype* is

$$\left.\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top}\\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\top}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top}\\ \mathbf{0} & \mathbf{I}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}, \tag{73}$$

measuring stabilized developmental feedback across the phenotype. The transpose of the matrix of *stabilized effects of a focal individual's controls on the metaphenotype* is

$$\left.\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{y}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top};\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\top};\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}N_\mathrm{c}}, \tag{74a}$$

measuring stabilized developmental bias from controls on the metaphenotype. The transpose of the matrix of *stabilized effects of a focal individual's environment on the metaphenotype* is

$$\left.\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\top};\frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\epsilon}^\top};\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}N_\mathrm{e}}, \tag{74b}$$

measuring stabilized plasticity of the metaphenotype. Finally, the transpose of the matrix of *stabilized effects of a focal individual's metaphenotype on the metaphenotype* is

$$\begin{aligned}\left.\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{m}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\top} & \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\top} & \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\top} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\\ \mathbf{0} & \mathbf{I} & \mathbf{0}\\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{x}^\top} & \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\top} & \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\top}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &\in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},\end{aligned} \tag{75}$$

measuring stabilized developmental feedback across the metaphenotype.

Layer 6: genetic covariation

We now move to the next layer of the evo-devo process, that of genetic covariation. To present this layer, we first define breeding value under our adaptive dynamics assumptions, which allows us to define additive genetic covariance matrices under our assumptions. Then, we define (socio-devo) stabilized breeding value, which generalizes the notion of breeding value to consider the effects of social development. Using stabilized breeding value, we define additive socio-genetic cross-covariance matrices, which generalize the notion of additive genetic covariance to consider the effects of social development.

We follow the standard definition of breeding value to define it under our assumptions. The breeding value of a trait is defined under under quantitative genetics assumptions as the best linear prediction of the trait from gene content (Lynch and Walsh 1998; Walsh and Lynch 2018). Specifically, under quantitative genetics assumptions, a trait value x is written as $x = \sum_i \alpha_i y_i + e$, where y_i is the i-th predictor (gene content in i-th locus), α_i is the least-square regression coefficient for the i-th predictor, and e is the error; the breeding value of x is $a = \sum_i \alpha_i y_i$. Accordingly, we define the breeding value $\mathbf{a}_{\boldsymbol{\zeta}}$ of a vector $\boldsymbol{\zeta}$ as its first-order prediction with respect to controls $\mathbf{y}$ around the resident controls $\bar{\mathbf{y}}$:

$$\mathbf{a}_{\boldsymbol{\zeta}} \equiv \boldsymbol{\zeta}|_{\mathbf{y}=\bar{\mathbf{y}}} + \left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}}) = \bar{\boldsymbol{\zeta}} + \left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}}). \tag{76}$$

With this definition, the entries of $\mathrm{d}\boldsymbol{\zeta}/\mathrm{d}\mathbf{y}^{\intercal}|_{\mathbf{y}=\bar{\mathbf{y}}}$ correspond to Fisher's additive effects of gene content on trait value (his α; see Eq. I of Fisher 1918 and p. 72 of Lynch and Walsh 1998). Moreover, such matrix $\mathrm{d}\boldsymbol{\zeta}/\mathrm{d}\mathbf{y}^{\intercal}|_{\mathbf{y}=\bar{\mathbf{y}}}$ corresponds to Wagner's (1984, 1989) developmental matrix, particularly when $\boldsymbol{\zeta} = \mathbf{x}$ (his $\mathbf{B}$; see Eq. 1 of Wagner 1989).

Our definition of breeding value recovers Fisher's (1918) infinitesimal model under certain conditions, although we do not need to assume the infinitesimal model. According to Fisher's (1918) infinitesimal model, the normalized breeding value excess is normally distributed as the number of loci approaches infinity. Indeed, for the i-th entry of $\mathbf{a}_{\boldsymbol{\zeta}}$ we have the breeding value excess

$$a_{\zeta_i} - \bar{\zeta}_i = \sum_{k=1}^{N_\mathrm{c}} \sum_{a=1}^{N_\mathrm{a}} \left.\frac{\mathrm{d}\zeta_i}{\mathrm{d}y_{ka}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (y_{ka} - \bar{y}_{ka}).$$

Let us denote the mutational variance for the k-th control at age a by

$$\sigma_{ka}^2 = \mathrm{E}[(y_{ka} - \bar{y}_{ka})^2],$$

and let us denote the total mutational variance by

$$s_{N_\mathrm{c}N_\mathrm{a}}^2 = \sum_{k=1}^{N_\mathrm{c}} \sum_{a=1}^{N_\mathrm{a}} \sigma_{ka}^2.$$

If the Lyapunov's condition is satisfied, from the Lyapunov central limit theorem we have that, as either the number of controls N_c or the number of ages N_a tends to infinity (e.g., by reducing the age bin size), the normalized breeding value excess

$$\frac{1}{s_{N_\mathrm{c}N_\mathrm{a}}}(a_{\zeta_i} - \bar{\zeta}_i)$$

is normally distributed with mean zero and variance 1. Thus, this limit yields the so-called Fisher's (1918) infinitesimal model, although note we do not need to assume such limit. Consequently, our framework recovers the infinitesimal model as a particular case, when either N_c or N_a approaches infinity.

From our definition of breeding value, we have that the breeding value of controls is simply the controls themselves. From Eq. (76), the expected breeding value of vector $\boldsymbol{\zeta}$ is

$$\bar{\mathbf{a}}_{\boldsymbol{\zeta}} \equiv \mathrm{E}[\mathbf{a}_{\boldsymbol{\zeta}}] = \bar{\boldsymbol{\zeta}}.$$

In turn, the breeding value of controls $\mathbf{y}$ is

$$\mathbf{a}_{\mathbf{y}} = \bar{\mathbf{y}} + \left.\frac{\mathrm{d}\mathbf{y}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}}) = \bar{\mathbf{y}} + \mathbf{y} - \bar{\mathbf{y}} = \mathbf{y},$$

since $\mathrm{d}\mathbf{y}/\mathrm{d}\mathbf{y}^{\intercal}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{I}$ because, by assumption, controls do not have developmental constraints and are open-loop (Layer 4; Eq. 48).

We now define additive genetic covariance matrices under our assumptions. The additive genetic variance of a trait is defined under quantitative genetics assumptions as the variance of its breeding value, which is extended to the multivariate case so the additive genetic covariance matrix of a set of traits is the covariance matrix of the traits' breeding values (Lynch and Walsh 1998; Walsh and Lynch 2018). Accordingly, we define the additive genetic covariance matrix of a vector $\boldsymbol{\zeta} \in \mathbb{R}^{m\times 1}$ as the covariance matrix of its breeding value:

$$\begin{aligned}
\mathbf{G}_{\boldsymbol{\zeta}} &\equiv \mathrm{cov}[\mathbf{a}_{\boldsymbol{\zeta}}, \mathbf{a}_{\boldsymbol{\zeta}}] \\
&= \mathrm{E}[(\mathbf{a}_{\boldsymbol{\zeta}} - \bar{\mathbf{a}}_{\boldsymbol{\zeta}})(\mathbf{a}_{\boldsymbol{\zeta}} - \bar{\mathbf{a}}_{\boldsymbol{\zeta}})^{\intercal}] = \mathrm{E}[(\mathbf{a}_{\boldsymbol{\zeta}} - \bar{\boldsymbol{\zeta}})(\mathbf{a}_{\boldsymbol{\zeta}} - \bar{\boldsymbol{\zeta}})^{\intercal}] \\
&= \mathrm{E}\left[\left(\left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}})\right)\left(\left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}})\right)^{\intercal}\right] \\
&= \mathrm{E}\left[\left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} (\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^{\intercal} \left.\frac{\mathrm{d}\boldsymbol{\zeta}^{\intercal}}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right] \\
&= \left.\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \mathrm{E}\left[(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^{\intercal}\right] \left.\frac{\mathrm{d}\boldsymbol{\zeta}^{\intercal}}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left.\left(\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^{\intercal}} \mathbf{G}_{\mathbf{y}} \frac{\mathrm{d}\boldsymbol{\zeta}^{\intercal}}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times m},
\end{aligned} \tag{77}$$

where the fourth line follows from the property of the transpose of a product (i.e., $(\mathbf{AB})^{\intercal} = \mathbf{B}^{\intercal}\mathbf{A}^{\intercal}$) and the last line follows since the additive genetic covariance matrix of controls $\mathbf{y}$ is

$$\mathbf{G}_{\mathbf{y}} \equiv \mathrm{cov}[\mathbf{a}_{\mathbf{y}}, \mathbf{a}_{\mathbf{y}}] = \mathrm{cov}[\mathbf{y}, \mathbf{y}] \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}.$$

Eq. (77) corresponds to previous expressions of the additive genetic covariance matrix (see Eq. II of Fisher 1918, Eq. + of Wagner 1984, Eq. 3.5b of Barton and Turelli 1987, and Eq. 4.23b of Lynch and Walsh 1998; see also Eq. 22a of Lande 1980, Eq. 3 of Wagner 1989, and Eq. 9 of Charlesworth 1990).

In some cases, Eq. (77) allows one to immediately determine whether an additive genetic covariance matrix is singular. Indeed, since a matrix with fewer rows than columns is necessarily singular (Horn and Johnson 2013, p. 14), and since a well-defined product of matrices where the rightmost matrix is singular yields a singular matrix, from Eq. (77) it follows that $\mathbf{G}_{\boldsymbol{\zeta}}$ is necessarily singular if $\mathbf{y}$ has fewer entries than $\boldsymbol{\zeta}$ (i.e., if $N_\mathrm{a}N_\mathrm{c} < m$).

The additive genetic covariance matrix of states takes the following form. Evaluating Eq. (77) at $\boldsymbol{\zeta} = \mathbf{x}$, the additive genetic covariance matrix of states $\mathbf{x} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times 1}$ is

$$\mathbf{G}_{\mathbf{x}} = \left.\left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{y}^{\intercal}} \mathbf{G}_{\mathbf{y}} \frac{\mathrm{d}\mathbf{x}^{\intercal}}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}}, \tag{78}$$

which is singular because the developmental matrix $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is singular since initial states are not affected by any control and final controls do not affect any state (Appendix 5, Eq. A54). However, evolutionary dynamic equations for states alone having an associated $\mathbf{G_x}$-matrix are dynamically insufficient in general. This is because the evolutionary dynamics of states generally depends on the evolutionary dynamics of controls, in particular, because the developmental matrix depends on resident controls in general (Eq. 45; e.g., due to non-linearities in the developmental map involving products between controls, or between controls and states, or between controls and environmental variables, that is, gene-gene interaction, gene-phenotype interaction, and gene-environment interaction, respectively). To guarantee dynamic sufficiency, one needs to consider the evolutionary dynamics of both states and controls, that is, of the phenotype, which depends on an associated $\mathbf{G_z}$-matrix rather than $\mathbf{G_x}$ alone.

The additive genetic covariance matrix of the phenotype takes the following form. Evaluating Eq. (77) at $\boldsymbol{\zeta} = \mathbf{z}$, the additive genetic covariance matrix of the phenotype $\mathbf{z} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times 1}$ is

$$\mathbf{G_z} = \left(\frac{\mathrm{d}\mathbf{z}}{\mathrm{d}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}. \tag{79}$$

This matrix is necessarily singular because the phenotype $\mathbf{z}$ includes controls $\mathbf{y}$ so $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{y}$ has fewer rows than columns if $N_\mathrm{s} > 0$ (i.e., $N_\mathrm{a}N_\mathrm{c} < N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})$; Eq. 54). This entails that $\mathbf{G_z}$ has at least $N_\mathrm{a}N_\mathrm{s}$ eigenvalues that are exactly zero. That is, $\mathbf{G_z}$ is singular if there is at least one trait that is developmentally constructed according to the developmental map (Eq. 8).

Another way to see the singularity of $\mathbf{G_z}$ is the following. From Eq. (79), we can write the additive genetic covariance of the phenotype as

$$\mathbf{G_z} = \begin{pmatrix} \mathbf{G_{zx}} & \mathbf{G_{zy}} \end{pmatrix},$$

where the additive genetic cross-covariance matrix of $\mathbf{z}$ and $\mathbf{x}$ is

$$\mathbf{G_{zx}} = \left(\frac{\mathrm{d}\mathbf{z}}{\mathrm{d}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{s}},$$

and the additive genetic cross-covariance matrix of $\mathbf{z}$ and $\mathbf{y}$ is

$$\mathbf{G_{zy}} = \left(\frac{\mathrm{d}\mathbf{z}}{\mathrm{d}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{c}}.$$

Thus, using Eq. (48), we have that

$$\mathbf{G_{zx}} = \mathbf{G_{zy}}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{80}$$

That is, some columns of $\mathbf{G_z}$ (i.e., those in $\mathbf{G_{zx}}$) are linear combinations of other columns of $\mathbf{G_z}$ (i.e., those in $\mathbf{G_{zy}}$). Hence, $\mathbf{G_z}$ is singular.

The additive genetic covariance matrix of the phenotype is singular because the phenotype includes controls ("gene content"). This is because the breeding value of states is a linear combination of the breeding value of controls, by definition of breeding value, regardless of whether states are linear functions of controls and regardless of the number of states or controls. In quantitative genetics terms, this can be understood as the $\mathbf{G}$-matrix being a function of allele frequencies, say $\bar{\mathbf{y}}$, so dynamic sufficiency requires that allele frequencies are part of the dynamic variables considered; consequently, if the phenotypic vector $\bar{\mathbf{z}}$ includes allele frequencies $\bar{\mathbf{y}}$, then $\mathbf{G}$ is necessarily singular since by definition, breeding value under quantitative genetics assumptions is a linear combination of gene content. The singularity of $\mathbf{G_z}$ implies that if there is only one state and one control, with a single age each, then there is a perfect correlation between their breeding values (i.e., their correlation coefficient is 1). This also holds under quantitative genetics assumptions, where the breeding value a of a trait x is a linear combination of predictors y_i, so the additive genetic covariance matrix of $\mathbf{z} = (x;\mathbf{y})$ is singular; in particular, if there is only one predictor y, the breeding value a and predictor y are perfectly correlated (i.e., $\mathrm{cov}[a,y]/\sqrt{\mathrm{var}[a]\mathrm{var}[y]} = \mathrm{cov}[\alpha y,y]/\sqrt{\mathrm{var}[\alpha y]\mathrm{var}[y]} = (\alpha/\alpha)\mathrm{cov}[y,y]/\sqrt{\mathrm{var}[y]\mathrm{var}[y]} = 1$). The perfect correlation between breeding value and a single predictor arises because, by definition, breeding value excludes prediction error e. Note this does not mean that states and controls are linearly related: it is breeding values and controls that are linearly related by definition of breeding value (Eq. 76). A standard approach to remove the singularity of an additive genetic covariance matrix is to remove some traits from the analysis (Lande 1979). To remove the singularity of $\mathbf{G_z}$ we would need to remove either all states or all controls from the analysis. However, removing states from the analysis prevents study of the evolution of developed traits whereas removing controls from the analysis renders the analysis dynamically insufficient in general because some dynamic variables are not followed. Thus, to guarantee that a dynamically sufficient study of the evolution of developed traits is carried out, we must keep the singularity of $\mathbf{G_z}$.

Consider now the following slight generalization of the additive genetic covariance matrix. We define the additive genetic cross-covariance matrix of a vector $\boldsymbol{\zeta} \in \mathbb{R}^{m\times 1}$ and a vector $\boldsymbol{\xi} \in \mathbb{R}^{p\times 1}$ as the cross-covariance matrix of their breeding value:

$$\mathbf{G}_{\boldsymbol{\zeta}\boldsymbol{\xi}} \equiv \mathrm{cov}[\mathbf{a}_{\boldsymbol{\zeta}}, \mathbf{a}_{\boldsymbol{\xi}}] = \left(\frac{\mathrm{d}\boldsymbol{\zeta}}{\mathrm{d}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\boldsymbol{\xi}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times p}. \tag{81}$$

Thus, $\mathbf{G}_{\boldsymbol{\zeta}\boldsymbol{\zeta}} = \mathbf{G}_{\boldsymbol{\zeta}}$. Again, from Eq. (81) it follows that $\mathbf{G}_{\boldsymbol{\zeta}\boldsymbol{\xi}}$ is necessarily singular if there are fewer entries in $\mathbf{y}$ than in $\boldsymbol{\xi}$ (i.e., if $N_\mathrm{a}N_\mathrm{c} < p$).

We now use stabilized-effect matrices (Layer 5) to extend the notion of breeding value (Eq. 76). We define the stabilized breeding value of a vector $\boldsymbol{\zeta}$ as:

$$\mathbf{b}_{\boldsymbol{\zeta}} \equiv \boldsymbol{\zeta}|_{\mathbf{y}=\bar{\mathbf{y}}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}(\mathbf{y}-\bar{\mathbf{y}}) = \bar{\boldsymbol{\zeta}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}(\mathbf{y}-\bar{\mathbf{y}}). \tag{82}$$

Recall that the stabilized-effect matrix $\mathrm{s}\boldsymbol{\xi}/\mathrm{s}\mathbf{y}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ equals the total-effect matrix $\mathrm{d}\boldsymbol{\xi}/\mathrm{d}\mathbf{y}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ if development is non-social. Thus, if development is non-social, the stabilized breeding value $\mathbf{b}_{\boldsymbol{\zeta}}$ equals the breeding value $\mathbf{a}_{\boldsymbol{\zeta}}$. Also, note that $\mathrm{E}[\mathbf{b}_{\boldsymbol{\zeta}}] = \bar{\boldsymbol{\zeta}}$.

We extend the notion of additive genetic covariance matrix to include the effects of socio-devo stabilization as follows. We define the *additive socio-genetic cross-covariance matrix of* $\boldsymbol{\zeta} \in \mathbb{R}^{m\times 1}$ as

$$\mathbf{H}_{\boldsymbol{\zeta}} \equiv \mathrm{cov}[\mathbf{b}_{\boldsymbol{\zeta}}, \mathbf{a}_{\boldsymbol{\zeta}}] = \left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\boldsymbol{\zeta}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times m}. \tag{83}$$

Thus, if development is non-social, $\mathbf{H}_{\boldsymbol{\zeta}}$ equals $\mathbf{G}_{\boldsymbol{\zeta}}$.

Similarly, we generalize this notion and define the *additive socio-genetic cross-covariance matrix of* $\boldsymbol{\zeta} \in \mathbb{R}^{m\times 1}$ *and* $\boldsymbol{\xi} \in \mathbb{R}^{p\times 1}$ as

$$\mathbf{H}_{\boldsymbol{\zeta}\boldsymbol{\xi}} \equiv \mathrm{cov}[\mathbf{b}_{\boldsymbol{\zeta}}, \mathbf{a}_{\boldsymbol{\xi}}] = \left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G_y}\frac{\mathrm{d}\boldsymbol{\xi}^\intercal}{\mathrm{d}\mathbf{y}}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times p}. \tag{84}$$

Again, if development is non-social, $\mathbf{H}_{\boldsymbol{\zeta}\boldsymbol{\zeta}}$ equals $\mathbf{G}_{\boldsymbol{\zeta}\boldsymbol{\zeta}}$.

Therefore, an additive socio-genetic cross-covariance matrix $\mathbf{H}_{\boldsymbol{\zeta}\boldsymbol{\xi}}$ is singular if $\boldsymbol{\xi}$ has more entries than $\mathbf{y}$. Consequently, the matrix

$$\mathbf{H}_{\boldsymbol{\zeta}\mathbf{z}} = \left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_{\mathbf{y}} \frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})} \tag{85}$$

is singular if there is at least one state (i.e., if $N_\mathrm{s} > 0$). Moreover, $\mathbf{H}_{\boldsymbol{\zeta}\mathbf{z}}$ has at least $N_\mathrm{a}N_\mathrm{s}$ eigenvalues that are exactly zero. Now, the matrix

$$\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}} = \left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_{\mathbf{y}} \frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{y}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times (1+N_\mathrm{a})(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})} \tag{86}$$

is singular if there is at least one state or one environmental variable (i.e., if $N_\mathrm{s} > 0$ or $N_\mathrm{e} > 0$). Thus, $\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}}$ has at least $N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{e})$ eigenvalues that are exactly zero. In contrast, the additive socio-genetic cross-covariance matrix of $\boldsymbol{\zeta} \in \{\mathbf{y}, \mathbf{z}, \mathbf{m}\}$ and $\mathbf{y}$

$$\mathbf{H}_{\boldsymbol{\zeta}\mathbf{y}} = \left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_{\mathbf{y}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{m\times N_\mathrm{a}N_\mathrm{c}} \tag{87}$$

is non-singular if $\mathbf{G}_{\mathbf{y}}$ is non-singular (Appendices 10 and 12). The matrices of additive socio-genetic covariance share various properties with similar generalizations of the **G**-matrix arising in the indirect genetic effects literature (Kirkpatrick and Lande 1989; Moore *et al.* 1997; Townley and Ezard 2013).

Layer 7: evolutionary dynamics

Finally, we move to the top layer of the evo-devo process, that of evolutionary dynamics. This layer contains equations describing the evolutionary dynamics under explicit developmental and environmental constraints. In Appendices 1 and 9-12, we show that the evolutionary dynamics of states, controls, phenotype, environment, and metaphenotype (i.e., for $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}, \boldsymbol{\epsilon}, \mathbf{m}\}$) are given by

$$\frac{\mathrm{d}\bar{\boldsymbol{\zeta}}}{\mathrm{d}\tau} = \left(\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}} \frac{\partial w}{\partial \mathbf{m}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{88a}$$

which must satisfy both the developmental constraint

$$\bar{\mathbf{x}}_a + 1 = \mathbf{g}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \bar{\boldsymbol{\epsilon}}_a) \text{ for all } a \in \{1, \dots, N_\mathrm{a} - 1\} \text{ with fixed } \bar{\mathbf{x}}_1, \tag{88b}$$

and the environmental constraint

$$\bar{\boldsymbol{\epsilon}}_a = \mathbf{h}_a(\bar{\mathbf{z}}_a, \bar{\mathbf{z}}, \tau) \text{ for all } a \in \{1, \dots, N_\mathrm{a}\}. \tag{88c}$$

If $\boldsymbol{\zeta} = \mathbf{z}$ in Eq. (88a), then the equations in layers 2-6 guarantee that the developmental constraint is satisfied for all $\tau > \tau_1$ given that it is satisfied at the initial evolutionary time τ_1. If $\boldsymbol{\zeta} = \mathbf{m}$ in Eq. (88a), then the equations in layers 2-6 guarantee that both the developmental and environmental constraints are satisfied for all $\tau > \tau_1$ given that they are satisfied at the initial evolutionary time τ_1. Both the developmental and environmental constraints can evolve as the phenotype and environment evolve and such constraints can involve any family of curves (as long as they are differentiable).

Eq. (88a) describes the evolutionary dynamics as consisting of selection response and exogenous plastic response. Eq. (88a) contains the term

$$\left(\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}} \frac{\partial w}{\partial \mathbf{m}} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{89}$$

which comprises directional selection on the metaphenotype ($\partial w/\partial \mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$) and socio-genetic covariation of $\boldsymbol{\zeta}$ and the metaphenotype ($\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}}$). Thus, the term in Eq. (89) is the *selection response* of $\boldsymbol{\zeta}$ and is a generalization of Lande's (1979) generalization of the univariate breeder's equation (Lush 1937; Walsh and Lynch 2018). Additionally, Eq. (88a) contains the term

$$\left(\frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{90}$$

which comprises the vector of environmental change due to exogenous causes ($\partial\bar{\boldsymbol{\epsilon}}/\partial\tau$) and the matrix of stabilized plasticity ($\mathrm{s}\boldsymbol{\zeta}/\mathrm{s}\boldsymbol{\epsilon}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$). Thus, the term in Eq. (90) is the *exogenous plastic response* of $\boldsymbol{\zeta}$ and is a generalization of previous equations (cf. Eq. A3 of Chevin *et al.* 2010). Note that the *endogenous* plastic response of $\boldsymbol{\zeta}$ (i.e., the plastic response due to endogenous environmental change arising from niche construction) is part of both the selection response and the exogenous plastic response (Layers 2-6).

Selection response is relatively incompletely described by directional selection on the metaphenotype. We saw that the matrix $\mathbf{H}_{\boldsymbol{\zeta}\mathbf{m}}$ is always singular if there is at least one state or one environmental variable (Layer 6, Eq. 86). Consequently, evolutionary equilibria of $\boldsymbol{\zeta}$ can invariably occur with persistent directional selection on the metaphenotype, regardless of whether there is exogenous plastic response.

Selection response is also relatively incompletely described by semi-total selection on the phenotype. We can rewrite the selection response, so the evolutionary dynamics of $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}, \boldsymbol{\epsilon}, \mathbf{m}\}$ (Eq. 88a) is equivalently given by

$$\frac{\mathrm{d}\bar{\boldsymbol{\zeta}}}{\mathrm{d}\tau} = \left(\mathbf{H}_{\boldsymbol{\zeta}\mathbf{z}} \frac{\delta w}{\delta \mathbf{z}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{91}$$

This equation now depends on semi-total selection on the phenotype ($\delta w/\delta \mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$), which measures directional selection on the phenotype considering environmental constraints (Lande's selection gradient does not consider any constraints on the traits; Appendix 16). We saw that the semi-total selection gradient of the phenotype can be interpreted as pointing in the direction of steepest ascent on the fitness landscape in phenotype space after the landscape is modified by the interaction of niche construction and environmental sensitivity of selection (Layer 3, Eq. 40). We also saw that the matrix $\mathbf{H}_{\boldsymbol{\zeta}\mathbf{z}}$ is always singular if there is at least one state (Layer 6, Eq. 85). Consequently, evolutionary equilibria can invariably occur with persistent directional selection on the phenotype after niche construction has modified the phenotype's fitness landscape, regardless of whether there is exogenous plastic response.

In contrast, selection response is relatively completely described by total genetic selection. We can further rewrite selection response, so the evolutionary dynamics of $\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}, \boldsymbol{\epsilon}, \mathbf{m}\}$ (Eq. 88a) is equivalently given by

$$\frac{\mathrm{d}\bar{\boldsymbol{\zeta}}}{\mathrm{d}\tau} = \left(\mathbf{H}_{\boldsymbol{\zeta}\mathbf{y}} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{92}$$

This equation now depends on total genetic selection ($\mathrm{d}w/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$), which measures directional selection on controls considering developmental and environmental constraints. We saw that the total selection gradient of controls can be interpreted as pointing in the direction of steepest ascent on the fitness landscape in control space after the landscape is modified by the interaction of total developmental bias from controls and directional selection on developed traits and by the interaction of total niche construction by controls and environmental sensitivity of selection (Layer 4, Eq. 64). In contrast to the other arrangements of selection response, in Appendices 10 and 12 we show that $\mathbf{H}_{\boldsymbol{\zeta}\mathbf{y}}$ is non-singular for all $\boldsymbol{\zeta} \in \{\mathbf{y}, \mathbf{z}, \mathbf{m}\}$ if $\mathbf{G}_{\mathbf{y}}$ is non-singular (i.e., if there is mutational variation in all directions of control space). Consequently, evolutionary equilibria of controls, phenotype, or metaphenotype can only occur when total genetic selection vanishes if there is mutational variation in all directions of control space and if exogenous plastic response is absent.

Importantly, although Eq. (88a) and its equivalents describe the evolutionary dynamics of $\boldsymbol{\zeta}$, such equations are guaranteed to be dynamically sufficient only for certain $\boldsymbol{\zeta}$. Eq. (88a) and its equivalents are dynamically sufficient if $\boldsymbol{\zeta}$ is the controls, the phenotype, or the metaphenotype, provided that the developmental and environmental constrains are satisfied throughout and the five elementary components of the evo-devo process are known (Layer 1, Fig. 5). In contrast, Eq. (88a) and its equivalents are generally dynamically *insufficient* if $\boldsymbol{\zeta}$ is the states or the environment, because the evolution of controls is not followed but it generally affects the system.

In particular, the evolutionary dynamics of states are generally dynamically insufficient if considered on their own. Let us temporarily assume that the following four conditions hold: (1) development is non-social $(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$, and there is (2) no exogenous plastic response of states $([(\mathrm{d}\mathbf{x}/\mathrm{d}\boldsymbol{\epsilon}^\intercal)(\partial\bar{\boldsymbol{\epsilon}}/\partial\tau)]\,|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$, (3) no semi-total selection on controls $(\delta w/\delta\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$, and (4) no niche-constructed effects of states on fitness $([(\partial\boldsymbol{\epsilon}^\intercal/\partial\mathbf{x})(\partial w/\partial\boldsymbol{\epsilon})]\,|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$. Then, the evolutionary dynamics of states reduces to

$$\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} = \mathbf{G}_{\mathbf{x}} \left.\frac{\partial w}{\partial \mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{93}$$

This recovers Lande's (1979) equation for states, where the additive genetic covariance matrix of states (Layer 6, Eq. 78) is singular because initial states are not affected by any control and final controls do not affect any state (so $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has rows and columns that are zero; Appendix 5, Eq. A54). Yet, the evolutionary dynamics of states is not necessarily fully determined by the evolutionary dynamics of states alone because such system depends on resident controls whose evolution must also be followed. In particular, setting $\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau = \mathbf{0}$ does not generally imply an evolutionary equilibrium, or evolutionary stasis, but only an evolutionary isocline in states, that is, a transient lack of evolutionary change in states. To guarantee a complete description of the evolutionary dynamics of states, we must consider the evolutionary dynamics of states and controls, that is, the phenotype.

Indeed, the evolutionary dynamics of the phenotype is dynamically sufficient more generally. Let us instead assume that the following three conditions hold: (i) development is non-social $(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\bar{\mathbf{z}}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$, and there is (ii) no exogenous plastic response of states $([(\mathrm{d}\mathbf{x}/\mathrm{d}\boldsymbol{\epsilon}^\intercal)(\partial\bar{\boldsymbol{\epsilon}}/\partial\tau)]\,|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$, and (iii) no niche-constructed effects of the phenotype on fitness $([(\partial\boldsymbol{\epsilon}^\intercal/\partial\mathbf{z})(\partial w/\partial\boldsymbol{\epsilon})]\,|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0})$. Then, the evolutionary dynamics of the phenotype reduces to

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \mathbf{G}_{\mathbf{z}} \left.\frac{\partial w}{\partial \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{94}$$

This recovers Lande's (1979) equation, this time for the phenotype, where the additive genetic covariance matrix of the phenotype (Layer 6, Eq. 79) is singular because the phenotype $\mathbf{z}$ includes controls $\mathbf{y}$ (so $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{y}$ has fewer rows than columns; Layer 4, Eq. 54). That is, $\mathbf{G}_{\mathbf{z}}$ is singular if there is at least one trait that is developmentally constructed according to the developmental map (Eq. 88b). The evolutionary dynamics of the phenotype is now fully determined by Eq. (94) provided that i-iii hold and that the developmental (Eq. 88b) and environmental (Eq. 88c) constraints are met. In such case, setting $\mathrm{d}\bar{\mathbf{z}}/\mathrm{d}\tau = \mathbf{0}$ does imply an evolutionary equilibrium, but this does not imply absence of directional selection on the phenotype (i.e., it is possible that $\partial w/\partial\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$) since $\mathbf{G}_{\mathbf{z}}$ is always singular. Due to this singularity, if there is any evolutionary equilibrium, there is an infinite number of them. Kirkpatrick and Lofsvold (1992) showed that if $\mathbf{G}_{\mathbf{z}}$ is singular and constant, then the evolutionary equilibrium that is achieved depends on the initial conditions. Our results extend the relevance of Kirkpatrick and Lofsvold's (1992) insight by showing that $\mathbf{G}_{\mathbf{z}}$ is always singular and remains so as it evolves. Moreover, since both the developmental (Eq. 88b) and environmental (Eq. 88c) constraints must be satisfied throughout the evolutionary process, the developmental and environmental constraints determine the admissible evolutionary trajectory and the admissible evolutionary equilibria if mutational variation exists in all directions of control space.

Since selection response is relatively completely described by total genetic selection, further insight can be gained by rearranging Lande's equation for the phenotype (Eq. 94) in terms of total genetic selection. Using the rearrangement in Eq. (92) and making the assumptions i-iii in the previous paragraph, Lande's equation (Eq. 94) becomes

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \mathbf{H}_{\mathbf{zy}} \left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{95}$$

Here, if the mutational covariance matrix $\mathbf{G}_{\mathbf{y}}$ is non-singular, then the matrix $\mathbf{H}_{\mathbf{zy}}$ is non-singular so evolutionary equilibrium $(\mathrm{d}\bar{\mathbf{z}}/\mathrm{d}\tau = \mathbf{0})$ implies absence of total genetic selection (i.e., $\mathrm{d}w/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$). Hence, lack of total genetic selection provides a first-order condition for evolutionary equilibria in the absence of exogenous environmental change and of absolute mutational constraints. Consequently, evolutionary equilibria depend on development and niche construction since total genetic selection depends on Wagner's (1984, 1989) developmental matrix and on total niche construction by controls (Layer 4; Eq. 64). Since $\mathrm{d}w/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$ has only as many equations as there are controls and since there are not only controls but also states and environmental variables to determine, then $\mathrm{d}w/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{0}$ provides fewer equations than variables to solve for. Hence, absence of total genetic selection still implies an infinite number of evolutionary equilibria. Again, only the subset of evolutionary equilibria that satisfy the developmental (Eq. 88b) and environmental (Eq. 88c) constraints are admissible, and the number of admissible evolutionary equilibria may be finite. Therefore, admissible evolutionary equilibria have a dual dependence on developmental and environmental constraints: first, by the constraints' influence on total genetic selection and so on evolutionary equilibria; and second, by the constraints' specification of which equilibria are admissible.

Because we assume that mutants arise when residents are at carrying capacity, the analogous statements can be made for the evolutionary dynamics of a resident vector in terms of lifetime reproductive success (Eq. 28). Using the relationship between selection gradients in terms of fitness and of expected lifetime reproductive success (Eqs. 29), the evolutionary dynamics of

$\boldsymbol{\zeta} \in \{\mathbf{x}, \mathbf{y}, \mathbf{z}, \boldsymbol{\epsilon}, \mathbf{m}\}$ (Eq. 88a) are equivalently given by

$$\frac{\mathrm{d}\bar{\boldsymbol{\zeta}}}{\mathrm{d}\tau} = \left(\frac{1}{T} \mathbf{H}_{\zeta\mathbf{m}} \frac{\partial R_0}{\partial \mathbf{m}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{96a}$$

$$= \left(\frac{1}{T} \mathbf{H}_{\zeta\mathbf{z}} \frac{\delta R_0}{\delta \mathbf{z}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{96b}$$

$$= \left(\frac{1}{T} \mathbf{H}_{\zeta\mathbf{y}} \frac{\mathrm{d} R_0}{\mathrm{d} \mathbf{y}} + \frac{\mathrm{s}\boldsymbol{\zeta}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} . \tag{96c}$$

To close, the evolutionary dynamics of the environment can be written in a particular form that is insightful. In Appendix 11, we show that the evolutionary dynamics of the environment is given by

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}}{\mathrm{d}\tau} = \left(\frac{\partial(\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{z}^\intercal} \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} . \tag{97}$$

Thus, the evolutionary change of the environment comprises "inclusive" endogenous environmental change and exogenous environmental change.

Discussion

We have addressed the question of how development affects evolution by formulating a mathematical framework that integrates explicit developmental dynamics into evolutionary dynamics. Previous understanding suggested that development affects evolution by inducing genetic covariation and genetic constraints, although the nature of such constraints had remained uncertain. We have found that development has major evolutionary effects. First, the **G**-matrix is singular in phenotype space if controls are included in the analysis to achieve dynamic sufficiency, so genetic covariation is necessarily absent in some directions of phenotype space; that is, there necessarily are absolute genetic constraints. Second, since **G** is singular in phenotype space, directional selection is insufficient to identify evolutionary equilibria. In contrast, total genetic selection, which depends on development, is sufficient to identify evolutionary equilibria if there are no absolute mutational constraints and no exogenous plastic response. Third, since **G** is singular in phenotype space, if there is any evolutionary equilibrium and no exogenous plastic response, then there is an infinite number of evolutionary equilibria, and development determines the admissible evolutionary trajectory and so the admissible equilibria. We have derived a collection of equations that describe the evo-devo dynamics with explicit population and environmental dynamics. These equations provide a theory of constrained evolutionary dynamics, where the developmental and environmental constraints determine the admissible evolutionary path (Eq. 88).

We find that the **G**-matrix is necessarily singular in phenotype space if at least one trait is developmentally constructed according to the developmental map (Eq. 88b). This singularity arises because the evolution of both genetic and developed traits is followed for the evolutionary system to be dynamically sufficient in general. In quantitative genetics, the evolution of a multivariate phenotype is traditionally followed without simultaneously following allele frequency change (e.g., Lande 1979; Wagner 1984; Barton and Turelli 1987; Wagner 1989; Martin 2014; Morrissey 2014, 2015; Engen and Sæther 2021). We show that the **G**-matrix generally depends on resident controls (which play an analogous role to that of allele frequencies under quantitative genetics assumptions). Thus, following the evolution of developed traits without simultaneously tracking the evolution of controls is generally dynamically insufficient. The **G**-matrix generally depends on resident controls via both the mutational covariance matrix and the developmental matrix. The developmental matrix depends on resident controls particularly due to gene-gene interaction, gene-phenotype interaction, and gene-environment interaction (see text below Eq. 78). The analogous dependence of **G** on allele frequency should hold under quantitative genetics assumptions for the same reasons, thus requiring consideration of allele frequency as part of the dynamic variables. If under a quantitative genetics framework, allele frequency were considered as part of the multivariate phenotype in order to render the system dynamically sufficient in general, then the associated **G**-matrix would be necessarily singular, with at least as many zero eigenvalues as there are traits that are not allele frequency. This is because, by definition, breeding values are linear combinations of gene content; thus, some columns in **G** (the covariances between the breeding values of all traits and the breeding values of traits that are not gene content, $\mathbf{G}_{\mathbf{zx}}$) are linear combinations of other columns (the covariances between the breeding values of all traits and the breeding values of gene content, $\mathbf{G}_{\mathbf{zy}}$), which means that **G** is singular (Eq. 80). Including controls as part of the phenotype might seem to trivially enforce singularity of **G**, but such inclusion is needed to guarantee dynamic sufficiency. Consequently, lack of selection response in phenotype space generally occurs with persistent directional selection in phenotype space. The singularity of **G** in phenotype space persists despite evolution of the developmental map, regardless of the number of controls or states provided there is any state, and in the presence of endogenous or exogenous environmental change. The singularity remains if states directly depend on controls (Eq. 88b) so that there is genetic input fed directly into states, although the singularity may disappear if every state at every age is exclusively directly genetically encoded: that is, if there are no developed traits but only genetic traits (or in a standard quantitative genetics framework, if only allele frequency change is followed).

Extensive research efforts have been devoted to determining the relevance of constraints in adaptive evolution (Arnold 1992; Hine and Blows 2006; Hansen and Houle 2008; Jones *et al.* 2014; Hine *et al.* 2014; Engen and Sæther 2021). Empirical research has found that the smallest eigenvalue of **G** is often close to zero (Kirkpatrick and Lofsvold 1992; Hine and Blows 2006; McGuigan and Blows 2007). However, Mezey and Houle (2005) found a non-singular **G**-matrix for 20 traits in fruit flies; our results suggest **G** singularity would still arise in this case if enough traits are included so as to guarantee dynamic sufficiency (i.e., if allele frequency change were tracked). Previous theory has offered limited predictions as to when the **G**-matrix would be singular. These include that more traits render **G** more likely to be singular as traits are more likely to be genetically correlated, such as in infinite-dimensional traits (Gomulkiewicz and Kirkpatrick 1992; Kirkpatrick and Lofsvold 1992). But as noted by Kirkpatrick and Lofsvold (1992, p. 959), "The small number of evolutionary degrees of freedom found in the mouse population is a strictly empirical finding not predicted by [previous] theory." Our results are in line with those of Kirkpatrick and Lofsvold (1992, p. 962 onwards) who showed that, assuming that **G** is singular and constant, then the evolutionary trajectory and equilibria depend on the initial conditions. Our results substantiate Kirkpatrick and Lofsvold's (1992) assumption of singular **G** by our point that **G** is always singular in phenotype space, even with few traits and evolving **G**. Our results extend Kirkpatrick and Lofsvold's (1992) insight that the evolutionary trajectory and equilibria depend on the initial conditions by our observation that the evolutionary trajectory and equilibria depend on development. In Appendix 17, we show that such evolutionary trajectory corresponds to a "genetic line of least resistance" (a line parallel to a leading eigenvector of **G**) (Schluter 1996) if there is a single control and a single age (this may hold for an arbitrary number of controls and ages but we do not prove it). In this case of a single control and single age, developmental constraints can then be interpreted as determining genetic lines of least resistance, the number of which is infinite, and as determining the admissible one along which evolution proceeds.

Multiple mathematical models have addressed the question of the singularity of **G**. Recently, simulation work studying the effect of pleiotropy on the structure of the **G**-matrix found that the smallest eigenvalue of **G** is very small but positive (Engen and Sæther 2021, Tables 3 and 5). Our findings indicate that this model and others (e.g., Wagner 1984; Barton and Turelli 1987; Wagner 1989; Martin 2014; Morrissey 2014, 2015) would recover **G**-singularity by considering allele frequency as part of the phenotype. Other recent simulation work found that a singular **G**-matrix arising from few segregating alleles still allows the population to reach fitness optima as all directions of phenotype space are eventually available in the long run (Barton 2017, Fig. 3). Our results indicate that such a model would recover that unconstrained fitness optima in phenotype space are not necessarily achieved by incorporating developmental constraints, which induce convergence to constrained fitness optima. Convergence to constrained fitness optima rather than to unconstrained fitness optima still occurs with the fewest number of traits allowed in our framework: two, that is, one control and one state with one age each (or in a standard quantitative genetics framework, allele frequency at a locus and one quantitative trait that is a function of such allele frequency). Such constrained adaptation has substantial implications (see e.g., Kirkpatrick and Lofsvold 1992; Gomulkiewicz and Kirkpatrick 1992) and is consistent with empirical observations of lack of selection response in the wild despite selection and genetic variation (Merilä *et al.* 2001; Hansen and Houle 2004; Pujol *et al.* 2018), and of relative lack of stabilizing selection (Kingsolver *et al.* 2001; Kingsolver and Diamond 2011).

Our results provide a mechanistic theory of breeding value, thus allowing for insight regarding the structure and evolution of the **G**-matrix. We have obtained **G**-matrices in terms of total-effect matrices, in accordance with previous results (Fisher 1918; Wagner 1984; Barton and Turelli 1987; Lynch and Walsh 1998; Martin 2014; Morrissey 2014). Total-effect matrices correspond to Wagner's (1984, 1989) developmental matrix (denoted by him as **B**). Wagner (1984, 1989) constructed and analysed evolutionary models considering developmental maps, and wrote the **G**-matrix in terms of his developmental matrix to assess its impact on the maintenance of genetic variation. Yet, as is traditionally done, Wagner (1984, 1988, 1989) did not simultaneously track the evolution of what we call controls and states, so he did not conclude that the associated **G**-matrix is necessarily singular or that the developmental matrix affects evolutionary equilibria. Wagner's (1984, 1989) models have been used to devise models of constrained adaptation in a fitness landscape, borrowing ideas from computer science (Altenberg 1995, his Fig. 2). This and other models (Houle 1991, his Fig. 2 and Kirkpatrick and Lofsvold 1992, their Fig. 5) have suggested how constrained evolutionary dynamics could proceed although they have lacked a mechanistic theory of breeding value and thus of **G** and its evolutionary dynamics. Other models borrowing ideas from computer science have found that epistasis can cause the evolutionary dynamics to take an exponentially long time to reach fitness peaks (Kaznatcheev 2019). We obtain equations allowing one to mechanistically construct breeding value and the **G**-matrix from low-level mechanistic components, providing a mechanistic theory of breeding value and opening the door to further insight regarding the structure and evolution of **G**. Our point that the **G**-matrix in phenotype space has at least $N_\mathrm{a}N_\mathrm{s}$ eigenvalues that are exactly zero entails that even if there were infinite time, the population does not necessarily reach a fitness peak in phenotype space, although it may in control space.

We find that total genetic selection can provide more information than directional selection regarding selection response. As the **G**-matrix is singular in phenotype space, directional selection on the phenotype is insufficient to identify evolutionary equilibria as has been previously realized (Lande 1979; Via and Lande 1985; Kirkpatrick and Lofsvold 1992; Gomulkiewicz and Kirkpatrick 1992). Evolutionary analysis with singular **G**, including identification of evolutionary equilibria, has been hampered by the lack of mechanistic theory for breeding value and thus of **G** (Via and Lande 1985; Kirkpatrick and Lofsvold 1992; Gomulkiewicz and Kirkpatrick 1992). Our results show that evolutionary analysis despite singular **G** is facilitated by considering total genetic selection, revealing that evolutionary equilibria depend on development rather than exclusively on (unconstrained) selection. Additionally, development determines the admissible evolutionary trajectory along which developmental and environmental constraints are satisfied. These findings indicate that development has a major evolutionary role.

Total genetic selection is measured by a total selection gradient, and total selection gradients closely correspond to Morrissey's (2014, 2015) notion of extended selection gradient. Total selection gradients measure directional selection taking into account developmental and environmental constraints, as opposed to Lande's (1979) selection gradients which measure directional selection without considering constraints. We obtained compact expressions for total selection gradients as linear transformations of Lande's selection gradients, arising from the chain rule in matrix notation (Eq. 62). Morrissey (2014) defined the extended selection gradient as $\boldsymbol{\eta}=\mathbf{\Phi}\boldsymbol{\beta}$, where $\boldsymbol{\beta}$ is Lande's selection gradient and $\mathbf{\Phi}$ is the matrix of total effects of all traits on themselves. Morrissey (2014) provided an equation for $\mathbf{\Phi}$ (his Eq. 2), which has the form of our matrix describing developmental feedback among states ($\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$; Eq. 44). Thus, interpreting $\mathbf{\Phi}$ as our $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and $\boldsymbol{\beta}$ as our $\partial w/\partial\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$, then Eq. (63) shows that $\boldsymbol{\eta}=\mathbf{\Phi}\boldsymbol{\beta}$ corresponds to the total selection gradient of states $\mathrm{d}w/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ if there is no niche construction by states (i.e., if $\partial\boldsymbol{\epsilon}^\intercal/\partial\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}=\mathbf{0}$). The equation for $\mathbf{\Phi}$ provided by Morrissey (2014) (his Eq. 2) does not correspond to the expressions we found for other total-effect matrices (e.g., for $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ in Eq. 45, $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ in Eq. 55, or $\mathrm{d}\mathbf{m}^\intercal/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ in Eq. 60). Yet, if we interpret $\mathbf{\Phi}$ as our $\mathrm{d}\mathbf{z}^\intercal/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and $\boldsymbol{\beta}$ as our $\partial w/\partial\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$, then Eq. (66) shows that $\boldsymbol{\eta}=\mathbf{\Phi}\boldsymbol{\beta}$ corresponds to the total selection gradient of the phenotype $\mathrm{d}w/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ if there is no niche construction by the phenotype (i.e., if $\partial\boldsymbol{\epsilon}^\intercal/\partial\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}=\mathbf{0}$). Alternatively, if we interpret $\mathbf{\Phi}$ as our $\mathrm{d}\mathbf{m}^\intercal/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and $\boldsymbol{\beta}$ as our $\partial w/\partial\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$, then Eq. (67) shows that $\boldsymbol{\eta}=\mathbf{\Phi}\boldsymbol{\beta}$ corresponds to the total selection gradient of the metaphenotype $\mathrm{d}w/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ regardless of whether there is niche construction by states or the phenotype. We show in Appendices 10 and 12 that selection response can be written in terms of the total selection gradients of the phenotype $\mathrm{d}w/\mathrm{d}\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and metaphenotype $\mathrm{d}w/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$, but such total selection gradients are insufficient to predict evolutionary equilibria because they are premultiplied by a singular socio-genetic cross-covariance matrix. In a subsequent paper, Morrissey (2015) provided a symbolic definition for $\mathbf{\Phi}$ (his Eq. 6) which suggests interpreting it as our $\mathrm{d}\mathbf{m}^{\intercal}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ (although he used partial derivatives). Thus, interpreting $\mathbf{\Phi}$ as our $\mathrm{d}\mathbf{m}^{\intercal}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and $\boldsymbol{\beta}$ as our $\partial w/\partial \mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$, then Eq. (62) shows that $\boldsymbol{\eta} = \mathbf{\Phi}\boldsymbol{\beta}$ corresponds to the total selection gradient of controls $\mathrm{d}w/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$, which we have shown can predict evolutionary equilibria. Morrissey gave a different treatment to linear (Morrissey 2014) and non-linear (Morrissey 2015) (implicit) developmental maps, so in the latter case he did not write evolutionary change as a Lande's type equation. We obtain equations describing evolutionary change involving a Lande's type term despite non-linear developmental maps because we linearize invasion fitness by assuming weak mutation (Eq. 13) (Dieckmann and Law 1996).

Our results allow for the modelling of evo-devo dynamics in a wide array of settings. First, developmental and environmental constraints (Eqs. 88b and 88c) can mechanistically describe development, gene-gene interaction, and gene-environment interaction, while allowing for arbitrary non-linearities and evolution of the developmental map (or genotype-phenotype map). Many previous approaches have modelled gene-gene interaction, such as by considering multiplicative gene effects, but general frameworks mechanistically linking gene-gene interaction, gene-environment interaction, developmental dynamics, and evolutionary dynamics have previously remained elusive (Rice 1990; Hansen and Wagner 2001; Rice 2002; Hermisson *et al.* 2003; Carter *et al.* 2005). A historically dominant yet debated view is that gene-gene interaction has minor evolutionary effects as phenotypic evolution depends on additive rather than epistatic effects to a first-order of approximation, so epistasis would act by influencing a seemingly effectively non-singular $\mathbf{G}$ (Hansen 2013; Nelson *et al.* 2013; Paixão and Barton 2016; Barton 2017). Our results show that $\mathbf{G}$ is singular and that evolutionary equilibria depend on development and so on gene-gene and gene-environment interaction. Hence, gene-gene and gene-environment interaction may have strong and permanent evolutionary effects (e.g., via developmental feedbacks described by $\mathrm{d}\mathbf{x}^{\intercal}/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$).

Second, our results allow for the study of the evolution of the $\mathbf{G}$-matrix as an emergent property of the evolution of the phenotype and environment (i.e., the metaphenotype) rather than treating $\mathbf{G}$ as another dynamic variable as is traditionally done (Bulmer 1971; Lande 1979; Bulmer 1980; Lande 1980; Lande and Arnold 1983; Barton and Turelli 1987; Turelli 1988; Gavrilets and Hastings 1994; Carter *et al.* 2005). Third, our results allow for the study of the effects of developmental bias, biased genetic variation, and modularity (Wagner 1996; Pavlicev *et al.* 2011; Wagner and Zhang 2011; Pavlicev and Wagner 2012; Watson *et al.* 2013). Indeed, while we have assumed that mutation is unbiased for genetic traits, our equations allow for the developmental map to lead to biases in genetic variation for developed traits. This may lead to modular effects of mutations, whereby altering a control tends to affect some states but not others.

Fourth, our equations allow for the study of the evolutionary dynamics of life-history models with dynamic constraints. Life-history models with dynamic constraints have previously been restricted to evolutionary equilibria (e.g., González-Forero *et al.* 2017; González-Forero and Gardner 2018). Previous frameworks of evolutionary dynamics of functioned-valued traits allow for the modelling of evolutionary dynamics of traits that vary over age or stage, but such frameworks do not generally consider dynamic constraints (i.e., they consider the evolution of control variables but allow for state variables on a case by case basis at most) (Kirkpatrick and Heckman 1989; Dieckmann *et al.* 2006; Coulson *et al.* 2010; Parvinen *et al.* 2013; Metz *et al.* 2016; Rees and Ellner 2016). Fifth, our framework allows for the modelling of the evo-devo dynamics of pattern formation by implementing reaction-diffusion equations in discrete space in the developmental map (e.g., Eq. 6.1 of Turing 1952; Tomlin and Axelrod 2007). Sixth, our framework also allows for the mechanistic modelling of adaptive plasticity, for instance, by implementing reinforcement learning or supervised learning in the developmental map (Sutton and Barto 2018; Paenke *et al.* 2007). To model evo-devo dynamics, it may often be simpler to compute the evolutionary dynamics of controls and the developmental dynamics of states, rather than the evolutionary dynamics of the phenotype or metaphenotype. In such cases, after solving for the evo-devo dynamics, one can then compute the matrices composing the evolutionary dynamics of the phenotype and metaphenotype to gain a detailed understanding of the evolutionary factors at play, including the evolution of the $\mathbf{G}$-matrix.

By allowing development to be social, our framework allows for a mechanistic description of extra-genetic inheritance and indirect genetic effects. Extra-genetic inheritance can be described since the states at a given age can be an identical or modified copy of the states of social partners. Thus, social development allows for the modelling of social learning (Sutton and Barto 2018; Paenke *et al.* 2007) and epigenetic inheritance (Jablonka *et al.* 1992; Slatkin 2009; Day and Bonduriansky 2011). However, we have only considered social interactions among non-relatives, so our framework at present only allows for social learning or epigenetic inheritance from non-relatives. Additionally, indirect genetic effects, where genes partly or completely causing a phenotype may be located in another individual (Moore *et al.* 1997), can be mechanistically described by social development since the controls or states of social partners influence the developed phenotype. Indirect genetic effect approaches model the phenotype as a linear regression of individual's phenotype on social partner's phenotype (Kirkpatrick and Lande 1989; Moore *et al.* 1997; Townley and Ezard 2013), whereas our approach constructs individual's phenotype from development depending on social partners' phenotypes. We have found that social development generates social feedback (described by $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^{\intercal}|_{\mathbf{y}=\bar{\mathbf{y}}}$, Eq. 68), which closely though not entirely corresponds to social feedback found in the indirect genetic effects literature (Moore *et al.* 1997, Eq. 19b and subsequent text). The social feedback we obtain depends on total social developmental bias from states ($\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^{\intercal}|_{\mathbf{y}=\bar{\mathbf{y}}}$, Eq. 47); analogously, social feedback in the indirect genetic effects literature depends on the matrix of interaction coefficients ($\mathbf{\Psi}$) which contains the regression coefficients of phenotype on social partner's phenotype. Social development leads to a generalization of additive genetic covariance matrices $\mathbf{G} = \mathrm{cov}[\mathbf{a}, \mathbf{a}]$ into additive socio-genetic cross-covariance matrices $\mathbf{H} = \mathrm{cov}[\mathbf{b}, \mathbf{a}]$; similarly, indirect genetic effects involve a generalization of the $\mathbf{G}$-matrix, involving $\mathbf{C}_{\mathbf{az}} = \mathrm{cov}[\mathbf{a}, \mathbf{z}]$ which is the cross-covariance matrix between multivariate breeding value and phenotype (Kirkpatrick and Lande 1989; Moore *et al.* 1997; Townley and Ezard 2013). However, there are differences between our results and those in the indirect genetic effects literature: for instance, social feedback appears twice in the evolutionary dynamics under indirect genetic effects (see Eqs. 20 and 21 of Moore *et al.* 1997) while it only appears once in our evolutionary dynamics equations through $\mathrm{s}\mathbf{x}/\mathrm{s}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ (Eq. 84); additionally, our $\mathbf{H}$ matrices make the evolutionary dynamics equations depend on total social developmental bias from *controls* ($\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{y}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$, Eq. 69a) in a non-feedback manner (specifically, not in an inverse matrix) but this type of dependence does not occur in the evolutionary dynamics under indirect genetic effects (Eqs. 20 and 21 of Moore *et al.* 1997); moreover, "social selection" (i.e., $\partial w/\partial \bar{\mathbf{z}}$) plays no role in our results in principle because we assume there is no kin selection, but social selection plays an important role in the indirect genetic effects literature even if relatedness is zero (McGlothlin *et al.* 2010, e.g., setting $r = 0$ in their Eq. 10 still leaves an effect of social selection on selection response). This raises the question of whether some of these differences disappear if controls are closed-loop (e.g., if gene expression depends on social partners' phenotypes).

Our results clarify the role of several developmental factors previously suggested to be evolutionarily important. We have arranged the evo-devo process in a layered structure, where a given layer is formed by components of layers below (Fig. 5). This layered structure helps see that several developmental factors previously suggested to have important evolutionary effects (Laland *et al.* 2014) but with little clear connection (Welch 2017) can be viewed as basic elements of the evolutionary process. Direct-effect matrices (Layer 2) are basic in that they form all the components of the evolutionary dynamics (Layer 7) except mutational variation and exogenous environmental change. Direct-effect matrices quantify (i) directional selection, (ii) developmental bias, (iii) niche construction, (iv) social developmental bias (e.g., extra-genetic inheritance and indirect genetic effects; Moore *et al.* 1997), (v) social niche construction, (vi) environmental sensitivity of selection (Chevin *et al.* 2010), and (vii) phenotypic plasticity. These factors variously affect selection and development, thus affecting evolutionary equilibria and the admissible evolutionary trajectory.

Our approach uses discrete rather than continuous age, which substantially simplifies the mathematics. We recover Lande's (1979) equation—which slightly differs from Lande's (1982) age-structured equation—despite having age structure by discretizing age and making use of matrix calculus notation, which allows for compact expressions that incorporate the effects of age structure. This treatment allows for the derivation of analytic expressions for what is otherwise a difficult mathematical challenge if age is continuous (Kirkpatrick and Heckman 1989; Dieckmann *et al.* 2006; Avila *et al.* 2021). For instance, we obtain formulas for the total selection gradient of states (Eq. 63), and in Appendix 13 we show that such gradient is proportional to costate variables (Eq. A96). Costate variables are key in dynamic optimization as used in life-history models (Sydsæter *et al.* 2008), but formulas for costate variables are often unavailable and it can be difficult to interpret how costate variables relate to the evolutionary process. We show that the total selection gradient of states, and so costate variables, affect the evolutionary process by affecting total genetic selection (fifth line of Eq. 64), thus influencing evolutionary equilibria. Although discretization of age may induce numerical imprecision if the continuous age dependence were known (Kirkpatrick and Heckman 1989), precision may be increased by reducing the age bin size (e.g., to represent months or days rather than years; Caswell 2001), potentially at a computational cost.

By simplifying the mathematics, our approach yields insight that has been otherwise challenging to gain. Life-history models with dynamic constraints generally find that costate variables are non-zero under optimal controls (Gadgil and Bossert 1970; Taylor *et al.* 1974; León 1976; Schaffer 1983; Houston *et al.* 1988; Houston and McNamara 1999; Sydsæter *et al.* 2008). This means that there is persistent total selection on states at evolutionary equilibrium. Our findings clarify that this is to be expected because of the arrow of developmental time, since controls at a given age cannot adjust states at the same age but only at a later age (i.e., the matrix of semi-total effects of controls on states is singular; Eq. A48). Thus, total genetic selection may generally vanish with persistent total selection on states (fifth line of Eq. 64). Moreover, life-history models with explicit developmental constraints have found that their predictions can be substantially different from those found without explicit developmental constraints. In particular, with developmental constraints, the outcome of parent-offspring conflict over sex allocation has been found to be that preferred by the mother (Avila *et al.* 2019), whereas without developmental constraints the outcome has been found to be an intermediate between those preferred by mother and offspring (Reuter and Keller 2001). Our results show that the particular form of the developmental map may induce substantial changes in predictions by influencing total genetic selection and the admissible evolutionary equilibria.

We have obtained a term that we call exogenous plastic response, which is the plastic response to exogenous environmental change over an evolutionary time step (Eq. 90). An analogous term occurs in previous equations (Eq. A3 of Chevin *et al.* 2010). Additionally, *endogenous* plastic response may occur due to niche construction (i.e., endogenous environmental change) and it affects both the selection response and the exogenous plastic response. Exogenous plastic response does not involve change in gene frequency, but it affects the evolutionary dynamics. An immediate evolutionary effect of exogenous plastic response is as follows. At an evolutionary equilibrium where exogenous plastic response is absent, the introduction of exogenous plastic response generally changes socio-genetic covariation or directional selection at a subsequent evolutionary time, thereby inducing selection response. This constitutes a simple form of "plasticity-first" evolution (West-Eberhard 2003), whereby plastic change precedes genetic change, although the plastic change may not be adaptive and the induced genetic change may have a different direction to that of the plastic change.

To conclude, we have formulated a framework that synthesizes developmental and evolutionary dynamics yielding a theory of constrained evolutionary dynamics under age structure. This framework shows that development has major evolutionary effects as it affects both evolutionary equilibria and the admissible evolutionary path. Our results provide a tool to chart major territory on how development affects evolution.

Acknowledgements

We thank K.N. Laland, R. Lande, L.C. Mikula, A.J. Moore, and M.B. Morrissey for comments on previous versions of the manuscript, and D.M. Shuker for feedback. We thank M.B. Morrissey for discussion and explanation of his work. This work was funded by an ERC Consolidator Grant to AG (grant no. 771387). AG was also funded by a NERC Independent Research Fellowship (grant no. NE/K009524/1).

Literature Cited

Altenberg, L., 1995 Genome growth and the evolution of the genotype-phenotype map. In *Evolution and biocomputation*, edited by W. Banzhaf and F. H. Eeckman, volume 899 of *Lecture Notes in Computer Science*, pp. 205–259, Springer-Verlag.

Arnold, S. J., 1992 Constraints on phenotypic evolution. Am. Nat. **140**: S85–S107.

Arnold, S. J., R. Bürger, P. A. Hohenlohe, B. C. Ajie, and A. G. Jones, 2008 Understanding the evolution and stability of the G-matrix. Evolution **62**: 2451–2461.

Avila, P., L. Fromhage, and L. Lehmann, 2019 Sex-allocation conflict and sexual selection throughout the lifespan of eusocial colonies. Evolution **73**: 1116–1132.

Avila, P., T. Priklopil, and L. Lehmann, 2021 Hamilton's rule, gradual evolution, and the optimal (feedback) control of phenotypically plastic traits. J. Theor. Biol. p. 110602.

Baldwin, J. M., 1896 A new factor in evolution. Am. Nat. **30**: 441–451.

Barton, N. H., 2017 How does epistasis influence the response to selection? Heredity **118**: 96–109.

Barton, N. H. and M. Turelli, 1987 Adaptive landscapes, genetic distance and the evolution of quantitative characters. Genet. Res. **49**: 157–173.

Bienvenu, F. and S. Legendre, 2015 A new approach to the generation time in matrix population models. Am. Nat. **185**: 834–843.

Björklund, M., A. Husby, and L. Gustafsson, 2013 Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. J. Evol. Biol. **26**: 1–13.

Blows, M. W., 2007 A tale of two matrices: multivariate approaches in evolutionary biology. J. Evol. Biol. **20**: 1–8.

Blows, M. W. and A. A. Hoffmann, 2005 A reassessment of genetic limits to evolutionary change. Ecology **86**: 1371–1384.

Boyd, R. and P. J. Richerson, 1985 *Culture and the Evolutionary Process*. The Univ. of Chicago Press, Chicago, IL, USA.

Bulmer, M., 1994 *Theoretical Evolutionary Ecology*. Sinauer, Sunderland, MA, USA.

Bulmer, M. G., 1971 The effect of selection on genetic variability. Am. Nat. **105**: 201–211.

Bulmer, M. G., 1980 *The Mathematical Theory of Quantitative Genetics*. Oxford Univ. Press, Oxford, UK.

Carter, A. J. R., J. Hermisson, and T. F. Hansen, 2005 The role of epistatic interactions in the response to selection and the evolution of evolvability. Theor. Popul. Biol. **68**: 179–196.

Caswell, H., 1978 A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. **14**: 215–230.

Caswell, H., 2001 *Matrix Population Models*. Sinauer, Sunderland, MA, USA, second edition.

Caswell, H., 2009 Stage, age and individual stochasticity in demography. Oikos **118**: 1763–1782.

Caswell, H., 2019 *Sensitivity Analysis: Matrix Methods in Demography and Ecology*. Springer Open, Cham, Switzerland.

Caswell, H. and E. Shyu, 2017 4, pp. 56–82 in *Senescence, selection gradients and mortality*, edited by Shefferson, R. P., O. R. Jones, and R. Salguero-Gómez, Cambridge Univ. Press.

Cavalli-Sforza, L. L. and M. W. Feldman, 1981 *Cultural Transmission and Evolution*. Princeton Univ. Press, Princeton, NJ, USA.

Chantepie, S. and L.-M. Chevin, 2020 How does the strength of selection influence genetic correlations? Evol. Lett. **4-6**: 468–478.

Charlesworth, B., 1990 Optimization models, quantitative genetics, and mutation. Evolution **44**: 520–538.

Charlesworth, B., 1993 Natural selection on multivariate traits in age-structured populations. Proc. R. Soc. Lond. B **251**: 47–52.

Charlesworth, B., 1994 *Evolution in age-structured populations*. Cambridge Univ. Press, second edition.

Charlesworth, B., R. Lande, and M. Slatkin, 1982 A neo-Darwinian commentary on macroevolution. Evolution **36**: 474–498.

Cheverud, J. M., 1984 Quantitative genetics and developmental constraints on evolution by selection. J. Theor. Biol. **110**: 155–171.

Cheverud, J. M., J. J. Rutledge, and W. R. Atchley, 1983 Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution **37**: 895–905.

Chevin, L.-M., R. Lande, and G. M. Mace, 2010 Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLOS Biology **8**: 1–8.

Coulson, T., S. Tuljapurkar, and D. Z. Childs, 2010 Using evolutionary demography to link life history theory, quantitative genetics and population ecology. J. Anim. Ecol. **79**: 1226–1240.

Creanza, N. and M. W. Feldman, 2014 Complexity in models of cultural niche construction with selection and homophily. Proc. Natl. Acad. Sci. USA **111**: 10830–10837.

Creanza, N., L. Fogarty, and M. W. Feldman, 2012 Models of cultural niche construction with selection and assortative mating. PLOS ONE **7**: 1–11.

Crow, J. F. and M. Kimura, 1970 *An Introduction to Population Genetics Theory*. Blackburn Press, Caldwell, NJ, USA.

Day, T. and R. Bonduriansky, 2011 A unified approach to the evolutionary consequences of genetic and nongenetic inheritance. Am. Nat. **178**: E18–E36.

de Vries, C. and H. Caswell, 2018 Demography when history matters: construction and analysis of second-order matrix population models. Theor. Ecol. **11**: 129–140.

de Vries, C. and H. Caswell, 2019 Stage-structured evolutionary demography: linking life histories, population genetics, and ecological dynamics. Am. Nat. **193**: 545–559.

Dieckmann, U., M. Heino, and K. Parvinen, 2006 The adaptive dynamics of function-valued traits. J. Theor. Biol. **241**: 370–389.

Dieckmann, U. and R. Law, 1996 The dynamical theory of coevolution: a derivation from stochastic ecological processes. J. Math. Biol. **34**: 579–612.

Durinx, M., J. A. J. (Hans) Metz, and G. Meszéna, 2008 Adaptive dynamics for physiologically structured population models. J. Math. Biol. **56**: 673–742.

Engen, S. and B.-E. Sæther, 2021 Structure of the G-matrix in relation to phenotypic contributions to fitness. Theor. Popul. Biol. **138**: 43–56.

Falconer, D. S. and T. F. C. Mackay, 1996 *Introduction to Quantitative Genetics*. Pearson Prentice Hall, Harlow, England, fourth edition.

Fisher, R., 1918 XV.—The correlation between relatives on the supposition of Mendelian inheritance. Trans. Roy. Soc. Edinb. **52**: 399–433.

Fisher, R. A., 1922 XXI.—On the dominance ratio. Trans. Roy. Soc. Edinb. **42**: 321–341.

Fisher, R. A., 1927 The actuarial treatment of official birth records. Eugen. Rev. **19**: 103–108.

Frank, S. A., 2012 Natural selection. IV The Price equation. J. Evol. Biol. **25**: 1002–1019.

Gadgil, M. and W. H. Bossert, 1970 Life historical consequences of natural selection. Am. Nat. **104**: 1–24.

Gavrilets, S. and A. Hastings, 1994 A quantitative-genetic model for selection on developmental noise. Evolution **48**: 1478–1486.

Gimelfarb, A., 1982 Quantitative character dynamics: Gametic model. Theor. Popul. Biol. **22**: 324–366.

Gomulkiewicz, R. and M. Kirkpatrick, 1992 Quantitative genetics and the evolution of reaction norms. Evolution **46**: 390–411.

González-Forero, M., T. Faulwasser, and L. Lehmann, 2017 A model for brain life history evolution. PLOS Comp. Biol. **13**: e1005380.

González-Forero, M. and A. Gardner, 2018 Inference of ecological and social drivers of human brain-size evolution. Nature **557**: 554–557.

Gould, S. J. and R. C. Lewontin, 1979 The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. Lond. B **205**: 581–598.

Hamilton, W. D., 1966 The moulding of senescence by natural selection. J. Theor. Biol. **12**: 12–45.

Hansen, T. F., 2013 Why epistasis is important for selection and adaptation. Evolution **67**: 3501–3511.

Hansen, T. F. and D. Houle, 2004 Evolvability, stabilizing selection, and the problem of stasis. In *Phenotypic integration: studying ecology and evolution of complex phenotypes*, edited by M. Pigliucci and K. Preston, chapter 5, Oxford Univ. Press.

Hansen, T. F. and D. Houle, 2008 Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. **21**: 1201–1219.

Hansen, T. F. and G. P. Wagner, 2001 Modeling genetic architecture: a multilinear theory of gene interaction. Theor. Popul. Biol. **59**: 61–86.

Hermisson, J., T. F. Hansen, and G. P. Wagner, 2003 Epistasis in polygenic traits and the evolution of genetic architecture under stabilizing selection. Am. Nat. **161**: 708–734.

Hill, W. G. and R. Thompson, 1978 Probabilities of non-positive definite between-group or genetic covariance matrices. Biometrics **34**: 429–439.

Hine, E. and M. W. Blows, 2006 Determining the effective dimensionality of the genetic variance-covariance matrix. Genetics **173**: 1135–1144.

Hine, E., K. McGuigan, and M. W. Blows, 2014 Evolutionary constraints in high-dimensional traits sets. Am. Nat. **184**: 119–131.

Horn, R. A. and C. R. Johnson, 2013 *Matrix Analysis*. Cambridge Univ. Press, New York, NY, USA, second edition.

Houle, D., 1991 Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution **45**: 630–648.

Houle, D., 2001 Characters as the units of evolutionary change. In *The Character Concept in Evolutionary Biology*, edited by G. P. Wagner, pp. 109–140, Academic Press, San Diego, CA, USA.

Houston, A., C. Clark, J. McNamara, and M. Mangel, 1988 Dynamic models in behavioural and evolutionary ecology. Nature **332**: 29–34.

Houston, A. I. and J. M. McNamara, 1999 *Models of Adaptive Behaviour: an approach based on state*. Cambridge Univ. Press.

Jablonka, E., M. Lachmann, and M. J. Lamb, 1992 Evidence, mechanisms and models for the inheritance of acquired characters. J. Theor. Biol. **158**: 245–268.

Jones, A. G., S. J. Arnold, and R. Bürger, 2003 Stability of the G-matrix in a population experiencing pleiotropic mutation, stabilizing selection, and genetic drift. Evolution **57**: 1747–1760.

Jones, A. G., S. J. Arnold, and R. Bürger, 2004 Evolution and stability of the G-matrix on a landscape with a moving optimum. Evolution **58**: 1639–1654.

Jones, A. G., S. J. Arnold, and R. Bürger, 2007 The mutation matrix and the evolution of evolvability. Evolution .

Jones, A. G., R. Bürger, and S. J. Arnold, 2014 Epistasis and natural selection shape the mutational architecture of complex traits. Nat. Comm. **5**: 3709.

Jones, A. G., R. Bürger, S. J. Arnold, P. A. Hohenlohe, and J. C. Uyeda, 2012 The effects of stochastic and episodic movement of the optimum on the evolution of the g-matrix and the response of the trait mean to selection. J. Evol. Biol. **5**: 2210–2231.

Kaznatcheev, A., 2019 Computational complexity as an ultimate constraint on evolution. Genetics **212**: 245–265.

Kingsolver, J. G. and S. E. Diamond, 2011 Phenotypic selection in natural populations: What limits directional selection? Am. Nat. **177**: 346–357.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, *et al.*, 2001 The strength of phenotypic selection in natural populations. Am. Nat. **157**: 245–261.

Kirkpatrick, M., 2009 Patterns of quantitative genetic variation in multiple dimensions. Genetica **136**: 271–284.

Kirkpatrick, M. and N. Heckman, 1989 A quantitative genetic model for growth, shape, reaction norms, and other infinite-dimensional characters. J. Math. Biol. **27**: 429–450.

Kirkpatrick, M. and R. Lande, 1989 The evolution of maternal characters. Evolution **43**: 485–503.

Kirkpatrick, M. and D. Lofsvold, 1992 Measuring selection and constraint in the evolution of growth. Evolution **46**: 954–971.

Klingenberg, C. P., 2005 11. Developmental constraints, modules, and evolvability, pp. 219–247 in *Variation*, edited by Hallgrímsson, B. and B. K. Hall, Academic Press.

Klingenberg, C. P., 2010 Evolution and development of shape: integrating quantitative approaches. Nat. Rev. Genet. **11**: 623–635.

Kobayashi, Y., J. Y. Wakano, and H. Ohtsuki, 2019 Evolution of cumulative culture for niche construction. J. Theor. Biol. **472**: 67–76.

Laland, K., T. Uller, M. Feldman, K. Sterelny, G. B. Müller, *et al.*, 2014 Does evolutionary theory need a rethink? Yes, urgently. Nature **514**: 161–164.

Laland, K. N., F. J. Odling-Smee, and M. W. Feldman, 1996 The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. J. Evol. Biol. **9**: 293–316.

Laland, K. N., F. J. Odling-Smee, and M. W. Feldman, 1999 Evolutionary consequences of niche construction and their implications for ecology. Proc. Natl. Acad. Sci. USA **96**: 10242–10247.

Laland, K. N., J. Odling-Smee, and M. W. Feldman, 2001 Cultural niche construction and human evolution. J. Evol. Biol. **14**: 22–33.

Laland, K. N., T. Uller, M. W. Feldman, K. Sterelny, G. B. Müller, *et al.*, 2015 The extended evolutionary synthesis: its structure, assumptions and predictions. Proc. R. Soc. B **282**: 20151019.

Lande, R., 1979 Quantitative genetic analysis of multivariate evolution applied to brain: body size allometry. Evolution **34**: 402–416.

Lande, R., 1980 The genetic covariance between characters maintained by pleiotropic mutations. Genetics **94**: 203–215.

Lande, R., 1982 A quantitative genetic theory of life history evolution. Ecology **63**: 607–615.

Lande, R., 2009 Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J. Evol. Biol. **22**: 1435–1446.

Lande, R., 2014 Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. J. Evol. Biol. **27**: 866–875.

Lande, R., 2019 Developmental integration and evolution of labile plasticity in a complex quantitative character in a multiperiodic environment. Proc. Natl. Acad. Sci. USA **116**: 11361–11369.

Lande, R. and S. J. Arnold, 1983 The measurement of selection on correlated characters. Evolution **37**: 1210–1226.

Lehmann, L., 2007 The evolution of trans-generational altruism: kin selection meets niche construction. J. Evol. Biol. **20**: 181–189.

Lehmann, L., 2008 The adaptive dynamics of niche constructing traits in spatially subdivided populations: Evolving posthumous extended phenotypes. Evolution **62**: 549–566.

León, J. A., 1976 Life histories as adaptive strategies. J. Theor. Biol. **60**: 301–335.

Lush, J. L., 1937 *Animal Breeding Plans*. Iowa State Univ. Press, Ames, IA, USA.

Lynch, M. and B. Walsh, 1998 *Genetics and Analysis of Quantitative Traits*. Sinauer, Sunderland, MA, USA.

Martin, G., 2014 Fisher's geometrical model emerges as a property of complex integrated phenotypic networks. Genetics **197**: 237–255.

Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, *et al.*, 1985 Developmental constraints and evolution. Q. Rev. Biol. .

McGlothlin, J. W., A. J. Moore, J. B. Wolf, and E. D. Brodie III, 2010 Interacting phenotypes and the evolutionary process. III. Social evolution. Evolution **64**: 2558–2574.

McGuigan, K. and M. Blows, 2007 The phenotypic and genetic covariance structure of Drosophilid wings. Evolution **61**: 902–911.

Medawar, P. B., 1952 *An unsolved problem of biology*. H. K. Lewis, London, UK.

Merilä, J., B. Sheldon, and L. Kruuk, 2001 Explaining stasis: microevolutionary studies in natural populations. Genetica **112**: 199–222.

Metz, J. A. J., K. Staňková, and J. Johansson, 2016 The canonical equation of adaptive dynamics for life histories: from fitness-returns to selection gradients and Pontryagin's maximum principle. J. Math. Biol. **72**: 1125–1152.

Meyer, K. and M. Kirkpatrick, 2008 Perils of parsimony: Properties of reduced-rank estimates of genetic covariance matrices. Genetics **180**: 1153–1166.

Mezey, J. G. and D. Houle, 2005 The dimensionality of genetic variation for wing shape in *Drosophila melanogaster*. Evolution **59**: 1027–1038.

Michel, M. J., L.-M. Chevin, and J. H. Knouft, 2014 Evolution of phenotype–environment associations by genetic responses to selection and phenotypic plasticity in a temporally autocorrelated environment. Evolution **68**: 1374–1384.

Milocco, L. and I. Salazar-Ciudad, 2020 Is evolution predictable? quantitative genetics under complex genotype-phenotype maps. Evolution **74**: 230–244.

Moore, A. J., E. D. Brodie III, and J. B. Wolf, 1997 Interacting phenotypes and the evolutionary process: I. direct and indirect genetic effects of social interactions. Evolution **51**: 1352–1362.

Morrissey, M. B., 2014 Selection and evolution of causally covarying traits. Evolution **68**: 1748–1761.

Morrissey, M. B., 2015 Evolutionary quantitative genetics of nonlinear developmental systems. Evolution **69**: 2050–2066.

Mullon, C. and L. Lehmann, 2017 Invasion fitness for gene-culture co-evolution in family-structured populations and an application to cumulative culture under vertical transmission. Theor. Popul. Biol. **116**: 33–46.

Mullon, C. and L. Lehmann, 2018 Eco-evolutionary dynamics in metacommunities: Ecological inheritance, helping within species, and harming between species. Am. Nat. **192**: 664–686.

Mullon, C., J. Y. Wakano, and H. Ohtsuki, 2021 Coevolutionary dynamics of genetic traits and their long-term extended effects under non-random interactions. J. Theor. Biol. p. 110750.

Mylius, S. D. and O. Diekmann, 1995 On evolutionarily stable life histories, optimization and the need to be specific about density dependence. Oikos **74**: 218–224.

Nelson, R. M., M. E. Pettersson, and Ö. Carlborg, 2013 A century after Fisher: time for a new paradigm in quantitative genetics. Trends Genet. **29**: 669–676.

Noble, D. W. A., R. Radersma, and T. Uller, 2019 Plastic responses to novel environments are biased towards phenotype dimensions with high additive genetic variation. Proc. Natl. Acad. Sci. USA **116**: 13452–13461.

Otto, S. P. and T. Day, 2007 *A Biologist's Guide to Mathematical Models in Ecology and Evolution*. Princeton Univ. Press, Woodstock, UK.

Paenke, I., B. Sendhoff, and T. J. Kawecki, 2007 Influence of plasticity and learning on evolution under directional selection. Am. Nat. **170**: E47–E58.

Paixão, T. and N. H. Barton, 2016 The effect of gene interactions on the long-term response to selection. Proc. Natl. Acad. Sci. USA **113**: 4422–4427.

Parvinen, K., M. Heino, and U. Dieckmann, 2013 Function-valued adaptive dynamics and optimal control theory. J. Math. Biol. **67**: 509–533.

Pavlicev, M., J. M. Cheverud, and G. P. Wagner, 2011 Evolution of adaptive phenotypic variation patterns by direct selection for evolvability. Proc. R. Soc. B **278**: 1903–1912.

Pavlicev, M. and G. P. Wagner, 2012 A model of developmental evolution: selection, pleiotropy and compensation. Trends. Ecol. Evol. **27**: 316–322.

Pavlicev, M., G. P. Wagner, and J. M. Cheverud, 2009 Measuring evolutionary constraints through the dimensionality of the phenotype: adjusted bootstrap method to estimate rank of phenotypic covariance matrices. Evol. Biol. **36**: 339–353.

Price, G. R., 1970 Selection and covariance. Nature **227**: 520–521.

Priklopil, T. and L. Lehmann, 2020 Invasion implies substitution in ecological communities with class-structured populations. Theor. Popul. Biol. **134**: 36–52.

Pujol, B., S. Blanchet, A. Charmantier, E. Danchin, B. Facon, *et al.*, 2018 The missing response to selection in the wild. Trends Ecol. Evol. **33**: 337–346.

Rees, M. and S. P. Ellner, 2016 Evolving integral projection models: evolutionary demography meets eco-evolutionary dynamics. Methods Ecol. Evol. **7**: 157–170.

Rendell, L., L. Fogarty, and K. N. Laland, 2011 Runaway cultural niche construction. Phil. Trans. R. Soc. B **366**: 823–835.

Reuter, M. and L. Keller, 2001 Sex ratio conflict and worker production in eusocial hymenoptera. Am. Nat. **158**: 166–177.

Rice, S. H., 1990 A geometric model for the evolution of development. J. Theor. Biol. **143**: 319–342.

Rice, S. H., 2002 A general population genetic theory for the evolution of developmental interactions. Proc. Natl. Acad. Sci.

USA **99**: 15518–15523.

Salazar-Ciudad, I. and J. Jernvall, 2002 A gene network model accounting for development and evolution of mammalian teeth. Proc. Natl. Acad. Sci. USA **99**: 8116–8120.

Salazar-Ciudad, I. and M. Marín-Riera, 2013 Adaptive dynamics under development-based genotype–phenotype maps. Nature **497**: 361–364.

Samuelson, P. A., 1947 *Foundations of economic analysis*. Harvard Univ. Press, Cambridge, MA, USA.

Schaffer, W. M., 1983 The application of optimal control theory to the general life history problem. Am. Nat. **121**: 418–431.

Schluter, D., 1996 Adaptive radiation along genetic lines of least resistance. Evolution **50**: 1766–1774.

Slatkin, M., 2009 Epigenetic inheritance and the missing heritability problem. Genetics **182**: 845–850.

Sternberg, S., 2010 *Dynamical Systems*. Dover Publications, Inc., Mineola, NY, USA.

Sutton, R. S. and A. G. Barto, 2018 *Reinforcement Learning: An Introduction*. The MIT Press, Cambridge, Massachusetts, USA, second edition.

Sydsæter, K., P. Hammond, A. Seierstad, and A. Strom, 2008 *Further Mathematics for Economic Analysis*. Prentice Hall, second edition.

Taylor, H. M., R. S. Gourley, C. E. Lawrence, and R. S. Kaplan, 1974 Natural selection of life history attributes: an analytical approach. Theor. Popul. Biol. **5**: 104–122.

Tomlin, C. J. and J. D. Axelrod, 2007 Biology by numbers: mathematical modelling in developmental biology. Nat. Rev. Genet. **8**: 331–340.

Townley, S. and T. H. G. Ezard, 2013 A G matrix analogue to capture the cumulative effects of nongenetic inheritance. J. Evol. Biol. **26**: 1234–1243.

Turelli, M., 1988 Phenotypic evolution, constant covariances, and the maintenance of additive variance. Evolution **42**: 1342–1347.

Turing, A. M., 1952 The chemical basis of morphogenesis. Phil. Trans. R. Soc. Lond. B **237**: 37–72.

Via, S. and R. Lande, 1985 Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution **39**: 505–522.

Waddington, C. H., 1959 Evolutionary adaptation. Perspect. Biol. Med. **2**: 379–401.

Wagner, G. P., 1984 On the eigenvalue distribution of genetic and phenotypic dispersion matrices: Evidence for a nonrandom organization of quantitative character variation. J. Math. Biol. **21**: 77–95.

Wagner, G. P., 1988 The influence of variation and of developmental constraints on the rate of multivariate phenotypic evolution. J. Evol. Biol. **1**: 45–66.

Wagner, G. P., 1989 Multivariate mutation-selection balance with constrained pleiotropic effects. Genetics **122**: 223–234.

Wagner, G. P., 1996 Homologues, natural kinds and the evolution of modularity. Am. Zool. **36**: 36–43.

Wagner, G. P. and J. Zhang, 2011 The pleiotropic structure of the genotype-phenotype map: the evolvability of complex organisms. Nat. Rev. Genet. **12**: 204–213.

Walsh, B. and M. W. Blows, 2009 Abundant genetic variation + strong selection = multivariate genetic constraints: A geometric view of adaptation. Annu. Rev. Ecol. Evol. Syst. **40**: 41–59.

Walsh, B. and M. Lynch, 2018 *Evolution and Selection of Quantitative Traits*. Oxford Univ. Press, Oxford, UK.

Watson, R. A., G. P. Wagner, M. Pavlicev, D. M. Weinreich, and R. Mills, 2013 The evolution of phenotypic correlations and "developmental memory". Evolution **68**: 1124–1138.

Welch, J. J., 2017 What's wrong with evolutionary biology? Biol. Philos. **32**: 263–279.

West-Eberhard, M. J., 2003 *Developmental Plasticity and Evolution*. Oxford Univ. Press, Oxford, UK.

Wild, G. and A. Traulsen, 2007 The different limits of weak selection and the evolutionary dynamics of finite populations. J. Theor. Biol. **247**: 382–390.

Wright, S., 1942 Statistical genetics and evolution. Bull. Amer. Math. Soc. **48**: 223–246.

Appendix 1: canonical equation

Here we derive the equation describing the evolutionary dynamics of controls. This derivation closely follows that of Dieckmann and Law (1996) except in a few places, particularly in that we consider deterministic population dynamics so the only source of stochasticity in our framework is due to mutation. Denote by $\bar{\mathbf{y}}'(\tau+\Delta\tau)$ a multivariate random variable describing the possible residents at time $\tau+\Delta\tau$ following fixation of mutants arising at time τ. Let this random variable have probability density function $P(\bar{\mathbf{y}}',\tau+\Delta\tau)$ at time $\tau+\Delta\tau$, with support in $\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}$. Hence, the expected resident controls at time $\tau+\Delta\tau$ are

$$\mathrm{E}[\bar{\mathbf{y}}'(\tau+\Delta\tau)] = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' P(\bar{\mathbf{y}}',\tau+\Delta\tau)\mathrm{d}\bar{\mathbf{y}}' \equiv \bar{\mathbf{y}}(\tau+\Delta\tau).$$

The evolutionary change in resident controls thus satisfies

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} &= \frac{\mathrm{E}[\bar{\mathbf{y}}'(\tau+\Delta\tau)] - \mathrm{E}[\bar{\mathbf{y}}'(\tau)]}{\Delta\tau}\\ &= \frac{1}{\Delta\tau}\left(\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' P(\bar{\mathbf{y}}',\tau+\Delta\tau)\mathrm{d}\bar{\mathbf{y}}' - \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' P(\bar{\mathbf{y}}',\tau)\mathrm{d}\bar{\mathbf{y}}'\right).\end{aligned}$$

Factorizing yields

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} &= \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' \frac{P(\bar{\mathbf{y}}',\tau+\Delta\tau) - P(\bar{\mathbf{y}}',\tau)}{\Delta\tau}\mathrm{d}\bar{\mathbf{y}}'\\ &= \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' \frac{\Delta P(\bar{\mathbf{y}}',\tau)}{\Delta\tau}\mathrm{d}\bar{\mathbf{y}}'.\end{aligned}$$

Now, the evolutionary change in the resident-control distribution satisfies the master equation

$$\frac{\Delta P(\bar{\mathbf{y}}',\tau)}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \left[\omega(\mathbf{y}\to\bar{\mathbf{y}}')P(\mathbf{y},\tau) - \omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)\right]\mathrm{d}\mathbf{y},$$

where $\omega(\mathbf{y}\to\bar{\mathbf{y}}')$ is the rate at which a resident $\mathbf{y}$ is replaced by $\bar{\mathbf{y}}'$. Then, the evolutionary change in controls is

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}' \Bigg(\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} &[\omega(\mathbf{y}\to\bar{\mathbf{y}}')P(\mathbf{y},\tau)\\ &- \omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)]\mathrm{d}\mathbf{y}\Bigg)\mathrm{d}\bar{\mathbf{y}}'.\end{aligned}$$

Since the integral is a linear operator, we have

$$\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}'\omega(\mathbf{y}\to\bar{\mathbf{y}}')P(\mathbf{y},\tau)\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'$$

$$-\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}'\omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'.$$

Exchanging $\mathbf{y}$ for $\bar{\mathbf{y}}'$ in the first term since they are dummy variables yields

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = &\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \mathbf{y}\omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'\\ &-\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \bar{\mathbf{y}}'\omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'.\end{aligned}$$

Factorizing yields

$$\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} (\mathbf{y}-\bar{\mathbf{y}}')\omega(\bar{\mathbf{y}}'\to\mathbf{y})P(\bar{\mathbf{y}}',\tau)\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'. \tag{A1}$$

Assuming that invasion implies fixation, we let the rate at which resident $\bar{\mathbf{y}}'$ is replaced by $\mathbf{y}$ be

$$\omega(\bar{\mathbf{y}}'\to\mathbf{y}) = \delta(\bar{\mathbf{y}}'-\bar{\mathbf{y}})\frac{M(\mathbf{y},\bar{\mathbf{y}}')}{P(\bar{\mathbf{y}}',\tau)}[\lambda(\mathbf{y},\bar{\mathbf{y}}')-1], \tag{A2}$$

where $\delta(\cdot)$ is the Dirac delta function. This expression for $\omega(\bar{\mathbf{y}}'\to\mathbf{y})$ can be understood as comprising the probability density $\delta(\bar{\mathbf{y}}'-\bar{\mathbf{y}})$ that the resident $\bar{\mathbf{y}}'$ is $\bar{\mathbf{y}}$, times the conditional probability density $M(\mathbf{y},\bar{\mathbf{y}}')/P(\bar{\mathbf{y}}',\tau)$ that a mutant is $\mathbf{y}$ given that the resident is $\bar{\mathbf{y}}'$ at time τ, times the rate of substitution $\lambda(\mathbf{y},\bar{\mathbf{y}}')-1$ for a mutant $\mathbf{y}$ in the context of resident $\bar{\mathbf{y}}'$. Substituting Eq. (A2) into Eq. (A1) using Eq. (13) yields

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \Bigg\{&(\mathbf{y}-\bar{\mathbf{y}}')\delta(\bar{\mathbf{y}}'-\bar{\mathbf{y}})\frac{M(\mathbf{y},\bar{\mathbf{y}}')}{P(\bar{\mathbf{y}}',\tau)}\\ &\left[(\mathbf{y}-\bar{\mathbf{y}}')^\intercal\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}'}+O(||\mathbf{y}-\bar{\mathbf{y}}'||^2)\right]P(\bar{\mathbf{y}}',\tau)\Bigg\}\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'.\end{aligned}$$

Cancelling $P(\bar{\mathbf{y}}',\tau)$ produces

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \Bigg\{&(\mathbf{y}-\bar{\mathbf{y}}')\delta(\bar{\mathbf{y}}'-\bar{\mathbf{y}})M(\mathbf{y},\bar{\mathbf{y}}').\\ &\left[(\mathbf{y}-\bar{\mathbf{y}}')^\intercal\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}'}+O(||\mathbf{y}-\bar{\mathbf{y}}'||^2)\right]\Bigg\}\mathrm{d}\mathbf{y}\mathrm{d}\bar{\mathbf{y}}'.\end{aligned}$$

Using the integration property of the Dirac delta function [i.e., $\int_{\mathbb{R}^n}F(\mathbf{y})\delta(\mathbf{y}-\bar{\mathbf{y}})\mathrm{d}\mathbf{y}=F(\bar{\mathbf{y}})$ for any function $F(\mathbf{y})$ with $\mathbf{y}\in\mathbb{R}^n$],

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} \Bigg\{&(\mathbf{y}-\bar{\mathbf{y}})M(\mathbf{y},\bar{\mathbf{y}})\\ &\left[(\mathbf{y}-\bar{\mathbf{y}})^\intercal\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}+O(||\mathbf{y}-\bar{\mathbf{y}}||^2)\right]\Bigg\}\mathrm{d}\mathbf{y}.\end{aligned}$$

Since the integral is a linear operator and because the evaluation at $\mathbf{y}=\bar{\mathbf{y}}$ makes the gradient constant with respect to $\mathbf{y}$, then

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = &\left[\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}}(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal M(\mathbf{y},\bar{\mathbf{y}})\mathrm{d}\mathbf{y}\right]\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &+\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} M(\mathbf{y},\bar{\mathbf{y}})O\left((\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal(\mathbf{y}-\bar{\mathbf{y}})\right)\mathrm{d}\mathbf{y}.\end{aligned}$$

By definition of covariance matrix, we have

$$\begin{aligned}\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = &\,\mathrm{cov}[\mathbf{y},\mathbf{y}]\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &+O\left(\int\limits_{\mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}} M(\mathbf{y},\bar{\mathbf{y}})\left[(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal(\mathbf{y}-\bar{\mathbf{y}})\right]\mathrm{d}\mathbf{y}\right).\end{aligned}$$

The matrix $\mathrm{cov}[\mathbf{y},\mathbf{y}]$ is *the mutational covariance matrix* (of controls). The big-O term on the right in the last equality is on the order of a measure of skewness of the mutational distribution. As we assume that the mutational distribution is symmetric, skewness vanishes, which yields

$$\frac{\Delta\bar{\mathbf{y}}}{\Delta\tau} = \mathrm{cov}[\mathbf{y},\mathbf{y}]\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A3}$$

This recovers a form of the canonical equation of adaptive dynamics (cf. Eq. 6.1 of Dieckmann and Law 1996 and Eq. 23 of Durinx *et al.* 2008).

We can rewrite the right-hand side of the canonical equation (A3) in a form that is reminiscent of the Price equation (Price 1970). Indeed, subtracting $\mathrm{E}[\lambda]$ from Eq. (13) yields

$$\lambda-\mathrm{E}[\lambda] = 1-\mathrm{E}[\lambda]+(\mathbf{y}-\bar{\mathbf{y}})^\intercal\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}+O(||\mathbf{y}-\bar{\mathbf{y}}||^2),$$

and premultiplying by $(\mathbf{y}-\bar{\mathbf{y}})$ produces

$$\begin{aligned}(\mathbf{y}-\bar{\mathbf{y}})(\lambda-\mathrm{E}[\lambda]) = &\,(\mathbf{y}-\bar{\mathbf{y}})(1-\mathrm{E}[\lambda])\\ &+(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &+O\left((\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal(\mathbf{y}-\bar{\mathbf{y}})\right).\end{aligned} \tag{A4}$$

Taking the expectation over the mutational distribution yields

$$\begin{aligned}\mathrm{E}[(\mathbf{y}-\bar{\mathbf{y}})(\lambda-\mathrm{E}[\lambda])] = &\,\mathrm{E}[(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal]\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &+O\left(\mathrm{E}[(\mathbf{y}-\bar{\mathbf{y}})(\mathbf{y}-\bar{\mathbf{y}})^\intercal(\mathbf{y}-\bar{\mathbf{y}})]\right),\end{aligned} \tag{A5}$$

where the total selection gradient of controls is outside of the expectation because the evaluation at $\mathbf{y}=\bar{\mathbf{y}}$ makes the gradient constant with respect to $\mathbf{y}$. From the definition of cross-covariance matrix, and since we assume that the mutational distribution is symmetric, Eq. (A5) becomes

$$\mathrm{cov}[\mathbf{y},\lambda] = \mathrm{cov}[\mathbf{y},\mathbf{y}]\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A6}$$

The left-hand side of Eq. (A6) is reminiscent of the Price equation (Price 1970; Frank 2012), which states that the evolutionary change of a univariate trait in the absence of transmission bias equals the covariance of the trait and relative fitness. Yet, note that there are differences between invasion fitness and relative fitness; in particular, invasion fitness is not the relative number of descendants at evolutionary time $\tau+1$ of rare mutants at τ (for *any* $\lambda>1$ all residents at $\tau+1$ are descendants of mutants at τ, yet for *any* $\lambda<1$ none is).

When deriving the evolutionary dynamics of the phenotype $\mathbf{z}$, we will obtain dynamic equations in terms of additive genetic covariance matrices. In particular, we will see that the mutational covariance matrix $\mathrm{cov}[\mathbf{y},\mathbf{y}]$ that we obtained in the canonical equation (A3) equals the additive genetic covariance matrix of controls. Indeed, in Eq. (77), we define the *additive* *genetic covariance matrix* $\mathbf{G}_\zeta$ of a vector $\zeta \in \mathbb{R}^{m\times 1}$ under our adaptive dynamics assumptions, and show that

$$\mathbf{G}_\zeta = \left.\left(\frac{\mathrm{d}\zeta}{\mathrm{d}\mathbf{y}^\intercal}\mathrm{cov}[\mathbf{y},\mathbf{y}]\frac{\mathrm{d}\zeta^\intercal}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

In particular, as we will later show that, since controls do not have developmental constraints and are open-loop so $\mathrm{d}\mathbf{y}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{I}$ (Eq. A51), it follows that the additive genetic covariance matrix of controls $\mathbf{G}_\mathbf{y}$ equals the mutational covariance matrix $\mathrm{cov}[\mathbf{y},\mathbf{y}]$. This and Eq. (A3) yield Eq. (14a).

Appendix 2: stable age distribution and reproductive values

The mutant stable age distribution and mutant reproductive value are given by dominant left and right eigenvectors $\mathbf{v}$ and $\mathbf{u}$ of the mutant's local stability matrix $\mathbf{J}$ in Eq. (11). That is, $\mathbf{v}$ and $\mathbf{u}$ are defined respectively by $\lambda\mathbf{u} = \mathbf{J}\mathbf{u}$ and $\lambda\mathbf{v}^\intercal = \mathbf{v}^\intercal\mathbf{J}$. Expanding these equations yields

$$\lambda u_1 = \sum_{j=1}^{N_\mathrm{a}} f_j u_j \tag{A7a}$$

$$\lambda u_j = p_{j-1}u_{j-1} \quad \text{for } j \in \{2,\ldots,N_\mathrm{a}\} \tag{A7b}$$

$$\lambda v_j = v_1 f_j + v_{j+1}p_j \quad \text{for } j \in \{1,\ldots,N_\mathrm{a}\}, \tag{A7c}$$

since $v_{N_\mathrm{a}+1} = 0$ without loss of generality. Eqs. (A7b) and (A7c) give the recurrence equations

$$\begin{aligned} u_j &= \lambda^{-1}p_{j-1}u_{j-1} \\ v_j &= \frac{1}{p_{j-1}}\lambda v_{j-1} - \frac{1}{p_{j-1}}v_1 f_{j-1}, \end{aligned}$$

for $j \in \{2,\ldots,N_\mathrm{a}\}$, which iterating yield

$$u_j = \lambda^{-j+1}\ell_j u_1 \tag{A9a}$$

$$\begin{aligned} v_j &= \frac{1}{\ell_j}\lambda^{j-1}v_1 - v_1\sum_{k=1}^{j-1}\frac{\lambda^{j-1-k}}{\ell_j/\ell_k}f_k \\ &= \frac{1}{\ell_j}\lambda^{j-1}v_1\left(1 - \sum_{k=1}^{j-1}\lambda^{-k}\ell_k f_k\right), \end{aligned} \tag{A9b}$$

where $\ell_j = \prod_{k=1}^{j-1} p_k$ is mutant survivorship from age 1 to age j. Eq. (A9b) can be rewritten in the standard form of Fisher's (1927) reproductive value in discrete time using the Euler-Lotka equation as follows. Defining $\ell_1 = 1$ and since $\lambda^0 = 1$, substituting Eq. (A9a) in Eq. (A7a) and dividing both sides of the equation by λu_1 yields

$$1 = \sum_{j=1}^{N_\mathrm{a}} \lambda^{-j}\ell_j f_j, \tag{A10}$$

which is the Euler-Lotka equation in discrete time (Charlesworth 1994, Eq. 1.42 and Caswell 2001, Eq. 4.42). Partitioning the sum in Eq. (A10) yields

$$1 - \sum_{j=1}^{m-1}\lambda^{-j}\ell_j f_j = \sum_{j=m}^{N_\mathrm{a}}\lambda^{-j}\ell_j f_j, \tag{A11}$$

which substituted in Eq. (A9b) yields

$$v_j = \frac{1}{\ell_j}\lambda^{j-1}v_1\sum_{k=j}^{N_\mathrm{a}}\lambda^{-k}\ell_k f_k. \tag{A12}$$

This equation is the standard form of Fisher's (1927) reproductive value in discrete time (Eq. 4.89 of Caswell 2001). Hence, from Eqs. (A9a) and (A12), we obtain the mutant stable age distribution and mutant reproductive value:

$$\begin{aligned} u_j &= \lambda^{-j+1}\ell_j u_1 \\ v_j &= \frac{1}{\ell_j}\lambda^{j-1}v_1\sum_{k=j}^{N_\mathrm{a}}\lambda^{-k}\ell_k f_k, \end{aligned}$$

for $j \in \{2,\ldots,N_\mathrm{a}\}$, where u_1 and v_1 can take any positive value. Evaluating at neutrality ($\mathbf{y} = \bar{\mathbf{y}}$), we have that $\lambda^\circ = \lambda|_{\mathbf{y}=\bar{\mathbf{y}}} = 1$, which yields Eqs. (19).

Bienvenu and Legendre (2015) find that generation time can be measured by

$$T = \frac{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}{\mathbf{v}^{\circ\intercal}\mathbf{F}^\circ\mathbf{u}^\circ},$$

where we evaluate at resident trait values given our adaptive dynamics assumptions, and where $\mathbf{F}$ is given by Eq. (11) setting all p_j to zero. Using Eq. (A7a), it is easily checked that $\mathbf{v}^{\circ\intercal}\mathbf{F}^\circ\mathbf{u}^\circ = v_1^\circ u_1^\circ$. In turn, we have that the numerator is

$$\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ = \sum_{j=1}^{N_\mathrm{a}} v_j^\circ u_j^\circ.$$

Thus, using Eqs. (19) yields

$$\begin{aligned} T = \frac{\mathbf{v}^{\circ\intercal}\mathbf{u}^\circ}{v_1^\circ u_1^\circ} &= \frac{v_1^\circ u_1^\circ + \sum_{j=2}^{N_\mathrm{a}} v_j^\circ u_j^\circ}{v_1^\circ u_1^\circ} \\ &= \frac{v_1^\circ u_1^\circ + v_1^\circ u_1^\circ \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ}{v_1^\circ u_1^\circ} \\ &= 1 + \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ. \end{aligned} \tag{A14}$$

We further manipulate this expression to recover a standard expression of generation time (Charlesworth 1994, Eq. 1.47c; Bulmer 1994, Eq. 25, Ch. 25; Bienvenu and Legendre 2015, Eq. 5). Evaluating the Euler-Lotka equation (A10) at the resident controls (so $\lambda|_{\mathbf{y}=\bar{\mathbf{y}}} = 1$), we obtain that a neutral mutant's expected lifetime reproductive success is

$$R_0^\circ = \sum_{j=1}^{N_\mathrm{a}}\ell_j^\circ f_j^\circ = 1. \tag{A15}$$

Therefore, Eq. (A14) is

$$\begin{aligned} T = 1 + \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ &= R_0^\circ + \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ \\ &= \sum_{j=1}^{N_\mathrm{a}}\ell_j^\circ f_j^\circ + \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ \\ &= \ell_1^\circ f_1^\circ + \sum_{j=2}^{N_\mathrm{a}}\ell_j^\circ f_j^\circ + \sum_{j=2}^{N_\mathrm{a}}\sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ \\ &= \ell_1^\circ f_1^\circ + \sum_{j=2}^{N_\mathrm{a}}\left(\ell_j^\circ f_j^\circ + \sum_{k=j}^{N_\mathrm{a}}\ell_k^\circ f_k^\circ\right). \end{aligned}$$

Expanding the rightmost sum yields

$$T = \ell_1^\circ f_1^\circ + \sum_{j=2}^{N_\mathrm{a}} \left(\ell_j^\circ f_j^\circ + \ell_j^\circ f_j^\circ + \ell_{j+1}^\circ f_{j+1}^\circ + \cdots + \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \right)$$

Expanding the remaining sum yields

$$\begin{aligned} T = \ell_1^\circ f_1^\circ &+ \left(\ell_2^\circ f_2^\circ + \ell_2^\circ f_2^\circ + \ell_3^\circ f_3^\circ + \cdots + \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \right) \\ &+ \left(\ell_3^\circ f_3^\circ + \ell_3^\circ f_3^\circ + \ell_4^\circ f_4^\circ + \cdots + \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \right) \\ &+ \cdots \\ &+ \left(\ell_{N_\mathrm{a}-1}^\circ f_{N_\mathrm{a}-1}^\circ + \ell_{N_\mathrm{a}-1}^\circ f_{N_\mathrm{a}-1}^\circ + \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \right) \\ &+ \left(\ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ + \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \right). \end{aligned}$$

Collecting common terms yields

$$\begin{aligned} T &= \ell_1^\circ f_1^\circ + 2\ell_2^\circ f_2^\circ + 3\ell_3^\circ f_3^\circ + 4\ell_4^\circ f_4^\circ \\ &\quad + \cdots + N_\mathrm{a} \ell_{N_\mathrm{a}}^\circ f_{N_\mathrm{a}}^\circ \\ &= \sum_{j=1}^{N_\mathrm{a}} j \ell_j^\circ f_j^\circ, \end{aligned} \tag{A16}$$

which is Eq. (21). This expression recovers a standard measure of generation time (Charlesworth 1994, Eq. 1.47c; Bulmer 1994, Eq. 25, Ch. 25; Bienvenu and Legendre 2015, Eq. 5).

Appendix 3: selection gradient in terms of R_0

Following Hamilton (1966) (see also Eqs. 58-61 in Caswell 2009), we differentiate the Euler-Lotka equation (A10) implicitly with respect to a mutant trait value ζ, which yields

$$0 = \sum_{j=1}^{N_\mathrm{a}} \left(\lambda^{-j} \frac{\partial \ell_j f_j}{\partial \zeta} - j \ell_j f_j \lambda^{-j-1} \frac{\partial \lambda}{\partial \zeta} \right) \bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Noting that $\lambda|_{\mathbf{y}=\bar{\mathbf{y}}} = 1$ and solving for the selection gradient, we obtain

$$\begin{aligned} \frac{\partial \lambda}{\partial \zeta}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \frac{1}{\sum_{j=1}^{N_\mathrm{a}} j \ell_j^\circ f_j^\circ} \sum_{j=1}^{N_\mathrm{a}} \frac{\partial \ell_j f_j}{\partial \zeta}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \frac{1}{T} \frac{\partial R_0}{\partial \zeta}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned} \tag{A17}$$

where we use Eqs. (28) and (A16). This is Eq. (29a). The same procedure using total derivatives yields Eq. (29b).

Appendix 4: total selection gradient of states

Here we derive the total selection gradient of states $\mathrm{d}\lambda/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$, which is part of and simpler to derive than the total selection gradient of controls $\mathrm{d}\lambda/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$.

Total selection gradient of states in terms of direct fitness effects

We start by considering the total selection gradient entry for the i-th state variable at age a. By this, we mean the total selection gradient of a perturbation of x_{ia} taken as initial condition of the recurrence equation (8) when applied at the ages $\{a, \ldots, n\}$. Consequently, a state perturbation at a given age does not affect states at earlier ages, in short, due to *the arrow of developmental time*. By letting ζ in Eq. (27) be x_{ia}, we have

$$\frac{\mathrm{d}\lambda}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}w}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_\mathrm{a}} \frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A18}$$

Note that the total derivatives of a mutant's relative fitness at age j in Eq. (A18) are with respect to the individual's state variables at possibly another age a. From Eq. (24), we have that a mutant's relative fitness at age j, $w_j(\mathbf{z}_j, \bar{\mathbf{z}}, \mathbf{h}_j(\mathbf{z}_j, \bar{\mathbf{z}}, \tau))$, depends on the individual's state variables at the current age (recall $\mathbf{z}_j = (\mathbf{x}_j; \mathbf{y}_j)$), but from the developmental constraint in Eq. (8) the state variables at a given age depend on state variables at previous ages. We must then calculate the total derivatives of fitness in Eq. (A18) in terms of direct (i.e., partial) derivatives, thus separating the effects of state variables at the current age from those of state variables at other ages.

To do this, we start by applying the chain rule, and since we assume that controls are open-loop (hence, controls do not depend on states, so $\mathrm{d}\mathbf{y}_j/\mathrm{d}x_{ia} = \mathbf{0}$ for all $i \in \{1, \ldots, N_\mathrm{s}\}$ and all $a, j \in \{1, \ldots, N_\mathrm{a}\}$), we obtain

$$\frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\sum_{k=1}^{N_\mathrm{s}} \frac{\partial w_j}{\partial x_{kj}} \frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}} + \sum_{k=1}^{N_\mathrm{s}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial w_j}{\partial \epsilon_{rj}} \frac{\partial \epsilon_{rj}}{\partial x_{kj}} \frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}} \right) \bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation (Appendix 14), this is

$$\frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}} \frac{\partial w_j}{\partial \mathbf{x}_j} + \sum_{k=1}^{N_\mathrm{s}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial x_{kj}} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}} \right) \bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation again yields

$$\frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}} \frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \right) \bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Factorizing, we have

$$\frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left[\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}} \left(\frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \right) \right] \bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A19}$$

Eq. (A19) now contains only partial derivatives of age-specific fitness.

We now write Eq. (A19) in terms of partial derivatives of lifetime fitness. Consider the *selection gradient of states at age j* or, equivalently, the column vector of *direct effects of a mutant's states at age j on fitness* defined as

$$\frac{\partial w}{\partial \mathbf{x}_j}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left(\frac{\partial w}{\partial x_{1j}}, \ldots, \frac{\partial w}{\partial x_{N_\mathrm{s}j}} \right)^\intercal \bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{s} \times 1}.$$

Such selection gradient of states at age j forms the selection gradient of states for all ages (Eq. 30). Similarly, the column vector of *direct effects of a mutant's environment at age j on fitness* is

$$\frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left(\frac{\partial w}{\partial \epsilon_{1j}}, \ldots, \frac{\partial w}{\partial \epsilon_{N_\mathrm{e}j}} \right)^\intercal \bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{e} \times 1},$$

and the matrix of *direct effects of a mutant's states at age j on her environment at age j* is

$$\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \begin{pmatrix} \dfrac{\partial \epsilon_{1j}}{\partial x_{1j}} & \cdots & \dfrac{\partial \epsilon_{N_\mathrm{e}j}}{\partial x_{1j}} \\ \vdots & \ddots & \vdots \\ \dfrac{\partial \epsilon_{1j}}{\partial x_{N_\mathrm{s}j}} & \cdots & \dfrac{\partial \epsilon_{N_\mathrm{e}j}^\intercal}{\partial x_{N_\mathrm{s}j}} \end{pmatrix} \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{s} \times N_\mathrm{e}}.$$

From Eq. (26), w only depends directly on $\mathbf{x}_j$, $\mathbf{y}_j$, and $\boldsymbol{\epsilon}_j$ through w_j. So,

$$\frac{\partial w_j}{\partial \mathbf{x}_j} = \frac{\partial w}{\partial \mathbf{x}_j} \tag{A20a}$$

$$\frac{\partial w_j}{\partial \mathbf{y}_j} = \frac{\partial w}{\partial \mathbf{y}_j} \tag{A20b}$$

$$\frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} = \frac{\partial w}{\partial \boldsymbol{\epsilon}_j}, \tag{A20c}$$

which substituted in Eq. (A19) yields

$$\begin{aligned}\left.\frac{\mathrm{d}w_j}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left[\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}}\left(\frac{\partial w}{\partial \mathbf{x}_j}+\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}}\frac{\delta w}{\delta \mathbf{x}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned} \tag{A21}$$

where the *semi-total selection gradient of states at age j* or, equivalently, the column vector of *semi-total effects of a mutant's states at age j on fitness* (i.e., the total gradient considering environmental but not developmental constraints) is

$$\left.\frac{\delta w}{\delta \mathbf{x}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial w}{\partial \mathbf{x}_j}+\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{s}\times 1}. \tag{A22}$$

Consider now the semi-total selection gradient of states for all ages. The block column vector of *semi-total effects of a mutant's states on fitness* is

$$\left.\frac{\delta w}{\delta \mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\delta w}{\delta \mathbf{x}_1};\cdots;\frac{\delta w}{\delta \mathbf{x}_{N_\mathrm{a}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times 1}.$$

Using Eq. (33d), we have that

$$\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}}\frac{\partial w}{\partial \boldsymbol{\epsilon}} = \left(\sum_{k=1}^{N_\mathrm{a}}\frac{\partial \boldsymbol{\epsilon}_k^\intercal}{\partial \mathbf{x}_j}\frac{\partial w}{\partial \boldsymbol{\epsilon}_k}\right) = \left(\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\right) \tag{A23}$$

is a block column vector whose j-th entry equals the rightmost term in Eq. (A22). Thus, from Eqs. (A22), (30), and (A23), it follows that the semi-total selection gradient of states is given by Eq. (40).

Now, we write the total selection gradient of x_{ia} in terms of the semi-total selection gradient of states. Substituting Eq. (A21) in Eq. (A18) yields

$$\left.\frac{\mathrm{d}w}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_\mathrm{a}}\left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}}\frac{\delta w}{\delta \mathbf{x}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}x_{ia}}\frac{\delta w}{\delta \mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},$$

where we use the block row vector

$$\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}x_{ia}} = \left(\frac{\mathrm{d}\mathbf{x}_0^\intercal}{\mathrm{d}x_{ia}},\dots,\frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}x_{ia}}\right) \in \mathbb{R}^{1\times N_\mathrm{a}N_\mathrm{s}}.$$

Therefore, the total selection gradient of all state variables across all ages is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\delta w}{\delta \mathbf{x}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times 1}, \tag{A24}$$

where the semi-total selection gradient of states is given by Eq. (40) and the block matrix of *total effects of a mutant's states on her states* is

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{x}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\partial \mathbf{x}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}}.$$

Using Eq. (40), expression (A24) is now in terms of partial derivatives of fitness, partial derivatives of the environment, and total effects of a mutant's states on her states, $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}$, which we now proceed to write in terms of partial derivatives only.

Matrix of total effects of a mutant's states on her states

From the developmental constraint (8) for the k-th state variable at age $j \in \{2,\dots,N_\mathrm{a}\}$ we have that $x_{kj} = g_{k,j-1}(\mathbf{z}_{j-1},\bar{\mathbf{z}},\mathbf{h}_{j-1}(\mathbf{z}_{j-1},\bar{\mathbf{z}},\tau))$, so using the chain rule since controls are open-loop we obtain

$$\begin{aligned}\left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(&\sum_{l=1}^{N_\mathrm{s}}\frac{\partial g_{k,j-1}}{\partial x_{l,j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}x_{ia}} \\ &+\left.\sum_{l=1}^{N_\mathrm{s}}\sum_{r=1}^{N_\mathrm{e}}\frac{\partial g_{k,j-1}}{\partial \epsilon_{r,j-1}}\frac{\partial \epsilon_{r,j-1}}{\partial x_{l,j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}x_{ia}}\Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Applying matrix calculus notation (Appendix 14), this is

$$\left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}}+\sum_{l=1}^{N_\mathrm{s}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial x_{l,j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}x_{ia}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation again yields

$$\left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}}+\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Factorizing, we have

$$\left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\left(\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}}+\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Rewriting $g_{k,j-1}$ as x_{kj} yields

$$\left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\left(\frac{\partial x_{kj}}{\partial \mathbf{x}_{j-1}}+\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial x_{kj}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Hence,

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}x_{ia}}\left(\frac{\partial \mathbf{x}_j^\intercal}{\partial \mathbf{x}_{j-1}}+\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial \mathbf{x}_j^\intercal}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A25}$$

where we use the matrix of *direct effects of a mutant's states at age j on her states at age j + 1*

$$\left.\frac{\partial \mathbf{x}_{j+1}^\intercal}{\partial \mathbf{x}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{\partial x_{1,j+1}}{\partial x_{1j}} & \cdots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial x_{1j}} \\ \vdots & \ddots & \vdots \\ \frac{\partial x_{1,j+1}}{\partial x_{N_\mathrm{s}j}} & \cdots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial x_{N_\mathrm{s}j}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{s}\times N_\mathrm{s}},$$

and the matrix of *direct effects of a mutant's environment at age j on her states at age $j+1$*

$$\left.\frac{\partial \mathbf{x}_{j+1}^{\intercal}}{\partial \boldsymbol{\epsilon}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial x_{1,j+1}}{\partial \epsilon_{1j}} & \cdots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial \epsilon_{1j}} \\ \vdots & \ddots & \vdots \\ \frac{\partial x_{1,j+1}}{\partial \epsilon_{N_\mathrm{e}j}} & \cdots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial \epsilon_{N_\mathrm{e}j}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{e}\times N_\mathrm{s}}.$$

We can more succinctly write Eq. (A25) as

$$\left.\frac{\mathrm{d}\mathbf{x}_j^{\intercal}}{\mathrm{d}x_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^{\intercal}}{\mathrm{d}x_{ia}}\frac{\delta \mathbf{x}_j^{\intercal}}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A26}$$

where we use the matrix of *semi-total effects of a mutant's states at age j on her states at age $j+1$*

$$\left.\frac{\delta \mathbf{x}_{j+1}^{\intercal}}{\delta \mathbf{x}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial \mathbf{x}_{j+1}^{\intercal}}{\partial \mathbf{x}_j} + \frac{\partial \boldsymbol{\epsilon}_j^{\intercal}}{\partial \mathbf{x}_j}\frac{\partial \mathbf{x}_{j+1}^{\intercal}}{\partial \boldsymbol{\epsilon}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{s}\times N_\mathrm{s}}. \tag{A27}$$

The block matrix of *semi-total effects a mutant's states on her states* is

$$\begin{aligned}\left.\frac{\delta \mathbf{x}^{\intercal}}{\delta \mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\delta \mathbf{x}_1^{\intercal}}{\delta \mathbf{x}_1} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\delta \mathbf{x}_1} \\ \vdots & \ddots & \vdots \\ \frac{\delta \mathbf{x}_1^{\intercal}}{\delta \mathbf{x}_{N_\mathrm{a}}} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\delta \mathbf{x}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{I} & \frac{\delta \mathbf{x}_2^{\intercal}}{\delta \mathbf{x}_1} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{I} & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\delta \mathbf{x}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{I} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}}.\end{aligned} \tag{A28}$$

The equality (A28) follows because semi-total effects of a mutant's states on her states are only non-zero at the next age (from the developmental constraint (8)) or when a variable is differentiated with respect to itself. Using Eqs. (33d) and (33c), we have that

$$\frac{\partial \boldsymbol{\epsilon}^{\intercal}}{\partial \mathbf{x}}\frac{\partial \mathbf{x}^{\intercal}}{\partial \boldsymbol{\epsilon}} = \left(\sum_{k=1}^{N_\mathrm{a}} \frac{\partial \boldsymbol{\epsilon}_k^{\intercal}}{\partial \mathbf{x}_a}\frac{\partial \mathbf{x}_j^{\intercal}}{\partial \boldsymbol{\epsilon}_k}\right) = \left(\begin{cases} \frac{\partial \boldsymbol{\epsilon}_a^{\intercal}}{\partial \mathbf{x}_a}\frac{\partial \mathbf{x}_j^{\intercal}}{\partial \boldsymbol{\epsilon}_a} & \text{for } j=a+1 \\ \mathbf{0} & \text{for } j\neq a+1 \end{cases}\right), \tag{A29}$$

which equals the rightmost term in Eq. (A27) for $j=a+1$. Thus, from Eqs. (A27), (33a), (A28), and (A29), it follows that the block matrix of semi-total effects of a mutant's states on her states satisfies Eq. (42).

Eq. (A26) gives the matrix of total effects of a mutant's i-th state at age a on her states at age j. Then, it follows that the matrix of total effects of all of a mutant's states at age a on her states at age j is

$$\left.\frac{\mathrm{d}\mathbf{x}_j^{\intercal}}{\mathrm{d}\mathbf{x}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^{\intercal}}{\mathrm{d}\mathbf{x}_a}\frac{\delta \mathbf{x}_j^{\intercal}}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A30}$$

Eq. (A30) is a recurrence equation for $\mathrm{d}\mathbf{x}_j^{\intercal}/\mathrm{d}\mathbf{x}_a$ over age $j \in \{2,\dots,N_\mathrm{a}\}$. Because of the arrow of developmental time (due to the developmental constraint (8)), perturbations in an individual's late state variables do not affect the individual's early state variables (i.e., $\mathrm{d}\mathbf{x}_j^{\intercal}/\mathrm{d}\mathbf{x}_a = \mathbf{0}$ for $j<a$ and $j \in \{1,\dots,N_\mathrm{a}-1\}$)[1]. Additionally, from the arrow of developmental time (Eq. 8), a perturbation in an individual's state variable at a given age does not affect any other of the individual's state variables at the *same* age (i.e., $\mathrm{d}\mathbf{x}_a^{\intercal}/\mathrm{d}\mathbf{x}_a = \mathbf{I}$ where $\mathbf{I}$ is the identity matrix). Hence, expanding the recurrence in Eq. (A30), we obtain for $j \in \{1,\dots,N_\mathrm{a}\}$ that

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{x}_j^{\intercal}}{\mathrm{d}\mathbf{x}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_a^{\intercal}}{\mathrm{d}\mathbf{x}_a}\frac{\delta \mathbf{x}_{a+1}^{\intercal}}{\delta \mathbf{x}_a}\cdots\frac{\delta \mathbf{x}_j^{\intercal}}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j>a \\ \left.\frac{\mathrm{d}\mathbf{x}_a^{\intercal}}{\mathrm{d}\mathbf{x}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j=a \\ \mathbf{0} & \text{for } j<a \end{cases} \\ &= \begin{cases} \left.\left(\frac{\delta \mathbf{x}_{a+1}^{\intercal}}{\delta \mathbf{x}_a}\cdots\frac{\delta \mathbf{x}_j^{\intercal}}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j>a \\ \mathbf{I} & \text{for } j=a \\ \mathbf{0} & \text{for } j<a. \end{cases}\end{aligned} \tag{A31}$$

Thus, the block matrix of *total effects of a mutant's states on her states* is

$$\begin{aligned}\left.\frac{\mathrm{d}\mathbf{x}^{\intercal}}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}_1^{\intercal}}{\mathrm{d}\mathbf{x}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\mathrm{d}\mathbf{x}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^{\intercal}}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{I} & \frac{\mathrm{d}\mathbf{x}_2^{\intercal}}{\mathrm{d}\mathbf{x}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^{\intercal}}{\mathrm{d}\mathbf{x}_1} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\mathrm{d}\mathbf{x}_1} \\ \mathbf{0} & \mathbf{I} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^{\intercal}}{\mathrm{d}\mathbf{x}_2} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\mathrm{d}\mathbf{x}_2} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{I} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^{\intercal}}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{I} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}},\end{aligned} \tag{A32}$$

which is block upper triangular and its aj-th entry is given by

$$\frac{\mathrm{d}\mathbf{x}_j^{\intercal}}{\mathrm{d}\mathbf{x}_a} = \begin{cases} \overset{\curvearrowright}{\prod_{k=a}^{j-1}} \frac{\delta \mathbf{x}_{k+1}^{\intercal}}{\delta \mathbf{x}_k} = \frac{\delta \mathbf{x}_{a+1}^{\intercal}}{\delta \mathbf{x}_a}\cdots\frac{\delta \mathbf{x}_j^{\intercal}}{\delta \mathbf{x}_{j-1}} & \text{for } j>a \\ \mathbf{I} & \text{for } j=a \\ \mathbf{0} & \text{for } j<a. \end{cases} \tag{A33}$$

Since matrix multiplication is not commutative, the $\curvearrowright$ denotes right multiplication. Eqs. (A32) and (A33) write the matrix of total effects of a mutant's states on her states in terms of partial derivatives, given Eq. (A27), as we sought.

---

[1] More specifically, we take the derivative $\mathrm{d}\mathbf{x}_j^{\intercal}/\mathrm{d}x_{ia}$ as referring to the effect on $\mathbf{x}_j^{\intercal}$ of a perturbation of the initial condition $\mathbf{x}_a$ of the difference equation (8) applied at the ages $\{a,\dots,n\}$. Hence, if $j<a$, $\mathbf{x}_j^{\intercal}$ is unmodified by a change in the initial condition of (8) applied at the ages $\{a,\dots,n\}$.

From Eq. (A32), it follows that the matrix of total effects of a mutant's states on her states $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is invertible. Indeed, since $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is square and block upper triangular, then its determinant is

$$\det\left(\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right)=\det\left(\left.\frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{x}_1}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right)\cdots\det\left(\left.\frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\right)$$

(Horn and Johnson 2013, p. 32). Since $\mathrm{d}\mathbf{x}_a^\intercal/\mathrm{d}\mathbf{x}_a|_{\mathbf{y}=\bar{\mathbf{y}}}=\mathbf{I}$, then $\det(\mathrm{d}\mathbf{x}_a^\intercal/\mathrm{d}\mathbf{x}_a|_{\mathbf{y}=\bar{\mathbf{y}}})=1$ for all $a\in\{1,\ldots,N_\mathrm{a}\}$. Hence, $\det(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}})\neq 0$, so $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is invertible.

We now obtain a more compact expression for the matrix of total effects of a mutant's states on her states in terms of partial derivatives. From Eq. (A28), it follows that

$$\left.\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}-\mathbf{I}=\left.\begin{pmatrix}\mathbf{0} & \frac{\delta\mathbf{x}_2^\intercal}{\delta\mathbf{x}_1} & \cdots & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0}\\ \vdots & \vdots & \ddots & \vdots & \vdots\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\delta\mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta\mathbf{x}_{N_\mathrm{a}-1}}\\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A34}$$

which is block 1-superdiagonal (i.e., only the entries in its first block super diagonal are non-zero). By definition of matrix power, we have that $(\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I})^0=\mathbf{I}$. Now, from Eq. (A34), we have that

$$\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}=\left(\begin{cases}\frac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_a} & \text{if } j=a+1\\ \mathbf{0} & \text{otherwise}\end{cases}\right).$$

Using Eq. (A34), taking the second power yields

$$\begin{aligned}\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^2&=\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)\\ &=\left(\begin{cases}\frac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{x}_a}\frac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{a+1}} & \text{if } j=a+2\\ \mathbf{0} & \text{otherwise}\end{cases}\right),\end{aligned}$$

which is block 2-superdiagonal. This suggests the inductive hypothesis that

$$\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i=\left(\begin{cases}\overset{\curvearrowright}{\prod_{k=a}^{j-1}}\frac{\delta\mathbf{x}_{k+1}^\intercal}{\delta\mathbf{x}_k} & \text{if } j=a+i\\ \mathbf{0} & \text{otherwise}\end{cases}\right) \tag{A35}$$

holds for some $i\in\{0,1,\ldots\}$, which is a block i-superdiagonal matrix. If this is the case, then we have that

$$\begin{aligned}\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^{i+1}&=\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)\\ &=\left(\begin{cases}\overset{\curvearrowright}{\prod_{k=a}^{a+i-1}}\frac{\delta\mathbf{x}_{k+1}^\intercal}{\delta\mathbf{x}_k}\frac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{a+i}} & \text{if } j=a+i+1\\ \mathbf{0} & \text{otherwise}\end{cases}\right)\\ &=\left(\begin{cases}\overset{\curvearrowright}{\prod_{k=a}^{j-1}}\frac{\delta\mathbf{x}_{k+1}^\intercal}{\delta\mathbf{x}_k} & \text{if } j=a+i+1\\ \mathbf{0} & \text{otherwise}\end{cases}\right).\end{aligned}$$

This proves by induction that Eq. (A35) holds for every $i\in\{0,1,\ldots\}$, which together with Eq. (A33) proves that

$$\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i=\left(\begin{cases}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_a} & \text{if } j=a+i\\ \mathbf{0} & \text{otherwise}\end{cases}\right)$$

holds for all $i\in\{0,1,\ldots,N_\mathrm{a}\}$. Evaluating this result at various i, note that

$$\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^0=\left(\begin{cases}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_a} & \text{if } j=a\\ \mathbf{0} & \text{otherwise}\end{cases}\right)=\left(\begin{cases}\mathbf{I} & \text{if } j=a\\ \mathbf{0} & \text{otherwise}\end{cases}\right)$$

is a block matrix of zeros except in its block main diagonal which coincides with the block main diagonal of Eq. (A32). Similarly,

$$\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^1=\left(\begin{cases}\frac{\mathrm{d}\mathbf{x}_{a+1}^\intercal}{\mathrm{d}\mathbf{x}_a} & \text{if } j=a+1\\ \mathbf{0} & \text{otherwise}\end{cases}\right)$$

is a block matrix of zeros except in its first block super diagonal which coincides with the first block super diagonal of Eq. (A32). Indeed,

$$\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i=\left(\begin{cases}\frac{\mathrm{d}\mathbf{x}_{a+i}^\intercal}{\mathrm{d}\mathbf{x}_a} & \text{if } j=a+i\\ \mathbf{0} & \text{otherwise}\end{cases}\right)$$

is a block matrix of zeros except in its i-th block super diagonal which coincides with the i-th block super diagonal of Eq. (A32) for all $i\in\{1,\ldots,N_\mathrm{a}-1\}$. Therefore, since any non-zero entry of the matrix $(\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I})^i$ corresponds to a zero entry for the matrix $(\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I})^j$ for any $i\neq j$ with $i,j\in\{0,\ldots,N_\mathrm{a}-1\}$, it follows that

$$\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}=\sum_{i=0}^{N_\mathrm{a}-1}\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i. \tag{A36}$$

From the geometric series of matrices we have that

$$\begin{aligned}\sum_{i=0}^{N_\mathrm{a}-1}\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^i&=\left[\mathbf{I}-\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)\right]^{-1}\left[\mathbf{I}-\left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}-\mathbf{I}\right)^{N_\mathrm{a}}\right]\\ &=\left(2\mathbf{I}-\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{x}}\right)^{-1}.\end{aligned} \tag{A37}$$

The last equality follows because $\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I}$ is strictly block triangular with block dimension N_a and so $\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I}$ is nilpotent with index smaller than or equal to N_a, which implies that $(\delta\mathbf{x}^\intercal/\delta\mathbf{x}-\mathbf{I})^{N_\mathrm{a}}=\mathbf{0}$. From Eq. (A28), the matrix $2\mathbf{I}-\delta\mathbf{x}^\intercal/\delta\mathbf{x}$ is block upper triangular with only identity matrices in its block main diagonal, so all the eigenvalues of $2\mathbf{I}-\delta\mathbf{x}^\intercal/\delta\mathbf{x}$ equal one and the matrix is invertible; thus, the inverse matrix in Eq. (A37) exists. Finally, using Eq. (A37) in (A36) yields (44), which is a compact expression for the matrix of total effects of a mutant's states on her states in terms of partial derivatives only, once Eq. (42) is used.

Conclusion

Form 1 Using Eqs. (A24) and (40) for $\boldsymbol{\zeta}=\mathbf{x}$, we have that the total selection gradient of states is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{x}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}=\left.\left[\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\left(\frac{\partial w}{\partial\mathbf{x}}+\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\frac{\partial w}{\partial\boldsymbol{\epsilon}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Thus, using Eq. (49) yields the first line of Eq. (63).

Form 2 Using Eq. (A24), the total selection gradient of states is given by the second line of Eq. (63).

Form 3 Using Eqs. (A24), (40) for $\boldsymbol{\zeta} = \mathbf{z}$, and (53), we have that the total selection gradient of states is given by the third line of Eq. (63), where the *semi-total selection gradient of the phenotype* is

$$\left.\frac{\delta w}{\delta \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \dfrac{\delta w}{\delta \mathbf{x}} \\ \dfrac{\delta w}{\delta \mathbf{y}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times 1}. \tag{A38}$$

Form 4 Finally, using the first line of Eqs. (63) and (56), we obtain the fourth line of Eq. (63).

Appendix 5: total selection gradient of controls

Total selection gradient of controls in terms of direct fitness effects

Here we derive the total selection gradient of controls following an analogous procedure to the one used in Appendix 4 for the total selection gradient of states. For the i-th control variable at age a, letting ζ in Eq. (27) be y_{ia}, we have

$$\left.\frac{\mathrm{d}\lambda}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\mathrm{d}w}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_\mathrm{a}} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A39}$$

The total derivatives of a mutant's relative fitness at age j in Eq. (A39) are with respect to the individual's control variables at possibly another age a. We now seek to express such selection gradient entry in terms of partial derivatives only.

From Eq. (24), we have $w_j(\mathbf{z}_j, \bar{\mathbf{z}}, \mathbf{h}_j(\mathbf{z}_j, \bar{\mathbf{z}}, \tau))$ and $\mathbf{z}_j = (\mathbf{x}_j; \mathbf{y}_j)$, so applying the chain rule, we obtain

$$\begin{aligned} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(& \sum_{k=1}^{N_\mathrm{s}} \frac{\partial w_j}{\partial x_{kj}} \frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}} + \sum_{k=1}^{N_\mathrm{c}} \frac{\partial w_j}{\partial y_{kj}} \frac{\mathrm{d}y_{kj}}{\mathrm{d}y_{ia}} \\ & + \sum_{k=1}^{N_\mathrm{s}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial w_j}{\partial \epsilon_{rj}} \frac{\partial \epsilon_{rj}}{\partial x_{kj}} \frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}} \\ & \left. + \sum_{k=1}^{N_\mathrm{c}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial w_j}{\partial \epsilon_{rj}} \frac{\partial \epsilon_{rj}}{\partial y_{kj}} \frac{\mathrm{d}y_{kj}}{\mathrm{d}y_{ia}} \Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Applying matrix calculus notation (Appendix 14), this is

$$\begin{aligned} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(& \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial w_j}{\partial \mathbf{y}_j} + \sum_{k=1}^{N_\mathrm{s}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial x_{kj}} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}} \\ & \left. + \sum_{k=1}^{N_\mathrm{c}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial y_{kj}} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \frac{\mathrm{d}y_{kj}}{\mathrm{d}y_{ia}} \Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Applying matrix calculus notation again yields

$$\begin{aligned} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(& \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial w_j}{\partial \mathbf{y}_j} + \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \\ & \left. + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Factorizing, we have

$$\begin{aligned} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg[& \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \left(\frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \right) \\ & \left. + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \left(\frac{\partial w_j}{\partial \mathbf{y}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j} \right) \Bigg]\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned} \tag{A40}$$

We now write Eq. (A40) in terms of partial derivatives of lifetime fitness. Consider the *selection gradient of controls at age j* or, equivalently, the column vector of *direct effects of a mutant's controls at age j on fitness*

$$\left.\frac{\partial w}{\partial \mathbf{y}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial w}{\partial y_{1j}}, \ldots, \frac{\partial w}{\partial y_{N_\mathrm{c}j}} \right)^\intercal\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{c}\times 1},$$

and the matrix of *direct effects of a mutant's controls at age j on her environment at age j*

$$\left.\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \dfrac{\partial \epsilon_{1j}}{\partial y_{1j}} & \cdots & \dfrac{\partial \epsilon_{N_\mathrm{e}j}}{\partial y_{1j}} \\ \vdots & \ddots & \vdots \\ \dfrac{\partial \epsilon_{1j}}{\partial y_{N_\mathrm{c}j}} & \cdots & \dfrac{\partial \epsilon_{N_\mathrm{e}j}^\intercal}{\partial y_{N_\mathrm{c}j}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{c}\times N_\mathrm{e}}.$$

Using Eqs. (A20) and (A22) in Eq. (A40) yields

$$\begin{aligned} \left.\frac{\mathrm{d}w_j}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \Bigg[\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \left(\frac{\partial w}{\partial \mathbf{x}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j} \right) \\ &\qquad \left. + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \left(\frac{\partial w}{\partial \mathbf{y}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j} \right) \Bigg]\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\delta w}{\delta \mathbf{x}_j} + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\delta w}{\delta \mathbf{y}_j} \right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned} \tag{A41}$$

where we use the *semi-total selection gradient of controls at age j* or, equivalently, the *semi-total effects of a mutant's controls at age j on fitness*

$$\left.\frac{\delta w}{\delta \mathbf{y}_j}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\partial w}{\partial \mathbf{y}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j} \right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{c}\times 1}. \tag{A42}$$

Consider now the semi-total selection gradient of controls for all ages. The *semi-total selection gradient of controls* or, equivalently, the block column vector of *semi-total effects of a mutant's controls on fitness* is

$$\left.\frac{\delta w}{\delta \mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\delta w}{\delta \mathbf{y}_1}; \cdots; \frac{\delta w}{\delta \mathbf{y}_{N_\mathrm{a}}} \right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times 1}.$$

Using Eq. (33d), we have that

$$\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}} \frac{\partial w}{\partial \boldsymbol{\epsilon}} = \left(\sum_{k=1}^{N_\mathrm{a}} \frac{\partial \boldsymbol{\epsilon}_k^\intercal}{\partial \mathbf{y}_j} \frac{\partial w}{\partial \boldsymbol{\epsilon}_k} \right) = \left(\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j} \right) \tag{A43}$$

is a block column vector whose j-th entry is the rightmost term in Eq. (A42). Thus, from Eqs. (A42), (31), and (A43), it follows that the semi-total selection gradient of controls satisfies Eq. (40).

Now, we write the total selection gradient of y_{ia} in terms of the semi-total selection gradient of controls. Substituting Eq. (A41) in Eq. (A39) yields

$$\left.\frac{\mathrm{d}w}{\mathrm{d}y_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_\mathrm{a}} \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\delta w}{\delta \mathbf{x}_j} + \frac{\mathrm{d}\mathbf{y}_j^\intercal}{\mathrm{d}y_{ia}} \frac{\delta w}{\delta \mathbf{y}_j} \right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}y_{ia}}\frac{\delta w}{\delta \mathbf{x}} + \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}y_{ia}}\frac{\delta w}{\delta \mathbf{y}}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}},$$

where we use the block row vectors

$$\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}y_{ia}} \equiv \left(\frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}y_{ia}},\dots,\frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}y_{ia}}\right) \in \mathbb{R}^{1\times N_\mathrm{a} N_\mathrm{s}}$$

$$\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}y_{ia}} \equiv \left(\frac{\mathrm{d}\mathbf{y}_1^\intercal}{\mathrm{d}y_{ia}},\dots,\frac{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}^\intercal}{\mathrm{d}y_{ia}}\right) \in \mathbb{R}^{1\times N_\mathrm{a} N_\mathrm{c}}.$$

Therefore, the total selection gradient of all control variables across all ages is

$$\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\delta w}{\delta \mathbf{x}} + \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\delta w}{\delta \mathbf{y}}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times 1}, \tag{A44}$$

where we use the block matrix of *total effects of a mutant's controls on her states*

$$\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{y}_1} & \dots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\partial\mathbf{y}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} & \dots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{s}},$$

and the block matrix of *total effects of a mutant's controls on her controls*

$$\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{y}_1^\intercal}{\mathrm{d}\mathbf{y}_1} & \dots & \frac{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}^\intercal}{\partial\mathbf{y}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{y}_1^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} & \dots & \frac{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}.$$

Expression (A44) is now in terms of partial derivatives of fitness, partial derivatives of the environment, total effects of a mutant's controls on her states, $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}$, and total effects of a mutant's controls on her controls, $\mathrm{d}\mathbf{y}^\intercal/\mathrm{d}\mathbf{y}$, once Eq. (40) is used. We now proceed to write $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{y}$ and $\mathrm{d}\mathbf{y}^\intercal/\mathrm{d}\mathbf{y}$ in terms of partial derivatives only.

Matrix of total effects of a mutant's controls on her states and her controls

From the developmental constraint (8) for the k-th state variable at age $j \in \{2,\dots,N_\mathrm{a}\}$ we have that $x_{kj} = g_{k,j-1}(\mathbf{z}_{j-1},\bar{\mathbf{z}},\mathbf{h}_{j-1}(\mathbf{z}_{j-1},\bar{\mathbf{z}},\tau))$, so using the chain rule we obtain

$$\begin{aligned}\frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(&\sum_{l=1}^{N_\mathrm{s}}\frac{\partial g_{k,j-1}}{\partial x_{l,j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}y_{ia}} + \sum_{l=1}^{N_\mathrm{c}}\frac{\partial g_{k,j-1}}{\partial y_{l,j-1}}\frac{\mathrm{d}y_{l,j-1}}{\mathrm{d}y_{ia}}\\ &+\sum_{l=1}^{N_\mathrm{s}}\sum_{r=1}^{N_\mathrm{e}}\frac{\partial g_{k,j-1}}{\partial \epsilon_{r,j-1}}\frac{\partial \epsilon_{r,j-1}}{\partial x_{l,j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}y_{ia}}\\ &+\sum_{l=1}^{N_\mathrm{c}}\sum_{r=1}^{N_\mathrm{e}}\frac{\partial g_{k,j-1}}{\partial \epsilon_{r,j-1}}\frac{\partial \epsilon_{r,j-1}}{\partial y_{l,j-1}}\frac{\mathrm{d}y_{l,j-1}}{\mathrm{d}y_{ia}}\Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Applying matrix calculus notation (Appendix 14), this is

$$\begin{aligned}\frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(&\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}} + \frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{y}_{j-1}}\\ &+\sum_{l=1}^{N_\mathrm{s}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial x_{l,j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}y_{ia}}\\ &+\sum_{l=1}^{N_\mathrm{c}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial y_{l,j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\frac{\mathrm{d}y_{l,j-1}}{\mathrm{d}y_{ia}}\Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Applying matrix calculus notation again yields

$$\begin{aligned}\frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg(&\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}} + \frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial g_{k,j-1}}{\partial \mathbf{y}_{j-1}}\\ &+\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\\ &+\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{y}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Factorizing, we have

$$\begin{aligned}\frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg[&\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial g_{k,j-1}}{\partial \mathbf{x}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\\ &+\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial g_{k,j-1}}{\partial \mathbf{y}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{y}_{j-1}}\frac{\partial g_{k,j-1}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\Bigg]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Rewriting $g_{k,j-1}$ as x_{kj} yields

$$\begin{aligned}\frac{\mathrm{d}x_{kj}}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg[&\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial x_{kj}}{\partial \mathbf{x}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial x_{kj}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\\ &+\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial x_{kj}}{\partial \mathbf{y}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{y}_{j-1}}\frac{\partial x_{kj}}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\Bigg]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Hence,

$$\begin{aligned}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \Bigg[&\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial \mathbf{x}_j^\intercal}{\partial \mathbf{x}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{x}_{j-1}}\frac{\partial \mathbf{x}_j^\intercal}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\\ &+\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\left(\frac{\partial \mathbf{x}_j^\intercal}{\partial \mathbf{y}_{j-1}} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^\intercal}{\partial \mathbf{y}_{j-1}}\frac{\partial \mathbf{x}_j^\intercal}{\partial \boldsymbol{\epsilon}_{j-1}}\right)\Bigg]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned} \tag{A45}$$

where we use the matrix of *direct effects of a mutant's controls at age j on her states at age j + 1*

$$\frac{\partial \mathbf{x}_{j+1}^\intercal}{\partial \mathbf{y}_j}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial x_{1,j+1}}{\partial y_{1j}} & \dots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial y_{1j}} \\ \vdots & \ddots & \vdots \\ \frac{\partial x_{1,j+1}}{\partial y_{N_\mathrm{c}j}} & \dots & \frac{\partial x_{N_\mathrm{s},j+1}}{\partial y_{N_\mathrm{c}j}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{c}\times N_\mathrm{s}}.$$

We can write Eq. (A45) more succinctly as

$$\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}y_{ia}}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}} + \frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}y_{ia}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A46}$$

where we use the matrix of *semi-total effects of a mutant's controls at age j on her states at age j + 1*

$$\frac{\delta \mathbf{x}_{j+1}^\intercal}{\delta \mathbf{y}_j}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\partial \mathbf{x}_{j+1}^\intercal}{\partial \mathbf{y}_j} + \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{y}_j}\frac{\partial \mathbf{x}_{j+1}^\intercal}{\partial \boldsymbol{\epsilon}_j}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{c}\times N_\mathrm{s}}. \tag{A47}$$

We also define the corresponding matrix across all ages. Specifically, the block matrix of *semi-total effects of a mutant's controls on her states* is

$$\begin{aligned}\left.\frac{\delta \mathbf{x}^\intercal}{\delta \mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix} \frac{\delta \mathbf{x}_1^\intercal}{\delta \mathbf{y}_1} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \mathbf{y}_1} \\ \vdots & \ddots & \vdots \\ \frac{\delta \mathbf{x}_1^\intercal}{\delta \mathbf{y}_{N_\mathrm{a}}} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \mathbf{y}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{0} & \frac{\delta \mathbf{x}_2^\intercal}{\delta \mathbf{y}_1} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \mathbf{y}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{s}}. \end{aligned} \tag{A48}$$

The equality (A48) follows because semi-total effects of a mutant's controls on her states are only non-zero at the next age (from the developmental constraint (8)). Using Eqs. (33d) and (33c), we have that

$$\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}}\frac{\partial \mathbf{x}^\intercal}{\partial \boldsymbol{\epsilon}} = \left(\sum_{k=1}^{N_\mathrm{a}} \frac{\partial \boldsymbol{\epsilon}_k^\intercal}{\partial \mathbf{y}_a}\frac{\partial \mathbf{x}_j^\intercal}{\partial \boldsymbol{\epsilon}_k}\right) = \left(\begin{cases} \frac{\partial \boldsymbol{\epsilon}_a^\intercal}{\partial \mathbf{y}_a}\frac{\partial \mathbf{x}_j^\intercal}{\partial \boldsymbol{\epsilon}_a} & \text{for } j=a+1 \\ \mathbf{0} & \text{for } j\neq a+1 \end{cases}\right), \tag{A49}$$

which equals the rightmost term in Eq. (A47) for $j = a+1$. Thus, from Eqs. (A47)–(A49), it follows that the block matrix of semi-total effects of a mutant's controls on her states satisfies Eq. (42).

Eq. (A46) gives the matrix of total effects of a mutant's i-th control at age a on her states at age j. Then, it follows that the matrix of total effects of all of a mutant's controls at age a on her states at age j is

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}} + \frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A50}$$

Eq. (A50) is a recurrence equation for $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}\mathbf{y}_a$ over age $j \in \{2,\dots,N_\mathrm{a}\}$. Since a given entry of the operator $\mathrm{d}/\mathrm{d}\mathbf{y}$ takes the total derivative with respect to a given y_{ia} while keeping all the other controls constant and controls are open-loop, a perturbation in an individual's control does not affect any other of the individual's control variables (i.e., $\mathrm{d}\mathbf{y}_a^\intercal/\mathrm{d}\mathbf{y}_a = \mathbf{I}$ and $\mathrm{d}\mathbf{y}_j^\intercal/\mathrm{d}\mathbf{y}_a = \mathbf{0}$ for $j \neq a$). Thus, the matrix of total effects of a mutant's controls on her controls is

$$\begin{aligned}\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} &= \begin{pmatrix} \frac{\mathrm{d}\mathbf{y}_1^\intercal}{\mathrm{d}\mathbf{y}_1} & \cdots & \frac{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{y}_1^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} \end{pmatrix} = \begin{pmatrix} \mathbf{I} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{I} \end{pmatrix} \\ &= \mathbf{I} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{c}}. \end{aligned} \tag{A51}$$

Moreover, because of the arrow of developmental time (due to the developmental constraint (8)), perturbations in an individual's late control variables do not affect the individual's early state variables (i.e., $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}\mathbf{y}_a = \mathbf{0}$ for $j < a$ and $j \in \{1,\dots,N_\mathrm{a}-1\}$)[2]. Additionally, from the arrow of developmental time (Eq. 8), a perturbation in an individual's control variable at a given age does not affect any of the individual's state variables at the *same* age (i.e., $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}\mathbf{y}_a = \mathbf{0}$ for $j = a$). Consequently, Eq. (A50) for $j \in \{1,\dots,N_\mathrm{a}\}$ reduces to

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}} + \underbrace{\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}}_{\mathbf{0},\text{ from (A51)}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1>a \\ \left.\left(\underbrace{\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}}_{\mathbf{0},\text{ from (8)}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}} + \underbrace{\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}}_{\mathbf{I},\text{ from (A51)}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1=a \\ \left.\left(\underbrace{\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}}_{\mathbf{0},\text{ from (8)}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}} + \underbrace{\frac{\mathrm{d}\mathbf{y}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}}_{\mathbf{0},\text{ from (A51)}}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1<a. \end{cases}$$

That is,

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\mathbf{y}_a}\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1>a \\ \left.\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{y}_{j-1}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1=a \\ \mathbf{0} & \text{for } j-1<a. \end{cases}$$

Expanding this recurrence yields

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{a+1}^\intercal}{\mathrm{d}\mathbf{y}_a}\frac{\delta \mathbf{x}_{a+2}^\intercal}{\delta \mathbf{x}_{a+1}}\cdots\frac{\delta \mathbf{x}_j^\intercal}{\delta \mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1>a \\ \left.\frac{\delta \mathbf{x}_{a+1}^\intercal}{\delta \mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1=a \\ \mathbf{0} & \text{for } j-1<a. \end{cases} \tag{A52}$$

Evaluating Eq. (A52) at $j = a+1$ yields

$$\left.\frac{\mathrm{d}\mathbf{x}_{a+1}^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\delta \mathbf{x}_{a+1}^\intercal}{\delta \mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}},$$

---

[2] Again, we take the derivative $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}y_{ia}$ as referring to the effect on $\mathbf{x}_j^\intercal$ of a perturbation of the initial condition $\mathbf{y}_a$ of the difference equation (8) applied at the ages $\{a,\dots,n\}$. Hence, if $j < a$, $\mathbf{x}_j^\intercal$ is unmodified by a change in the initial condition of (8) applied at the ages $\{a,\dots,n\}$.

which substituted back in the top line of Eq (A52) yields

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\dfrac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\dfrac{\delta\mathbf{x}_{a+2}^\intercal}{\delta\mathbf{x}_{a+1}}\cdots\dfrac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1>a \\ \left.\dfrac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1=a \\ \mathbf{0} & \text{for } j-1<a. \end{cases} \tag{A53}$$

Hence, the block matrix of *total effects of a mutant's controls on her states* is

$$\begin{aligned} \left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix} \dfrac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{y}_1} & \cdots & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_1} \\ \vdots & \ddots & \vdots \\ \dfrac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} & \cdots & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \mathbf{0} & \dfrac{\mathrm{d}\mathbf{x}_2^\intercal}{\mathrm{d}\mathbf{y}_1} & \cdots & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\mathbf{y}_1} & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_1} \\ \mathbf{0} & \mathbf{0} & \cdots & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\mathbf{y}_2} & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_2} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \dfrac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\mathbf{y}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}\times N_\mathrm{a}N_\mathrm{s}}, \end{aligned} \tag{A54}$$

whose aj-th entry is given by

$$\begin{aligned} \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a} &= \begin{cases} \dfrac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\dfrac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_{a+1}} & \text{for } j>a \\ \mathbf{0} & \text{for } j\le a \end{cases} \\ &= \begin{cases} \dfrac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\displaystyle\prod_{k=a+1}^{\overset{\curvearrowright}{j-1}}\dfrac{\delta\mathbf{x}_{k+1}^\intercal}{\delta\mathbf{x}_k} & \text{for } j>a \\ \mathbf{0} & \text{for } j\le a \end{cases} \\ &= \begin{cases} \dfrac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\dfrac{\delta\mathbf{x}_{a+2}^\intercal}{\delta\mathbf{x}_{a+1}}\cdots\dfrac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{j-1}} & \text{for } j>a \\ \mathbf{0} & \text{for } j\le a, \end{cases} \end{aligned} \tag{A55}$$

where we use Eq. (A33) and adopt the empty-product convention that

$$\frac{\mathrm{d}\mathbf{x}_{a+1}^\intercal}{\mathrm{d}\mathbf{x}_{a+1}} = \prod_{k=a+1}^{\overset{\curvearrowright}{a}}\frac{\delta\mathbf{x}_{k+1}^\intercal}{\delta\mathbf{x}_k} = \mathbf{I}.$$

Eqs. (A54) and (A55) write the matrix of total effects of a mutant's controls on her states in terms of partial derivatives, given Eq. (A47), as we sought.

We now obtain a more compact expression for the matrix of total effects of a mutant's controls on her states in terms of partial derivatives. To do this, we note a relationship between the matrix of total effects of a mutant's controls on her states with the matrix of total effects of a mutant's states on her states. Note that the aj-th entry of $(\delta\mathbf{x}^\intercal/\delta\mathbf{y})(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x})$ is

$$\begin{aligned} \left(\frac{\delta\mathbf{x}^\intercal}{\delta\mathbf{y}}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\right)_{aj} &= \sum_{k=1}^{N_\mathrm{a}}\frac{\delta\mathbf{x}_k^\intercal}{\delta\mathbf{y}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_k} \\ &= \frac{\delta\mathbf{x}_{a+1}^\intercal}{\delta\mathbf{y}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_{a+1}} \\ &= \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{y}_a}, \end{aligned}$$

where we use Eq. (A48) in the second equality and Eq. (A55) in the third equality, noting that $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}\mathbf{x}_{a+1}=\mathbf{0}$ and $\mathrm{d}\mathbf{x}_j^\intercal/\mathrm{d}\mathbf{y}_a=\mathbf{0}$ for $j\le a$. Hence, Eq. (45) follows, which is a compact expression for the matrix of total effects of a mutant's controls on her states in terms of partial derivatives only, once Eqs. (44) and (42) are used.

Conclusion

Form 1 Using Eqs. (A44), (A51), and (40) for $\boldsymbol{\zeta}\in\{\mathbf{x},\mathbf{y}\}$, we have that the total selection gradient of controls is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\left(\frac{\partial w}{\partial\mathbf{x}}+\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\frac{\partial w}{\partial\boldsymbol{\epsilon}}\right)+\frac{\partial w}{\partial\mathbf{y}}+\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{y}}\frac{\partial w}{\partial\boldsymbol{\epsilon}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Thus, using Eq. (50) yields the first line of Eq. (64).

Form 2 Using Eqs. (A44) and (A51), the total selection gradient of controls is given by the second line of Eq. (64).

Form 3 Using Eqs. (A44), (A38), and (54), we have that the total selection gradient of controls is given by the third line of Eq. (64).

Form 4 Using the first line of Eqs. (64) and (57), we obtain the fourth line of Eq. (64).

Form 5 Finally, we can rearrange total genetic selection (64) in terms of total selection on states. Using Eq. (45) in the second line of Eq. (64), and then using the second line of Eq. (63), we have that the total selection gradient of controls is given by the fifth line of Eq. (64).

Appendix 6: total selection gradient of the environment

Here proceed analogously to derive the total selection gradient of the environment, which allows us to write an equation describing the evolutionary dynamics of the metaphenotype.

Total selection gradient of the environment in terms of direct fitness effects

As before, we start by considering the total selection gradient entry for the i-th environmental variable at age a. By this, we mean the total selection gradient of a perturbation of ϵ_{ia} taken as initial condition of the developmental constraint (8) when applied at the ages $\{a,\ldots,n\}$. Consequently, an environmental perturbation at a given age does not affect states at earlier ages due to the arrow of developmental time. By letting ζ in Eq. (27) be ϵ_{ia}, we have

$$\left.\frac{\mathrm{d}\lambda}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\mathrm{d}w}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \sum_{j=1}^{N_\mathrm{a}}\left.\frac{\mathrm{d}w_j}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A56}$$

The total derivatives of a mutant's relative fitness at age j in Eq. (A56) are with respect to the individual's environmental variables at possibly another age a. We now seek to express such selection gradient in terms of partial derivatives only.

From Eq. (24), we have $w_j(\mathbf{z}_j, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_j)$ and $\mathbf{z}_j = (\mathbf{x}_j; \mathbf{y}_j)$, so applying the chain rule and, since we assume that controls are open-loop (hence, controls do not depend on the environment, so $\mathrm{d}\mathbf{y}_j/\mathrm{d}\epsilon_{ia} = \mathbf{0}$ for all $i \in \{1, \ldots, N_\mathrm{s}\}$ and all $a, j \in \{1, \ldots, N_\mathrm{a}\}$), we obtain

$$\begin{aligned}\left.\frac{\mathrm{d}w_j}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left(\sum_{k=1}^{N_\mathrm{s}} \frac{\partial w_j}{\partial x_{kj}} \frac{\mathrm{d}x_{kj}}{\mathrm{d}\epsilon_{ia}} + \sum_{k=1}^{N_\mathrm{e}} \frac{\partial w_j}{\partial \epsilon_{kj}} \frac{\mathrm{d}\epsilon_{kj}}{\mathrm{d}\epsilon_{ia}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w_j}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w_j}{\partial \boldsymbol{\epsilon}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

In the last equality we applied matrix calculus notation (Appendix 14). Using Eq. (A20) we have

$$\left.\frac{\mathrm{d}w_j}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A57}$$

Substituting Eq. (A57) in (A56) yields

$$\begin{aligned}\left.\frac{\mathrm{d}w}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \sum_{j=1}^{N_\mathrm{a}} \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \mathbf{x}_j} + \frac{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \boldsymbol{\epsilon}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \mathbf{x}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Therefore, the total selection gradient of all environmental variables across all ages is

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\partial w}{\partial \mathbf{x}} + \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a} N_\mathrm{e} \times 1}, \tag{A58}$$

where we use the block matrix of *total effects of a mutant's environment on her states*

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\partial \boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a} N_\mathrm{s} \times N_\mathrm{a} N_\mathrm{e}}$$

and the block matrix of *total effects of a mutant's environment on her environment*

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\boldsymbol{\epsilon}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\partial \boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\boldsymbol{\epsilon}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a} N_\mathrm{e} \times N_\mathrm{a} N_\mathrm{e}}.$$

Expression (A58) is now in terms of partial derivatives of fitness, total effects of a mutant's environment on her states, $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\boldsymbol{\epsilon}$, and total effects of a mutant's environment on her environment, $\mathrm{d}\boldsymbol{\epsilon}^\intercal/\mathrm{d}\boldsymbol{\epsilon}$. We now proceed to write $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\boldsymbol{\epsilon}$ and $\mathrm{d}\boldsymbol{\epsilon}^\intercal/\mathrm{d}\boldsymbol{\epsilon}$ in terms of partial derivatives only.

Matrix of total effects of a mutant's environment on her environment

From the environmental constraint (9) for the k-th environmental variable at age $j \in \{1, \ldots, N_\mathrm{a}\}$ we have that $\epsilon_{kj} = h_{kj}(\mathbf{z}_j, \bar{\mathbf{z}}, \tau)$, so using the chain rule since controls are open-loop yields

$$\begin{aligned}\left.\frac{\mathrm{d}\epsilon_{kj}}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \begin{cases} \left.\left(\sum_{l=1}^{N_\mathrm{s}} \frac{\partial h_{kj}}{\partial x_{lj}} \frac{\mathrm{d}x_{lj}}{\mathrm{d}\epsilon_{ia}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > a \\ \left.\frac{\partial \epsilon_{kj}}{\partial \epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j = a \\ 0 & \text{for } j < a \end{cases} \\ &= \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial \epsilon_{kj}}{\partial \mathbf{x}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > a \\ \left.\frac{\partial \epsilon_{kj}}{\partial \epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j = a \\ 0 & \text{for } j < a. \end{cases}\end{aligned}$$

In the last equality we used matrix calculus notation and rewrote h_{kj} as ϵ_{kj}. Since we assume that environmental variables are mutually independent, we have that $\partial \epsilon_{ka}/\partial \epsilon_{ia} = 1$ if $i = k$ or $\partial \epsilon_{ka}/\partial \epsilon_{ia} = 0$ otherwise; however, we leave the partial derivatives $\partial \epsilon_{ka}/\partial \epsilon_{ia}$ unevaluated as it is conceptually useful. Hence,

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > a \\ \left.\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j = a \\ \mathbf{0} & \text{for } j < a. \end{cases}$$

Then, the matrix of total effects of a mutant's environment at age a on her environment at age j is

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a} \frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \mathbf{x}_j}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > a \\ \left.\frac{\partial \boldsymbol{\epsilon}_j^\intercal}{\partial \boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j = a \\ \mathbf{0} & \text{for } j < a. \end{cases} \tag{A59}$$

Hence, the block matrix of *total effects of a mutant's environment on her environment* is

$$\left.\frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\boldsymbol{\epsilon}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\boldsymbol{\epsilon}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left.\begin{pmatrix} \frac{\partial\boldsymbol{\epsilon}_1^\intercal}{\partial\boldsymbol{\epsilon}_1} & \frac{\mathrm{d}\boldsymbol{\epsilon}_2^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} \\ \mathbf{0} & \frac{\partial\boldsymbol{\epsilon}_2^\intercal}{\partial\boldsymbol{\epsilon}_2} & \cdots & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_2} & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_2} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \frac{\partial\boldsymbol{\epsilon}_{N_\mathrm{a}-1}^\intercal}{\partial\boldsymbol{\epsilon}_{N_\mathrm{a}-1}} & \frac{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\partial\boldsymbol{\epsilon}_{N_\mathrm{a}}^\intercal}{\partial\boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{A60}$$

$$\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{e}}.$$

Note that the aj-th entry of $(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\boldsymbol{\epsilon})(\partial\boldsymbol{\epsilon}^\intercal/\partial\mathbf{x})$ for $j > a$ is

$$\left(\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\right)_{aj} = \sum_{k=1}^{N_\mathrm{a}} \frac{\mathrm{d}\mathbf{x}_k^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\boldsymbol{\epsilon}_j^\intercal}{\partial\mathbf{x}_k} = \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\boldsymbol{\epsilon}_j^\intercal}{\partial\mathbf{x}_j},$$

where we use Eq. (33d) in the second equality. Note also that since environmental variables are mutually independent, $\partial\boldsymbol{\epsilon}_j^\intercal/\partial\boldsymbol{\epsilon}_a = \mathbf{0}$ for $j \neq a$ from the environmental constraint (9). Finally, note that because of the arrow of developmental time, $\partial\mathbf{x}_j^\intercal/\partial\boldsymbol{\epsilon}_a = \mathbf{0}$ for $j < a$ due to the developmental constraint (8). Hence, Eq. (52) follows, which is a compact expression for the matrix of total effects of a mutant's environment on itself in terms of partial derivatives and the total effects of a mutant's environment on her states, which we now write in terms of partial derivatives only.

Matrix of total effects of a mutant's environment on her states

From the developmental constraint (8) for the k-th state variable at age $j \in \{2,\ldots,N_\mathrm{a}\}$ we have that $x_{kj} = g_{k,j-1}(\mathbf{z}_{j-1}, \bar{\mathbf{z}}, \boldsymbol{\epsilon}_{j-1})$, so using the chain rule since controls are open-loop yields

$$\begin{aligned} \left.\frac{\mathrm{d}x_{kj}}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left(\sum_{l=1}^{N_\mathrm{s}} \frac{\partial g_{k,j-1}}{\partial x_{l,j-1}}\frac{\mathrm{d}x_{l,j-1}}{\mathrm{d}\epsilon_{ia}} + \sum_{l=1}^{N_\mathrm{e}} \frac{\partial g_{k,j-1}}{\partial \epsilon_{l,j-1}}\frac{\mathrm{d}\epsilon_{l,j-1}}{\mathrm{d}\epsilon_{ia}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\epsilon_{ia}}\frac{\partial x_{kj}}{\partial\mathbf{x}_{j-1}} + \frac{\mathrm{d}\boldsymbol{\epsilon}_{j-1}^\intercal}{\mathrm{d}\epsilon_{ia}}\frac{\partial x_{kj}}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

In the last equality we used matrix calculus notation and rewrote $g_{k,j-1}$ as x_{kj}. Hence,

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\epsilon_{ia}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\epsilon_{ia}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\mathbf{x}_{j-1}} + \frac{\mathrm{d}\boldsymbol{\epsilon}_{j-1}^\intercal}{\mathrm{d}\epsilon_{ia}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Then, the matrix of total effects of a mutant's environment at age a on her states at age j is

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_j^\intercal}{\partial\mathbf{x}_{j-1}} + \frac{\mathrm{d}\boldsymbol{\epsilon}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (A59) yields

$$\begin{aligned} \left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_j^\intercal}{\partial\mathbf{x}_{j-1}} + \frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\partial\boldsymbol{\epsilon}_{j-1}^\intercal}{\partial\mathbf{x}_{j-1}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \\ \left.\left(\underbrace{\frac{\mathrm{d}\mathbf{x}_a^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}}_{\mathbf{0},\text{ from (8)}}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\mathbf{x}_a} + \frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\boldsymbol{\epsilon}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 = a \\ \left.\left(\underbrace{\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}}_{\mathbf{0},\text{ from (8)}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \end{cases} \\ &= \begin{cases} \left.\left[\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\left(\frac{\partial\mathbf{x}_j^\intercal}{\partial\mathbf{x}_{j-1}} + \frac{\partial\boldsymbol{\epsilon}_{j-1}^\intercal}{\partial\mathbf{x}_{j-1}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \\ \left.\left(\frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 = a \\ \mathbf{0} & \text{for } j-1 > a. \end{cases} \end{aligned}$$

Using Eq. (A27), this reduces to

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{j-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \\ \left.\left(\frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\boldsymbol{\epsilon}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 = a \\ \mathbf{0} & \text{for } j-1 > a. \end{cases}$$

Expanding this recurrence yields

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\mathrm{d}\mathbf{x}_{a+1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\frac{\delta\mathbf{x}_{a+2}^\intercal}{\delta\mathbf{x}_{a+1}}\cdots\frac{\delta\mathbf{x}_j^\intercal}{\delta\mathbf{x}_{j-1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \\ \left.\left(\frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\boldsymbol{\epsilon}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 = a \\ \mathbf{0} & \text{for } j-1 > a, \end{cases}$$

which using Eq. (A33) yields

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_{a+1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 > a \\ \left.\left(\frac{\partial\boldsymbol{\epsilon}_a^\intercal}{\partial\boldsymbol{\epsilon}_a}\frac{\partial\mathbf{x}_{a+1}^\intercal}{\partial\boldsymbol{\epsilon}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1 = a \\ \mathbf{0} & \text{for } j-1 > a. \end{cases} \tag{A61}$$

It will be useful to denote the matrix of *semi-total effects of a mutant's environment at age j on her states at age j* for $j > 0$ as

$$\left.\frac{\delta\mathbf{x}_j^\intercal}{\delta\boldsymbol{\epsilon}_{j-1}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\frac{\partial\boldsymbol{\epsilon}_{j-1}^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\frac{\partial\mathbf{x}_j^\intercal}{\partial\boldsymbol{\epsilon}_{j-1}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{e}\times N_\mathrm{s}}. \tag{A62}$$

The matrix of *direct effects of a mutant's environment on itself* is given by Eq. (34). In turn, the block matrix of *semi-total effects of* *a mutant's environment on her states* is

$$\left.\frac{\delta \mathbf{x}^\intercal}{\delta \boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\delta \mathbf{x}_1^\intercal}{\delta \boldsymbol{\epsilon}_1} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\delta \mathbf{x}_1^\intercal}{\delta \boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left.\begin{pmatrix} \mathbf{0} & \frac{\delta \mathbf{x}_2^\intercal}{\delta \boldsymbol{\epsilon}_1} & \cdots & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\delta \mathbf{x}_{N_\mathrm{a}}^\intercal}{\delta \boldsymbol{\epsilon}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{s}}, \tag{A63}$$

so Eq. (43) follows from Eqs. (A62), (34), and (33c).

Using Eq. (A62), Eq. (A61) becomes

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\delta \mathbf{x}_{a+1}^\intercal}{\delta \boldsymbol{\epsilon}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_{a+1}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1>a \\ \left.\frac{\delta \mathbf{x}_{a+1}^\intercal}{\delta \boldsymbol{\epsilon}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j-1=a \\ \mathbf{0} & \text{for } j-1>a. \end{cases}$$

Note that the aj-th entry of $(\delta\mathbf{x}^\intercal/\delta\boldsymbol{\epsilon})(\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x})$ is

$$\left(\frac{\delta \mathbf{x}^\intercal}{\delta \boldsymbol{\epsilon}}\right)_{aj} = \sum_{k=1}^{N_\mathrm{a}} \frac{\delta \mathbf{x}_k^\intercal}{\delta \boldsymbol{\epsilon}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_k} = \frac{\delta \mathbf{x}_{a+1}^\intercal}{\delta \boldsymbol{\epsilon}_a}\frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\mathbf{x}_{a+1}} = \frac{\mathrm{d}\mathbf{x}_j^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_a}, \tag{A64}$$

where we use Eq. (A63) in the second equality. Hence, Eq. (46) follows, where the block matrix of *total effects of a mutant's environment on her states* is

$$\left.\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left.\begin{pmatrix} \mathbf{0} & \frac{\mathrm{d}\mathbf{x}_2^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_1} \\ \mathbf{0} & \mathbf{0} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}-1}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_2} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_2} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \frac{\mathrm{d}\mathbf{x}_{N_\mathrm{a}}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}_{N_\mathrm{a}-1}} \\ \mathbf{0} & \mathbf{0} & \cdots & \mathbf{0} & \mathbf{0} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \tag{A65}$$

$$\in \mathbb{R}^{N_\mathrm{a}N_\mathrm{e}\times N_\mathrm{a}N_\mathrm{s}}.$$

Eqs. (46), (A63), and (44) write the matrix of total effects of a mutant's environment on her states in terms of partial derivatives. This is a compact expression for the matrix of total effects of a mutant's environment on her states in terms of partial derivatives only.

Conclusion

Form 1 Eq. (A58) gives the total selection gradient of the environment as in the first line of Eq. (65).

Form 2 Using Eqs. (A58) and (52) yields

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\boldsymbol{\epsilon}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\frac{\partial w}{\partial \mathbf{x}} + \left(\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \boldsymbol{\epsilon}} + \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}}\right)\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Collecting for $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\boldsymbol{\epsilon}$ and using Eq. (40) for $\boldsymbol{\zeta} = \mathbf{x}$ as well as Eq. (41), we have that the total selection gradient of the environment is given by the second line of Eq. (65).

Form 3 Using the first line of Eq. (65) and Eq. (58), we obtain the third line of Eq. (65).

Form 4 Finally, we can rearrange total selection on the environment in terms of total selection on states. Using Eq. (46) in the second line of Eq. (65), and then using the second line of Eq. (63), we have that the total selection gradient of the environment is given by the fourth line of Eq. (65).

Appendix 7: total selection gradient of the phenotype

We have that the mutant phenotype is $\mathbf{z} = (\mathbf{x};\mathbf{y})$. We first define the (direct), semi-total, and total selection gradients of the phenotype and write the total selection gradient of the phenotype in terms of the semi-total selection gradient of the phenotype and of the partial selection gradient of the metaphenotype.

We have the *selection gradient of the phenotype*

$$\left.\frac{\partial w}{\partial \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial w}{\partial \mathbf{x}};\frac{\partial w}{\partial \mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times 1},$$

the *semi-total selection gradient of the phenotype*

$$\left.\frac{\delta w}{\delta \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\delta w}{\delta \mathbf{x}};\frac{\delta w}{\delta \mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times 1},$$

and the *total selection gradient of the phenotype*

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\mathrm{d}w}{\mathrm{d}\mathbf{x}};\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times 1}.$$

Now, we write the semi-total selection gradient of the phenotype as a linear combination of the selection gradients of the phenotype and environment. Using Eq. (40) for $\boldsymbol{\zeta} \in \{\mathbf{x},\mathbf{y}\}$, we have that the semi-total selection gradient of the phenotype is

$$\begin{aligned}\left.\frac{\delta w}{\delta \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{\delta w}{\delta \mathbf{x}} \\ \frac{\delta w}{\delta \mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{\partial w}{\partial \mathbf{x}} + \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}}\frac{\partial w}{\partial \boldsymbol{\epsilon}} \\ \frac{\partial w}{\partial \mathbf{y}} + \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left[\begin{pmatrix}\frac{\partial w}{\partial \mathbf{x}} \\ \frac{\partial w}{\partial \mathbf{y}}\end{pmatrix} + \begin{pmatrix}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}}\frac{\partial w}{\partial \boldsymbol{\epsilon}} \\ \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned} \tag{A66}$$

Using Eq. (37), we have that

$$\left.\left(\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{z}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\begin{pmatrix}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}} \\ \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}}\end{pmatrix}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}}\frac{\partial w}{\partial \boldsymbol{\epsilon}} \\ \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}}\frac{\partial w}{\partial \boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Therefore, Eq. (A66) becomes Eq. (40) for $\boldsymbol{\zeta} = \mathbf{z}$.

Form 2 Now we bring together the total selection gradients of states and controls to write the total selection gradient of the phenotype as a linear transformation of the semi-total selection gradient of the phenotype.

Using the third lines of Eqs. (63) and (64), we have

$$\begin{aligned}\left.\frac{dw}{d\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{dw}{d\mathbf{x}}\\[4pt] \frac{dw}{d\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{d\mathbf{z}^\intercal}{d\mathbf{x}}\frac{\delta w}{\delta\mathbf{z}}\\[4pt] \frac{d\mathbf{z}^\intercal}{d\mathbf{y}}\frac{\delta w}{\delta\mathbf{z}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left[\begin{pmatrix}\frac{d\mathbf{z}^\intercal}{d\mathbf{x}}\\[4pt] \frac{d\mathbf{z}^\intercal}{d\mathbf{y}}\end{pmatrix}\frac{\delta w}{\delta\mathbf{z}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{d\mathbf{z}^\intercal}{d\mathbf{z}}\frac{\delta w}{\delta\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned}$$

which is the second line of Eq. (66).

Form 3 Now we use the expressions of the total selection gradients of states and controls as linear transformations of the metaphenotype to write the total selection gradient of the phenotype. Using the fourth lines of Eqs. (63) and (64), we have

$$\begin{aligned}\left.\frac{dw}{d\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{dw}{d\mathbf{x}}\\[4pt] \frac{dw}{d\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{d\mathbf{m}^\intercal}{d\mathbf{x}}\frac{\partial w}{\partial\mathbf{m}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\mathbf{y}}\frac{\partial w}{\partial\mathbf{m}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left[\begin{pmatrix}\frac{d\mathbf{m}^\intercal}{d\mathbf{x}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\mathbf{y}}\end{pmatrix}\frac{\partial w}{\partial\mathbf{m}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{d\mathbf{m}^\intercal}{d\mathbf{z}}\frac{\partial w}{\partial\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned}$$

which is the third line of Eq. (66).

Form 1 Now, we obtain the total selection gradient of the phenotype as a linear combination of selection gradients of the phenotype and environment. Using Eq. (40) for $\boldsymbol{\zeta}=\mathbf{z}$, the second line of Eq. (66) becomes

$$\left.\frac{dw}{d\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\frac{d\mathbf{z}^\intercal}{d\mathbf{z}}\left(\frac{\partial w}{\partial\mathbf{z}}+\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\frac{\partial w}{\partial\boldsymbol{\epsilon}}\right)\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A67}$$

We define the block matrix of total effects of a mutant's phenotype on her environment as

$$\left.\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{x}}\\[4pt] \frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}N_\mathrm{e}},$$

which using Eqs. (49) and (50) yields

$$\begin{aligned}\left.\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\begin{pmatrix}\frac{d\mathbf{z}^\intercal}{d\mathbf{x}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\\[4pt] \frac{d\mathbf{z}^\intercal}{d\mathbf{y}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\begin{pmatrix}\frac{d\mathbf{z}^\intercal}{d\mathbf{x}}\\[4pt] \frac{d\mathbf{z}^\intercal}{d\mathbf{y}}\end{pmatrix}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left(\frac{d\mathbf{z}^\intercal}{d\mathbf{z}}\frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned}$$

which is Eq. (51), where in the second equality we factorized and in the third equality we used Eq. (55). Using this in Eq. (A67), the first line of Eq. (66) follows.

Appendix 8: total selection gradient of the metaphenotype

We have that the mutant metaphenotype is $\mathbf{m}=(\mathbf{x};\mathbf{y};\boldsymbol{\epsilon})$. We now define the (direct), semi-total, and total selection gradients of the metaphenotype and write the total selection gradient of the metaphenotype in terms of the partial selection gradient of the metaphenotype.

We have the *selection gradient of the metaphenotype*

$$\left.\frac{\partial w}{\partial\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\left(\frac{\partial w}{\partial\mathbf{x}};\frac{\partial w}{\partial\mathbf{y}};\frac{\partial w}{\partial\boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times 1},$$

the *semi-total selection gradient of the metaphenotype*

$$\left.\frac{\delta w}{\delta\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\delta w}{\delta\mathbf{x}};\frac{\delta w}{\delta\mathbf{y}};\frac{\delta w}{\delta\boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times 1},$$

and the *total selection gradient of the metaphenotype*

$$\left.\frac{dw}{d\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{dw}{d\mathbf{x}};\frac{dw}{d\mathbf{y}};\frac{dw}{d\boldsymbol{\epsilon}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times 1}.$$

Now we use the expressions of the total selection gradients of states, controls, and environment as linear transformations of the metaphenotype to write the total selection gradient of the metaphenotype. Using the fourth lines of Eqs. (63) and (64) and the third line of Eq. (65), we have

$$\begin{aligned}\left.\frac{dw}{d\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &\equiv \left.\begin{pmatrix}\frac{dw}{d\mathbf{x}}\\[4pt] \frac{dw}{d\mathbf{y}}\\[4pt] \frac{dw}{d\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\frac{d\mathbf{m}^\intercal}{d\mathbf{x}}\frac{\partial w}{\partial\mathbf{m}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\mathbf{y}}\frac{\partial w}{\partial\mathbf{m}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\boldsymbol{\epsilon}}\frac{\partial w}{\partial\mathbf{m}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\left[\begin{pmatrix}\frac{d\mathbf{m}^\intercal}{d\mathbf{x}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\mathbf{y}}\\[4pt] \frac{d\mathbf{m}^\intercal}{d\boldsymbol{\epsilon}}\end{pmatrix}\frac{\partial w}{\partial\mathbf{m}}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{d\mathbf{m}^\intercal}{d\mathbf{m}}\frac{\partial w}{\partial\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}},\end{aligned}$$

which is Eq. (67).

To see that $\mathrm{d}\mathbf{m}^\intercal/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular, we factorize it as follows. We define the block matrix of *direct effects of a mutant's metaphenotype on her metaphenotype considering environmental constraints without considering developmental constraints* as

$$\left.\frac{\gamma\mathbf{m}^\intercal}{\gamma\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix}\mathbf{I} & \mathbf{0} & \frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{x}}\\[4pt] \mathbf{0} & \mathbf{I} & \frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\mathbf{y}}\\[4pt] \mathbf{0} & \mathbf{0} & \frac{\partial\boldsymbol{\epsilon}^\intercal}{\partial\boldsymbol{\epsilon}}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},$$

which is non-singular since it is square, block upper triangular, and $\partial\boldsymbol{\epsilon}^\intercal/\partial\boldsymbol{\epsilon}=\mathbf{I}$ (Eq. 34). We also define the block matrix of *total effects of a mutant's metaphenotype on her metaphenotype considering developmental constraints but not selective environmental constraints* as

$$\left.\frac{\beta \mathbf{m}^\intercal}{\beta \mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \mathbf{0} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \mathbf{0} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \mathbf{I} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})},$$

which is non-singular since it is square, block lower triangular, and $\mathrm{d}\mathbf{x}^\intercal/\mathrm{d}\mathbf{x}$ is non-singular (Eq. A32). Note that

$$\begin{aligned}
\left.\begin{pmatrix} \frac{\beta \mathbf{m}^\intercal}{\beta \mathbf{m}} & \frac{\gamma \mathbf{m}^\intercal}{\gamma \mathbf{m}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left.\left[\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \mathbf{0} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \mathbf{0} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{I} & \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}} \\ \mathbf{0} & \mathbf{I} & \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}} \\ \mathbf{0} & \mathbf{0} & \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \boldsymbol{\epsilon}} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}} + \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{y}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}}\frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \mathbf{x}} + \frac{\partial \boldsymbol{\epsilon}^\intercal}{\partial \boldsymbol{\epsilon}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\
&= \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{x}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\mathbf{y}} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} & \mathbf{0} & \frac{\mathrm{d}\boldsymbol{\epsilon}^\intercal}{\mathrm{d}\boldsymbol{\epsilon}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}},
\end{aligned}$$

where the last equality follows from Eqs. (49), (50), and (52). Using Eq. (60), we thus have that

$$\left.\frac{\mathrm{d}\mathbf{m}^\intercal}{\mathrm{d}\mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \frac{\beta \mathbf{m}^\intercal}{\beta \mathbf{m}} & \frac{\gamma \mathbf{m}^\intercal}{\gamma \mathbf{m}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Hence, $\mathrm{d}\mathbf{m}^\intercal/\mathrm{d}\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular since $\beta\mathbf{m}^\intercal/\beta\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ and $\gamma\mathbf{m}^\intercal/\gamma\mathbf{m}|_{\mathbf{y}=\bar{\mathbf{y}}}$ are square and non-singular.

Appendix 9: evolutionary dynamics of states

Here we derive an equation describing the evolutionary dynamics of states.

From Eqs. (14) and (27), we have that the evolutionary dynamics of controls satisfy the canonical equation

$$\frac{\Delta \bar{\mathbf{y}}}{\Delta \tau} = \mathbf{G}_\mathbf{y} \left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A68}$$

whereas the developmental dynamics of states satisfy the developmental constraint

$$\bar{\mathbf{x}}_{a+1} = \mathbf{g}_a^\circ,$$

for $a \in \{1, \ldots, N_\mathrm{a}-1\}$.

Let $\bar{\mathbf{z}}(\tau)$ be the resident phenotype at evolutionary time τ, specifically at the point where the socio-devo stable resident is at carrying capacity, marked in Fig. 3. The i-th mutant state at age $j+1$ at such evolutionary time τ is $x_{i,j+1} = g_{ij}(\mathbf{z}_j(\tau), \bar{\mathbf{z}}(\tau), \mathbf{h}_j(\mathbf{z}_j(\tau), \bar{\mathbf{z}}(\tau), \tau))$. Then, evolutionary change in the i-th resident state variable at age $a \in \{2, \ldots, N_\mathrm{a}\}$ is

$$\begin{aligned}
\frac{\Delta \bar{x}_{ia}}{\Delta \tau} = \frac{1}{\Delta\tau}\Big[g_{i,a-1}\Big(&\mathbf{z}_{a-1}(\tau+\Delta\tau), \bar{\mathbf{z}}(\tau+\Delta\tau), \\
&\mathbf{h}_{a-1}(\mathbf{z}_{a-1}(\tau+\Delta\tau), \bar{\mathbf{z}}(\tau+\Delta\tau), \tau+\Delta\tau)\Big) \\
&- g_{i,a-1}\left(\mathbf{z}_{a-1}(\tau), \bar{\mathbf{z}}(\tau), \mathbf{h}_{a-1}(\mathbf{z}_{a-1}(\tau), \bar{\mathbf{z}}(\tau), \tau)\right)\Big]\Big|_{\mathbf{y}=\bar{\mathbf{y}}}.
\end{aligned}$$

Taking the limit as $\Delta\tau \to 0$, this becomes

$$\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \left.\frac{\mathrm{d}g_{i,a-1}(\mathbf{z}_{a-1}(\tau), \bar{\mathbf{z}}(\tau), \mathbf{h}_{a-1}(\mathbf{z}_{a-1}(\tau), \bar{\mathbf{z}}(\tau), \tau))}{\mathrm{d}\tau}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying the chain rule, we obtain

$$\begin{aligned}
&\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \\
&\Bigg(\sum_{j=1}^{N_\mathrm{s}} \frac{\partial g_{i,a-1}}{\partial x_{j,a-1}} \frac{\mathrm{d}x_{j,a-1}}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{c}} \frac{\partial g_{i,a-1}}{\partial y_{j,a-1}} \frac{\mathrm{d}y_{j,a-1}}{\mathrm{d}\tau} + \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{s}} \frac{\partial g_{i,a-1}}{\partial \bar{x}_{jk}} \frac{\mathrm{d}\bar{x}_{jk}}{\mathrm{d}\tau} \\
&+ \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{c}} \frac{\partial g_{i,a-1}}{\partial \bar{y}_{jk}} \frac{\mathrm{d}\bar{y}_{jk}}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{s}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial g_{i,a-1}}{\partial \epsilon_{r,a-1}} \frac{\partial \epsilon_{r,a-1}}{\partial x_{j,a-1}} \frac{\mathrm{d}x_{j,a-1}}{\mathrm{d}\tau} \\
&+ \sum_{j=1}^{N_\mathrm{c}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial g_{i,a-1}}{\partial \epsilon_{r,a-1}} \frac{\partial \epsilon_{r,a-1}}{\partial y_{j,a-1}} \frac{\mathrm{d}y_{j,a-1}}{\mathrm{d}\tau} + \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{s}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial g_{i,a-1}}{\partial \epsilon_{r,a-1}} \frac{\partial \epsilon_{r,a-1}}{\partial \bar{x}_{jk}} \frac{\mathrm{d}\bar{x}_{jk}}{\mathrm{d}\tau} \\
&+ \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{c}} \sum_{r=1}^{N_\mathrm{e}} \frac{\partial g_{i,a-1}}{\partial \epsilon_{r,a-1}} \frac{\partial \epsilon_{r,a-1}}{\partial \bar{y}_{jk}} \frac{\mathrm{d}\bar{y}_{jk}}{\mathrm{d}\tau} + \sum_{r=1}^{N_\mathrm{e}} \frac{\partial g_{i,a-1}}{\partial \epsilon_{r,a-1}} \frac{\partial \epsilon_{r,a-1}}{\partial \tau} \Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.
\end{aligned}$$

Applying matrix calculus notation (Appendix 14), this is

$$\begin{aligned}
&\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \\
&\Bigg(\frac{\partial g_{i,a-1}}{\partial \mathbf{x}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \mathbf{y}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} + \sum_{k=1}^{N_\mathrm{a}} \frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{x}}_k^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}_k}{\mathrm{d}\tau} \\
&+ \sum_{k=1}^{N_\mathrm{a}} \frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{y}}_k^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}_k}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{s}} \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial x_{j,a-1}} \frac{\mathrm{d}x_{j,a-1}}{\mathrm{d}\tau} \\
&+ \sum_{j=1}^{N_\mathrm{c}} \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial y_{j,a-1}} \frac{\mathrm{d}y_{j,a-1}}{\mathrm{d}\tau} + \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{s}} \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{x}_{jk}} \frac{\mathrm{d}\bar{x}_{jk}}{\mathrm{d}\tau} \\
&+ \sum_{k=1}^{N_\mathrm{a}} \sum_{j=1}^{N_\mathrm{c}} \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{y}_{jk}} \frac{\mathrm{d}\bar{y}_{jk}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.
\end{aligned}$$

Applying matrix calculus notation again yields

$$\begin{aligned}
&\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \\
&\Bigg(\frac{\partial g_{i,a-1}}{\partial \mathbf{x}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \mathbf{y}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{y}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} \\
&+ \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{x}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{y}_{a-1}^\intercal} \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} \\
&+ \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{y}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^\intercal} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.
\end{aligned}$$

Factorizing, we have

$$\begin{aligned}\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \\ \Bigg[& \left(\frac{\partial g_{i,a-1}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial g_{i,a-1}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial g_{i,a-1}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial g_{i,a-1}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .\end{aligned}$$

Rewriting $g_{i,a-1}$ as x_{ia} yields

$$\begin{aligned}\frac{\mathrm{d}\bar{x}_{ia}}{\mathrm{d}\tau} = \\ \Bigg[& \left(\frac{\partial x_{ia}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} + \frac{\partial x_{ia}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial x_{ia}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} + \frac{\partial x_{ia}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial x_{ia}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} + \frac{\partial x_{ia}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial x_{ia}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} + \frac{\partial x_{ia}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial x_{ia}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .\end{aligned}$$

Hence, for all resident states at age $a \in \{2, \ldots, N_{\mathrm{a}}\}$, we have

$$\begin{aligned}\frac{\mathrm{d}\bar{\mathbf{x}}_{a}}{\mathrm{d}\tau} = \Bigg[& \left(\frac{\partial \mathbf{x}_{a}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} + \frac{\partial \mathbf{x}_{a}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{x}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial \mathbf{x}_{a}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} + \frac{\partial \mathbf{x}_{a}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \mathbf{y}_{a-1}^{\mathsf{T}}} \right) \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial \mathbf{x}_{a}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} + \frac{\partial \mathbf{x}_{a}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{x}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} \\ & + \left(\frac{\partial \mathbf{x}_{a}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} + \frac{\partial \mathbf{x}_{a}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \bar{\mathbf{y}}^{\mathsf{T}}} \right) \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial \mathbf{x}_{a}}{\partial \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} .\end{aligned} \tag{A69}$$

Here we used the following series of definitions. The matrix of *direct effects of social partner's states at age a on the mutant's states at age j* is

$$\left.\frac{\partial \mathbf{x}_j^{\mathsf{T}}}{\partial \bar{\mathbf{x}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial x_{1j}}{\partial \bar{x}_{1a}} & \cdots & \frac{\partial x_{N_{\mathrm{s}}j}}{\partial \bar{x}_{1a}} \\ \vdots & \ddots & \vdots \\ \frac{\partial x_{1j}}{\partial \bar{x}_{N_{\mathrm{s}}a}} & \cdots & \frac{\partial x_{N_{\mathrm{s}}j}}{\partial \bar{x}_{N_{\mathrm{s}}a}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{s}} \times N_{\mathrm{s}}},$$

and the block matrix of direct effects of social partners' states on a mutant's states is given by Eq. (35) with $\bar{\boldsymbol{\zeta}} = \bar{\mathbf{x}}$. The matrix $\partial \mathbf{x}_a^{\mathsf{T}} / \partial \bar{\mathbf{x}}$ is the a-th block column of $\partial \mathbf{x}^{\mathsf{T}} / \partial \bar{\mathbf{x}}$.

Similarly, the matrix of *direct effects of social partners' controls at age a on a mutant's states at age j* is

$$\left.\frac{\partial \mathbf{x}_j^{\mathsf{T}}}{\partial \bar{\mathbf{y}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial x_{1j}}{\partial \bar{y}_{1a}} & \cdots & \frac{\partial x_{N_{\mathrm{s}}j}}{\partial \bar{y}_{1a}} \\ \vdots & \ddots & \vdots \\ \frac{\partial x_{1j}}{\partial \bar{y}_{N_{\mathrm{c}}a}} & \cdots & \frac{\partial x_{N_{\mathrm{s}}j}}{\partial \bar{y}_{N_{\mathrm{c}}a}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{c}} \times N_{\mathrm{s}}},$$

and the block matrix of direct effects of social partners' controls on a mutant's states is given by Eq. (35) with $\bar{\boldsymbol{\zeta}} = \bar{\mathbf{y}}$. The matrix $\partial \mathbf{x}_a^{\mathsf{T}} / \partial \bar{\mathbf{y}}$ is the a-th block column of $\partial \mathbf{x}^{\mathsf{T}} / \partial \bar{\mathbf{y}}$.

In turn, the matrix of *direct effects of social partners' states at age a on a mutant's environment at age j* is

$$\left.\frac{\partial \boldsymbol{\epsilon}_j^{\mathsf{T}}}{\partial \bar{\mathbf{x}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial \epsilon_{1j}}{\partial \bar{x}_{1a}} & \cdots & \frac{\partial \epsilon_{N_{\mathrm{e}}j}}{\partial \bar{x}_{1a}} \\ \vdots & \ddots & \vdots \\ \frac{\partial \epsilon_{1j}}{\partial \bar{x}_{N_{\mathrm{s}}a}} & \cdots & \frac{\partial \epsilon_{N_{\mathrm{e}}j}}{\partial \bar{x}_{N_{\mathrm{s}}a}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{e}} \times N_{\mathrm{s}}},$$

and the block matrix of direct effects of social partners' states on a mutant's environment is given by Eq. (36) with $\bar{\boldsymbol{\zeta}} = \bar{\mathbf{x}}$. The matrix $\partial \boldsymbol{\epsilon}_a^{\mathsf{T}} / \partial \bar{\mathbf{x}}$ is the a-th block column of $\partial \boldsymbol{\epsilon}^{\mathsf{T}} / \partial \bar{\mathbf{x}}$.

Similarly, the matrix of *direct effects of social partners' controls at age a on a mutant's environment at age j* is

$$\left.\frac{\partial \boldsymbol{\epsilon}_j^{\mathsf{T}}}{\partial \bar{\mathbf{y}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\partial \epsilon_{1j}}{\partial \bar{y}_{1a}} & \cdots & \frac{\partial \epsilon_{N_{\mathrm{e}}j}}{\partial \bar{y}_{1a}} \\ \vdots & \ddots & \vdots \\ \frac{\partial \epsilon_{1j}}{\partial \bar{y}_{N_{\mathrm{c}}a}} & \cdots & \frac{\partial \epsilon_{N_{\mathrm{e}}j}}{\partial \bar{y}_{N_{\mathrm{c}}a}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_{\mathrm{e}} \times N_{\mathrm{c}}},$$

and the block matrix of *direct effects of social partners' controls on a mutant's environment* is given by Eq. (36) with $\bar{\boldsymbol{\zeta}} = \bar{\mathbf{y}}$. The matrix $\partial \boldsymbol{\epsilon}_a^{\mathsf{T}} / \partial \bar{\mathbf{y}}$ is the a-th block column of $\partial \boldsymbol{\epsilon}^{\mathsf{T}} / \partial \bar{\mathbf{y}}$.

Having made these definitions explicit, we now write Eq. (A69) as

$$\begin{aligned}\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \Bigg(& \frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^{\mathsf{T}}} \frac{\mathrm{d}\mathbf{x}_{a-1}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \mathbf{y}_{a-1}^{\mathsf{T}}} \frac{\mathrm{d}\mathbf{y}_{a-1}}{\mathrm{d}\tau} \\ & + \frac{\delta \mathbf{x}_a}{\delta \bar{\mathbf{x}}^{\mathsf{T}}} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \bar{\mathbf{y}}^{\mathsf{T}}} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \boldsymbol{\epsilon}_{a-1}^{\mathsf{T}}} \frac{\partial \boldsymbol{\epsilon}_{a-1}}{\partial \tau} \Bigg) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} ,\end{aligned} \tag{A70}$$

where we used the transpose of the semi-total effects of a mutant's states and controls on her states (Eqs. A27 and A47), and the the matrix of *semi-total effects of social partners' states or controls at age a on a mutant's states at age j*

$$\left.\frac{\delta \mathbf{x}_j^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \left.\left(\frac{\partial \mathbf{x}_j^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_a} + \frac{\partial \boldsymbol{\epsilon}_{j-1}^{\mathsf{T}}}{\partial \bar{\boldsymbol{\zeta}}_a} \frac{\partial \mathbf{x}_j^{\mathsf{T}}}{\partial \boldsymbol{\epsilon}_{j-1}} \right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > 1 \\ \mathbf{0} & \text{for } j = 1, \end{cases} \tag{A71}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$ since the initial states $\mathbf{x}_1$ are constant by assumption. We also define the corresponding matrix of *semi-total effects of social partners' states on a mutant's states* as

$$\left.\frac{\delta \mathbf{x}^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \equiv \left.\begin{pmatrix} \frac{\delta \mathbf{x}_1^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\delta \mathbf{x}_{N_{\mathrm{a}}}^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}_1} \\ \vdots & \ddots & \vdots \\ \frac{\delta \mathbf{x}_1^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} & \cdots & \frac{\delta \mathbf{x}_{N_{\mathrm{a}}}^{\mathsf{T}}}{\delta \bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left.\begin{pmatrix} \mathbf{0} & \frac{\delta \mathbf{x}_2^\top}{\delta \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\delta \mathbf{x}_{N_{\mathrm{a}}}^\top}{\delta \bar{\boldsymbol{\zeta}}_1} \\ \mathbf{0} & \frac{\delta \mathbf{x}_2^\top}{\delta \bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\delta \mathbf{x}_{N_{\mathrm{a}}}^\top}{\delta \bar{\boldsymbol{\zeta}}_1} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \frac{\delta \mathbf{x}_2^\top}{\delta \bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} & \cdots & \frac{\delta \mathbf{x}_{N_{\mathrm{a}}}^\top}{\delta \bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A72}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$. The matrix $\delta \mathbf{x}_a^\top / \delta \bar{\boldsymbol{\zeta}}$ is the a-th block column of $\delta \mathbf{x}^\top / \delta \bar{\boldsymbol{\zeta}}$. Using Eq. (33c) and since the initial states $\mathbf{x}_1$ are constant by assumption, we have that

$$\frac{\partial \boldsymbol{\epsilon}^\top}{\partial \bar{\boldsymbol{\zeta}}}\frac{\partial \mathbf{x}^\top}{\partial \boldsymbol{\epsilon}} = \left(\sum_{k=1}^{N_{\mathrm{a}}} \frac{\partial \boldsymbol{\epsilon}_k^\top}{\partial \bar{\boldsymbol{\zeta}}_a}\frac{\partial \mathbf{x}_j^\top}{\partial \boldsymbol{\epsilon}_k}\right) = \left(\begin{cases} \frac{\partial \boldsymbol{\epsilon}_{j-1}^\top}{\partial \bar{\boldsymbol{\zeta}}_a}\frac{\partial \mathbf{x}_j^\top}{\partial \boldsymbol{\epsilon}_{j-1}} & \text{for } j > 1 \\ \mathbf{0} & \text{for } j = 1 \end{cases}\right), \tag{A73}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$, which equals the rightmost terms in Eqs. (A71). Thus, from Eqs. (A71), (A72), and (A73), it follows that the block matrix of semi-total effects of social partners' states or controls on a mutant's states satisfies Eq. (42).

Noting that $\delta \mathbf{x}_a / \delta \bar{\mathbf{z}}^\top = (\delta \mathbf{x}_a / \delta \bar{\mathbf{x}}^\top, \delta \mathbf{x}_a / \delta \bar{\mathbf{y}}^\top)$ and that evaluation of $\mathrm{d}\mathbf{z}_a / \mathrm{d}\tau$ and $\partial \boldsymbol{\epsilon}_a / \partial \tau$ at $\mathbf{y} = \bar{\mathbf{y}}$ is $\mathrm{d}\bar{\mathbf{z}}_a / \mathrm{d}\tau$ and $\partial \bar{\boldsymbol{\epsilon}}_a / \partial \tau$ respectively, Eq. (A70) can be written as

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \Bigg(& \frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\mathrm{d}\bar{\mathbf{x}}_{a-1}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \mathbf{y}_{a-1}^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_{a-1}}{\mathrm{d}\tau} \\ & + \frac{\delta \mathbf{x}_a}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \boldsymbol{\epsilon}_{a-1}^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-1}}{\partial \tau} \Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned}$$

which is a recursion for $\mathrm{d}\bar{\mathbf{x}}_a / \mathrm{d}\tau$ over a. Expanding this recursion two steps yields

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \Bigg\{ & \frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\Bigg[\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{x}_{a-2}^\top}\Bigg(\frac{\delta \mathbf{x}_{a-2}}{\delta \mathbf{x}_{a-3}^\top}\frac{\mathrm{d}\bar{\mathbf{x}}_{a-3}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_{a-2}}{\delta \mathbf{y}_{a-3}^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_{a-3}}{\mathrm{d}\tau} \\ & + \frac{\delta \mathbf{x}_{a-2}}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_{a-2}}{\delta \boldsymbol{\epsilon}_{a-3}^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-3}}{\partial \tau}\Bigg) \\ & + \frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{y}_{a-1}^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_{a-2}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_{a-1}}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_{a-1}}{\delta \boldsymbol{\epsilon}_{a-2}^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-2}}{\partial \tau}\Bigg] \\ & + \frac{\delta \mathbf{x}_a}{\delta \mathbf{y}_{a-1}^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_{a-1}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \boldsymbol{\epsilon}_{a-1}^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-1}}{\partial \tau}\Bigg\}\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Collecting the derivatives with respect to τ yields

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = & \\ \Bigg[& \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{x}_{a-2}^\top}\frac{\delta \mathbf{x}_{a-2}}{\delta \mathbf{x}_{a-3}^\top}\right)\frac{\mathrm{d}\bar{\mathbf{x}}_{a-3}}{\mathrm{d}\tau} \\ & + \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{x}_{a-2}^\top}\frac{\delta \mathbf{x}_{a-2}}{\delta \mathbf{y}_{a-3}^\top}\right)\frac{\mathrm{d}\bar{\mathbf{y}}_{a-3}}{\mathrm{d}\tau} \\ & + \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{y}_{a-1}^\top}\right)\frac{\mathrm{d}\bar{\mathbf{y}}_{a-2}}{\mathrm{d}\tau} + \frac{\delta \mathbf{x}_a}{\delta \mathbf{y}_{a-1}^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_{a-1}}{\mathrm{d}\tau} \\ & + \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{x}_{a-2}^\top}\frac{\delta \mathbf{x}_{a-2}}{\delta \boldsymbol{\epsilon}_{a-3}^\top}\right)\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-3}}{\partial \tau} \\ & + \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \boldsymbol{\epsilon}_{a-2}^\top}\right)\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-2}}{\partial \tau} + \frac{\delta \mathbf{x}_a}{\delta \boldsymbol{\epsilon}_{a-1}^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_{a-1}}{\partial \tau} \\ & + \left(\frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \mathbf{x}_{a-2}^\top}\frac{\delta \mathbf{x}_{a-2}}{\delta \bar{\mathbf{z}}^\top} + \frac{\delta \mathbf{x}_a}{\delta \mathbf{x}_{a-1}^\top}\frac{\delta \mathbf{x}_{a-1}}{\delta \bar{\mathbf{z}}^\top} + \frac{\delta \mathbf{x}_a}{\delta \bar{\mathbf{z}}^\top}\right)\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\Bigg]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Inspection shows that by expanding the recursion completely and since we assume that initial states do not evolve (i.e., $\mathrm{d}\bar{\mathbf{x}}_1 / \mathrm{d}\tau = \mathbf{0}$), the resulting expression can be succinctly written as

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \Bigg(& \sum_{j=1}^{a-1} \overset{\curvearrowleft}{\prod_{k=j+1}^{a-1}} \frac{\delta \mathbf{x}_{k+1}}{\delta \mathbf{x}_k^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \mathbf{y}_j^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} \\ & + \sum_{j=1}^{a-1} \overset{\curvearrowleft}{\prod_{k=j+1}^{a-1}} \frac{\delta \mathbf{x}_{k+1}}{\delta \mathbf{x}_k^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \boldsymbol{\epsilon}_j^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_j}{\partial \tau} \\ & + \sum_{j=1}^{a-1} \overset{\curvearrowleft}{\prod_{k=j+1}^{a-1}} \frac{\delta \mathbf{x}_{k+1}}{\delta \mathbf{x}_k^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned}$$

where the $\curvearrowleft$ denotes left multiplication. Note that the products over k are the transpose of the total effects of a mutant's states at age $j+1$ on her states at age a (Eq. A33). Hence,

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \Bigg(& \sum_{j=1}^{a-1} \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_{j+1}^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \mathbf{y}_j^\top}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{a-1} \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_{j+1}^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \boldsymbol{\epsilon}_j^\top}\frac{\partial \bar{\boldsymbol{\epsilon}}_j}{\partial \tau} \\ & + \sum_{j=1}^{a-1} \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_{j+1}^\top}\frac{\delta \mathbf{x}_{j+1}}{\delta \bar{\mathbf{z}}^\top}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\Bigg)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned} \tag{A74}$$

Before simplifying Eq. (A74), we introduce a series of matrices that are analogous to those already provided, based on Eq. (A55). The matrix of *total effects of social partners' states or controls at age a on a mutant's states at age j* is

$$\left.\frac{\mathrm{d}\mathbf{x}_j^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{cases} \displaystyle\sum_{l=1}^{N_{\mathrm{a}}} \left.\left(\frac{\delta \mathbf{x}_l^\top}{\delta \bar{\boldsymbol{\zeta}}_a}\frac{\mathrm{d}\mathbf{x}_j^\top}{\mathrm{d}\mathbf{x}_l}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \text{for } j > 1 \\ \mathbf{0} & \text{for } j = 1, \end{cases} \tag{A75}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$. The block matrix of *total effects of social partners' states or controls on a mutant's states* is thus

$$\begin{aligned} \left.\frac{\mathrm{d}\mathbf{x}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} & \equiv \left.\begin{pmatrix} \frac{\mathrm{d}\mathbf{x}_1^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_{\mathrm{a}}}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_1} \\ \vdots & \ddots & \vdots \\ \frac{\mathrm{d}\mathbf{x}_1^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_{\mathrm{a}}}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ & = \left.\begin{pmatrix} \mathbf{0} & \frac{\mathrm{d}\mathbf{x}_2^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_1} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_{\mathrm{a}}}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_1} \\ \mathbf{0} & \frac{\mathrm{d}\mathbf{x}_2^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_2} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_{\mathrm{a}}}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_2} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{0} & \frac{\mathrm{d}\mathbf{x}_2^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} & \cdots & \frac{\mathrm{d}\mathbf{x}_{N_{\mathrm{a}}}^\top}{\mathrm{d}\bar{\boldsymbol{\zeta}}_{N_{\mathrm{a}}}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned} \tag{A76}$$

for $\bar{\boldsymbol{\zeta}} \in \{\bar{\mathbf{x}}, \bar{\mathbf{y}}\}$. Then, from Eq. (A75), the block matrix in Eq. (A76) satisfies Eq. (47).

Using Eqs. (A55) and (A64) and given the property of transpose of a product (i.e., $(\mathbf{AB})^\intercal = \mathbf{B}^\intercal\mathbf{A}^\intercal$), Eq. (A74) can be written more succinctly as

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{a-1}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{a-1}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{j=1}^{a-1}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_{j+1}^\intercal}\frac{\delta\mathbf{x}_{j+1}}{\delta\bar{\mathbf{z}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Note that from Eq. (A54), we have that $\mathrm{d}\mathbf{x}_a/\mathrm{d}\mathbf{y}_j^\intercal = \mathbf{0}$ for $j \geq a$, from Eq. (A65), we have that $\mathrm{d}\mathbf{x}_a/\mathrm{d}\boldsymbol{\epsilon}_j^\intercal = \mathbf{0}$ for $j \geq a$, and from Eq. (A32), we have that $\mathrm{d}\mathbf{x}_a/\mathrm{d}\mathbf{x}_{j+1}^\intercal = \mathbf{0}$ for $j+1 \geq a$. Hence, the same expression holds extending the upper bounds of the sums to the last possible age:

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{j=1}^{N_\mathrm{a}-1}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_{j+1}^\intercal}\frac{\delta\mathbf{x}_{j+1}}{\delta\bar{\mathbf{z}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Changing the sum index for the last terms yields

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{j=2}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_j^\intercal}\frac{\delta\mathbf{x}_j}{\delta\bar{\mathbf{z}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Expanding the matrix calculus notation for the entries of $\bar{\mathbf{z}}$ in the rightmost term yields

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{j=2}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_j^\intercal}\frac{\delta\mathbf{x}_j}{\delta\bar{\mathbf{x}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \sum_{j=2}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_j^\intercal}\frac{\delta\mathbf{x}_j}{\delta\bar{\mathbf{y}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Expanding again the matrix calculus notation for the entries of $\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$ in the two rightmost terms yields

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{l=1}^{N_\mathrm{a}}\sum_{j=2}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_j^\intercal}\frac{\delta\mathbf{x}_j}{\delta\bar{\mathbf{x}}_l^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}_l}{\mathrm{d}\tau} + \sum_{l=1}^{N_\mathrm{a}}\sum_{j=2}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{x}_j^\intercal}\frac{\delta\mathbf{x}_j}{\delta\bar{\mathbf{y}}_l^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_l}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using the transpose of the matrix in Eq. (A75) in the two rightmost terms, noting that $\delta\mathbf{x}_j/\delta\bar{\mathbf{x}}_l^\intercal = \mathbf{0}$ and $\delta\mathbf{x}_j/\delta\bar{\mathbf{y}}_l^\intercal = \mathbf{0}$ for $j = 1$ (from Eq. A72), yields

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}_j^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}_j^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}_j}{\partial\tau} + \sum_{l=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\bar{\mathbf{x}}_l^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}_l}{\mathrm{d}\tau} + \sum_{l=1}^{N_\mathrm{a}}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\bar{\mathbf{y}}_l^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_l}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation to each term yields

$$\frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} = \left(\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\mathbf{y}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\boldsymbol{\epsilon}^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}}{\partial\tau} + \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}},$$

for $a \in \{2, \ldots, N_\mathrm{a}\}$. Since $\mathrm{d}\bar{\mathbf{x}}_1/\mathrm{d}\tau = \mathbf{0}$, it follows that

$$\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} = \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{y}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\epsilon}^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}}{\partial\tau} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau}\right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \quad \text{(A77)}$$

which contains our desired $\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau$ on both sides of the equation.

The matrix premultiplying $\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau$ on the right-hand side of Eq. (A77) is $\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$, which is square. We now make use of our assumption that the absolute value of all the eigenvalues of $\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is strictly less than one, which guarantees that the resident phenotype is socio-devo stable (Appendix 15). Given this property of $\mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$, then $\mathbf{I} - \mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is invertible. Hence, we can define the transpose of the matrix of *stabilized effects of a focal individual' states on a social partners' states* (second equality of Eq. 68). Thus, solving for $\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau$ in Eq. (A77), we finally obtain an equation describing the evolutionary dynamics of states

$$\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} = \left[\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal}\left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{y}^\intercal} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\right)\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal}\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\epsilon}^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}}{\partial\tau}\right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Let us momentarily write $\mathbf{x} = \tilde{\mathbf{g}}(\mathbf{y}, \bar{\mathbf{y}})$ for some differentiable function $\tilde{\mathbf{g}}$ to highlight the dependence of a mutant's states $\mathbf{x}$ on her controls $\mathbf{y}$ and on the controls $\bar{\mathbf{y}}$ of resident social partners. Consider the resident states that develop in the context of mutant controls, denoted by $\check{\mathbf{x}} = \tilde{\mathbf{g}}(\bar{\mathbf{y}}, \mathbf{y})$. Hence,

$$\frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\tilde{\mathbf{g}}(\bar{\mathbf{y}}, \mathbf{y})}{\mathrm{d}\mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\tilde{\mathbf{g}}(\mathbf{y}, \bar{\mathbf{y}})}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \quad \text{(A78)}$$

where the second equality follows by exchanging dummy variables. Then, the transpose of the matrix of *total social effects of a mutant's controls on her and a partner's states* is

$$\begin{aligned}\frac{\mathrm{d}(\mathbf{x}+\check{\mathbf{x}})}{\mathrm{d}\mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{y}^\intercal} + \frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{y}^\intercal}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{y}^\intercal} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{y}}^\intercal}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{c}}. \quad \text{(A79)}\end{aligned}$$

Similarly, let us momentarily write $\mathbf{x} = \tilde{\tilde{\mathbf{g}}}(\mathbf{x}, \bar{\mathbf{x}})$ for some differentiable function $\tilde{\tilde{\mathbf{g}}}$ to highlight the dependence of a mutant's states $\mathbf{x}$ on her (developmentally earlier) states $\mathbf{x}$ and on the states $\bar{\mathbf{x}}$ of resident social partners. Consider the resident states that develop in the context of mutant states, denoted by $\check{\mathbf{x}} = \tilde{\tilde{\mathbf{g}}}(\bar{\mathbf{x}}, \mathbf{x})$. Hence,

$$\frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\tilde{\tilde{\mathbf{g}}}(\bar{\mathbf{x}}, \mathbf{x})}{\mathrm{d}\mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\tilde{\tilde{\mathbf{g}}}(\mathbf{x}, \bar{\mathbf{x}})}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \quad \text{(A80)}$$

where the second equality follows by exchanging dummy variables. Then, the transpose of the matrix of *total social effects of a mutant's states on her and a partner's states* is

$$\begin{aligned}\frac{\mathrm{d}(\mathbf{x}+\check{\mathbf{x}})}{\mathrm{d}\mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{x}^\intercal} + \frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{x}^\intercal}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left(\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\mathbf{x}^\intercal} + \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\intercal}\right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}}. \quad \text{(A81)}\end{aligned}$$

Thus, from Eq. (A80) and the second equality of Eq. (68), the transpose of the matrix of stabilized effects of a focal individual's states on social partners' states may also be written as

$$\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\mathbf{I} - \frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}\right)^{-1}$$

$$= \sum_{\theta=1}^{\infty} \left(\frac{\mathrm{d}\check{\mathbf{x}}}{\mathrm{d}\mathbf{x}^\intercal} \right)^{\theta-1} \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}\times N_\mathrm{a}N_\mathrm{s}},$$

where the last equality follows from the geometric series of matrices. This equation is the first and third equalities of (68).

Therefore, using Eqs. (69) and (69b), the evolutionary dynamics of states are given by

$$\begin{aligned} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} &= \left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}(\mathbf{x}+\check{\mathbf{x}})}{\mathrm{d}\mathbf{y}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\boldsymbol{\epsilon}^\intercal} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left(\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left(\mathbf{H}_{\mathbf{xy}} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned} \tag{A82}$$

where the second equality follows by using Eq. (A68) in the limit $\Delta\tau \to 0$, and the third equality follows from Eq. (87). The first line of Eq. A82 describing evolutionary change of states in terms of evolutionary change of controls is a generalization of previous equations describing the evolution of a multivariate phenotype in terms of allele frequency change (e.g., the first equation on p. 49 of Engen and Sæther 2021). Eq. (A82) is Eq. (92) for $\boldsymbol{\zeta} = \mathbf{x}$. Using the third line of Eq. (64) and Eq. (85) yields Eq. (91) for $\boldsymbol{\zeta} = \mathbf{x}$, whereas using the fourth line of Eq. (64) and Eq. (86) yields Eq. (88a) for $\boldsymbol{\zeta} = \mathbf{x}$.

Appendix 10: evolutionary dynamics of the phenotype

In terms of total genetic selection

Here we obtain an equation describing the evolutionary dynamics of the resident phenotype, that is, $\mathrm{d}\bar{\mathbf{z}}/\mathrm{d}\tau$. In this section, we write such an equation in terms of the total genetic selection. Since $\mathrm{d}\bar{\mathbf{z}}/\mathrm{d}\tau = (\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau; \mathrm{d}\bar{\mathbf{y}}/\mathrm{d}\tau)$, from Eqs. (A82) and (14a), we can write the evolutionary dynamics of the resident phenotype $\bar{\mathbf{z}}$ as

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \left[\begin{pmatrix} \mathbf{H}_{\mathbf{xy}} \\ \mathbf{G}_\mathbf{y} \end{pmatrix} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \\ \mathbf{0} \end{pmatrix} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A83}$$

Using Eqs. (87) and (70), this is

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\intercal} \end{pmatrix} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \end{pmatrix} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (72), this reduces to

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (87) yields Eq. (92) for $\boldsymbol{\zeta} = \mathbf{z}$. Using the third line of Eq. (64) and Eq. (85) yields Eq. (91) for $\boldsymbol{\zeta} = \mathbf{z}$, whereas using the fourth line of Eq. (64) and (86) yields Eq. (88a) for $\boldsymbol{\zeta} = \mathbf{z}$.

In contrast to other arrangements, the premultiplying matrix $\mathbf{H}_{\mathbf{zy}}$ is non-singular if $\mathbf{G}_\mathbf{y}$ is non-singular. Indeed, if

$$\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\intercal} \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} = \mathbf{0}$$

for some vector $\mathbf{r}$, then from Eqs. (72a) and (70b) we have

$$\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \mathbf{I} \end{pmatrix} \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} = \mathbf{0}.$$

Doing the multiplication yields

$$\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \Big|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} \\ \mathbf{r} \end{pmatrix} = \mathbf{0},$$

which implies that $\mathbf{r} = \mathbf{0}$, so $\mathrm{s}\mathbf{z}/\mathrm{s}\mathbf{y}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular. Thus, $\mathbf{H}_{\mathbf{zy}}$ is non-singular if $\mathbf{G}_\mathbf{y}$ is non-singular.

In terms of total selection on the phenotype

Here we write the evolutionary dynamics of the phenotype in terms of the total selection gradient of the phenotype.

First, using Eq. (77), we define the *additive genetic covariance matrix of the undeveloped phenotype* $\hat{\mathbf{z}} = (\bar{\mathbf{x}}; \mathbf{y})$ as

$$\mathbf{G}_{\hat{\mathbf{z}}} \equiv \mathrm{cov}[\mathbf{a}_{\hat{\mathbf{z}}}, \mathbf{a}_{\hat{\mathbf{z}}}] = \left(\frac{\mathrm{d}\hat{\mathbf{z}}}{\mathrm{d}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}\hat{\mathbf{z}}^\intercal}{\mathrm{d}\mathbf{y}} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}.$$

By definition of $\hat{\mathbf{z}}$, we have

$$\mathbf{G}_{\hat{\mathbf{z}}} = \left[\begin{pmatrix} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\mathbf{y}^\intercal} \\ \frac{\mathrm{d}\mathbf{y}}{\mathrm{d}\mathbf{y}^\intercal} \end{pmatrix} \mathbf{G}_\mathbf{y} \begin{pmatrix} \frac{\mathrm{d}\bar{\mathbf{x}}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} \end{pmatrix} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

From Eq. (2), resident states are independent of mutant controls, so

$$\mathbf{G}_{\hat{\mathbf{z}}} = \left[\begin{pmatrix} \mathbf{0} \\ \mathbf{I} \end{pmatrix} \mathbf{G}_\mathbf{y} \begin{pmatrix} \mathbf{0} & \mathbf{I} \end{pmatrix} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Doing the matrix multiplication yields

$$\mathbf{G}_{\hat{\mathbf{z}}} = \left[\begin{pmatrix} \mathbf{0} \\ \mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{G}_\mathbf{y} \end{pmatrix} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_\mathbf{y} \end{pmatrix}. \tag{A84}$$

The matrix $\mathbf{G}_{\hat{\mathbf{z}}}$ is singular because the undeveloped phenotype includes controls (i.e., $\mathrm{d}\hat{\mathbf{z}}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has fewer rows than columns). For this reason, the matrix $\mathbf{G}_{\hat{\mathbf{z}}}$ would still be singular even if the zero block entries in Eq. (A84) were non-zero (i.e., if $\mathrm{d}\bar{\mathbf{x}}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$).

Now, we write an alternative factorization of $\mathbf{H}_\mathbf{z}$ in terms of $\mathbf{G}_{\hat{\mathbf{z}}}$. Using Eqs. (55) and (73), consider the matrix

$$\begin{aligned} &\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal} \mathbf{G}_{\hat{\mathbf{z}}} \frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\intercal} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \mathbf{0} & \mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_\mathbf{y} \end{pmatrix} \begin{pmatrix} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{x}} & \mathbf{0} \\ \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{I} \end{pmatrix} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \end{aligned}$$

Doing the matrix multiplication yields

$$\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal} \mathbf{G}_{\hat{\mathbf{z}}} \frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}} \right) \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{x}^\intercal} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \mathbf{0} & \mathbf{I} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{G}_\mathbf{y} \frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{G}_\mathbf{y} \end{pmatrix} \right] \Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}$$

$$= \left.\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y} \\ \mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \mathbf{G}_\mathbf{y} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (70b), we have

$$\left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal}\mathbf{G}_{\hat{\mathbf{z}}}\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{x}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Notice that the matrix on the right-hand side is

$$\left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{H}_\mathbf{z}.$$

Hence, we obtain an alternative factorization for $\mathbf{H}_\mathbf{z}$ as

$$\mathbf{H}_\mathbf{z} = \left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal}\mathbf{G}_{\hat{\mathbf{z}}}\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Thus, we can write the selection response of the phenotype (in the form of Eq. 91) as

$$\mathbf{H}_\mathbf{z}\left.\frac{\delta w}{\delta \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal}\mathbf{G}_{\hat{\mathbf{z}}}\frac{\mathrm{d}\mathbf{z}^\intercal}{\mathrm{d}\mathbf{z}}\frac{\delta w}{\delta \mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using the relationship between the total and semi-total selection gradients of the phenotype (second line of Eq. 66), this becomes

$$\mathbf{H}_\mathbf{z}\left.\frac{\delta w}{\delta \mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal}\mathbf{G}_{\hat{\mathbf{z}}}\frac{\mathrm{d}w}{\mathrm{d}\mathbf{z}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

We can further simplify this equation by noticing the following. Using Eq. (84) and $\hat{\mathbf{z}} = (\bar{\mathbf{x}};\mathbf{y})$, we have that the *additive socio-genetic cross-covariance matrix of the phenotype and the undeveloped phenotype* is

$$\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}} = \left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y}\frac{\mathrm{d}\hat{\mathbf{z}}^\intercal}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}. \tag{A85}$$

Expanding, we have

$$\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}} = \left.\left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\intercal} \end{pmatrix}\mathbf{G}_\mathbf{y}\begin{pmatrix} \frac{\mathrm{d}\bar{\mathbf{x}}^\intercal}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^\intercal}{\mathrm{d}\mathbf{y}} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (70b) and since resident states do not depend on mutant controls, then

$$\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}} = \left.\left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \mathbf{I} \end{pmatrix}\mathbf{G}_\mathbf{y}\begin{pmatrix} \mathbf{0} & \mathbf{I} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Doing the matrix multiplication yields

$$\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}} = \left.\left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \mathbf{I} \end{pmatrix}\begin{pmatrix} \mathbf{0} & \mathbf{G}_\mathbf{y} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\begin{pmatrix} \mathbf{0} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal}\mathbf{G}_\mathbf{y} \\ \mathbf{0} & \mathbf{G}_\mathbf{y} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Notice that the last matrix equals

$$\left.\left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{z}^\intercal}\mathbf{G}_{\hat{\mathbf{z}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

We can then write the evolutionary dynamics of the resident phenotype $\bar{\mathbf{z}}$ in terms of the total selection gradient of the phenotype as

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} = \left.\left(\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}}\frac{\mathrm{d}w}{\mathrm{d}\mathbf{z}} + \frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal}\frac{\partial\bar{\boldsymbol{\epsilon}}}{\partial\tau}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A86}$$

The cross-covariance matrix $\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}}$ is singular because $\mathrm{d}\hat{\mathbf{z}}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has fewer rows than columns since the undeveloped phenotype includes controls. For this reason, $\mathbf{H}_{\mathbf{z}\hat{\mathbf{z}}}$ would still be singular even if the zero block entries in Eq. (A85) were non-zero (i.e., if $\mathrm{d}\bar{\mathbf{x}}^\intercal/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$). Then, evolutionary equilibria of the phenotype do not imply absence of total selection on the phenotype, even if exogenous plastic response is absent.

Appendix 11: evolutionary dynamics of the environment

In terms of endogenous and exogenous environmental change

Here we derive an equation describing the evolutionary dynamics of the environment. Let $\bar{\mathbf{z}}(\tau)$ be the resident phenotype at evolutionary time τ, specifically at the point where the socio-devo stable resident is at carrying capacity, marked in Fig. 3. The i-th environmental variable experienced by a mutant of age a at such evolutionary time τ is $\epsilon_{ia} = h_{ia}(\mathbf{z}_a(\tau), \bar{\mathbf{z}}(\tau), \tau))$. Then, evolutionary change in the i-th environmental variable experienced by residents at age a is

$$\frac{\Delta\bar{\epsilon}_{ia}}{\Delta\tau} = \frac{1}{\Delta\tau}\Big[h_{ia}\left(\mathbf{z}_a(\tau+\Delta\tau), \bar{\mathbf{z}}(\tau+\Delta\tau), \tau+\Delta\tau\right) \\ \left. - h_{ai}\left(\mathbf{z}_a(\tau), \bar{\mathbf{z}}(\tau), \tau\right)\Big]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Taking the limit as $\Delta\tau \to 0$, this becomes

$$\frac{\mathrm{d}\bar{\epsilon}_{ia}}{\mathrm{d}\tau} = \left.\frac{\mathrm{d}h_{ia}(\mathbf{z}_a(\tau), \bar{\mathbf{z}}(\tau), \tau)}{\mathrm{d}\tau}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying the chain rule, we obtain

$$\frac{\mathrm{d}\bar{\epsilon}_{ia}}{\mathrm{d}\tau} = \Bigg(\sum_{j=1}^{N_\mathrm{s}}\frac{\partial h_{ia}}{\partial x_{ja}}\frac{\mathrm{d}x_{ja}}{\mathrm{d}\tau} + \sum_{j=1}^{N_\mathrm{c}}\frac{\partial h_{ia}}{\partial y_{ja}}\frac{\mathrm{d}y_{ja}}{\mathrm{d}\tau} + \sum_{k=0}^{N_\mathrm{a}}\sum_{j=1}^{N_\mathrm{s}}\frac{\partial h_{ia}}{\partial \bar{x}_{jk}}\frac{\mathrm{d}\bar{x}_{jk}}{\mathrm{d}\tau} \\ \left. + \sum_{k=0}^{N_\mathrm{a}}\sum_{j=1}^{N_\mathrm{c}}\frac{\partial h_{ia}}{\partial \bar{y}_{jk}}\frac{\mathrm{d}\bar{y}_{jk}}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial\tau}\Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation, this is

$$\frac{\mathrm{d}\bar{\epsilon}_{ia}}{\mathrm{d}\tau} = \Bigg(\frac{\partial h_{ia}}{\partial \mathbf{x}_a^\intercal}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial \mathbf{y}_a^\intercal}\frac{\mathrm{d}\mathbf{y}_a}{\mathrm{d}\tau} + \sum_{k=0}^{N_\mathrm{a}}\frac{\partial h_{ia}}{\partial \bar{\mathbf{x}}_k^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}_k}{\mathrm{d}\tau} \\ \left. + \sum_{k=0}^{N_\mathrm{a}}\frac{\partial h_{ia}}{\partial \bar{\mathbf{y}}_k^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}_k}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial\tau}\Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Applying matrix calculus notation again yields

$$\frac{\mathrm{d}\bar{\epsilon}_{ia}}{\mathrm{d}\tau} = \Bigg(\frac{\partial h_{ia}}{\partial \mathbf{x}_a^\intercal}\frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial \mathbf{y}_a^\intercal}\frac{\mathrm{d}\mathbf{y}_a}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial \bar{\mathbf{x}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial h_{ia}}{\partial \bar{\mathbf{y}}^\intercal}\frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} \\ \left. + \frac{\partial h_{ia}}{\partial\tau}\Bigg)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Rewriting h_{ia} as ϵ_{ia}, we obtain

$$\frac{\mathrm{d}\bar{\epsilon}_{ia}}{\mathrm{d}\tau} = \left(\frac{\partial \epsilon_{ia}}{\partial \mathbf{x}_a^\intercal} \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\tau} + \frac{\partial \epsilon_{ia}}{\partial \mathbf{y}_a^\intercal} \frac{\mathrm{d}\mathbf{y}_a}{\mathrm{d}\tau} + \frac{\partial \epsilon_{ia}}{\partial \bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial \epsilon_{ia}}{\partial \bar{\mathbf{y}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial \epsilon_{ia}}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Hence, for all environmental variables at age a, we have

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}_a}{\mathrm{d}\tau} = \left(\frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{x}_a^\intercal} \frac{\mathrm{d}\mathbf{x}_a}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{y}_a^\intercal} \frac{\mathrm{d}\mathbf{y}_a}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \bar{\mathbf{y}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Note that evaluation of $\mathrm{d}\mathbf{z}_a/\mathrm{d}\tau$ and $\partial\boldsymbol{\epsilon}_a/\partial\tau$ at $\mathbf{y} = \bar{\mathbf{y}}$ is $\mathrm{d}\bar{\mathbf{z}}_a/\mathrm{d}\tau$ and $\partial\bar{\boldsymbol{\epsilon}}_a/\partial\tau$, respectively. Using Eqs. (33d) and (33d) yields

$$\begin{aligned} \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{x}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} &= \sum_{j=1}^{N_\mathrm{a}} \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{x}_j^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}_j}{\mathrm{d}\tau} = \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{x}_a^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}_a}{\mathrm{d}\tau} \\ \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{y}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} &= \sum_{j=1}^{N_\mathrm{a}} \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{y}_j^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}_j}{\mathrm{d}\tau} = \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{y}_a^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}_a}{\mathrm{d}\tau}. \end{aligned}$$

Then, we have

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}_a}{\mathrm{d}\tau} = \left(\frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{x}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{y}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \bar{\mathbf{x}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{x}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \bar{\mathbf{y}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{y}}}{\mathrm{d}\tau} + \frac{\partial \bar{\boldsymbol{\epsilon}}_a}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Now note that $\partial\boldsymbol{\epsilon}_a/\partial\mathbf{z}^\intercal = (\partial\boldsymbol{\epsilon}_a/\partial\mathbf{x}^\intercal, \partial\boldsymbol{\epsilon}_a/\partial\mathbf{y}^\intercal)$, so

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}_a}{\mathrm{d}\tau} = \left(\frac{\partial \boldsymbol{\epsilon}_a}{\partial \mathbf{z}^\intercal} \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}_a}{\partial \bar{\mathbf{z}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \bar{\boldsymbol{\epsilon}}_a}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Hence, for all environmental variables over all ages, we have

$$\begin{aligned} \frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}}{\mathrm{d}\tau} &= \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{z}^\intercal} \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{z}}^\intercal} \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left[\left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{z}^\intercal} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{z}}^\intercal} \right) \frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}\tau} + \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \end{aligned}$$

where we use Eq. (37) and the block matrix of direct effects of social partners' phenotype on a mutant's environment (Eq. 38; see also Eq. 36).

Let us momentarily write $\boldsymbol{\epsilon} = \tilde{\mathbf{h}}(\mathbf{z}, \bar{\mathbf{z}})$ for some differentiable function $\tilde{\mathbf{h}}$ to highlight the dependence of a mutant's environment $\boldsymbol{\epsilon}$ on her phenotype $\mathbf{z}$ and on the phenotype $\bar{\mathbf{x}}$ of resident social partners. Consider the environment a resident experiences when she is in the context of mutants, denoted by $\check{\boldsymbol{\epsilon}} = \tilde{\mathbf{h}}(\bar{\mathbf{z}}, \mathbf{z})$. Hence,

$$\frac{\partial \check{\boldsymbol{\epsilon}}}{\partial \mathbf{z}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\partial \tilde{\mathbf{h}}(\bar{\mathbf{z}}, \mathbf{z})}{\partial \mathbf{z}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\partial \tilde{\mathbf{h}}(\mathbf{z}, \bar{\mathbf{z}})}{\partial \bar{\mathbf{z}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{z}}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}}, \tag{A87}$$

where the second equality follows by exchanging dummy variables. Then, the transpose of the matrix of *direct social effects of a mutant's phenotype on her and a partner's environment* is

$$\begin{aligned} \frac{\partial (\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{z}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{z}^\intercal} + \frac{\partial \check{\boldsymbol{\epsilon}}}{\partial \mathbf{z}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{z}^\intercal} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{z}}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a} N_\mathrm{e} \times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c})}. \end{aligned} \tag{A88}$$

Similarly, the transpose of the matrix of *direct social effects of a mutant's states on her and a partner's environment* is

$$\begin{aligned} \frac{\partial (\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{x}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{x}^\intercal} + \frac{\partial \check{\boldsymbol{\epsilon}}}{\partial \mathbf{x}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{x}^\intercal} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{x}}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a} N_\mathrm{e} \times N_\mathrm{a} N_\mathrm{s}}, \end{aligned} \tag{A89}$$

and the transpose of the matrix of *direct social effects of a mutant's controls on her and a partner's environment* is

$$\begin{aligned} \frac{\partial (\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{y}^\intercal}\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} &= \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{y}^\intercal} + \frac{\partial \check{\boldsymbol{\epsilon}}}{\partial \mathbf{y}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} = \left(\frac{\partial \boldsymbol{\epsilon}}{\partial \mathbf{y}^\intercal} + \frac{\partial \boldsymbol{\epsilon}}{\partial \bar{\mathbf{y}}^\intercal} \right)\bigg|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &\in \mathbb{R}^{N_\mathrm{a} N_\mathrm{e} \times N_\mathrm{a} N_\mathrm{c}}. \end{aligned} \tag{A90}$$

Consequently, the evolutionary dynamics of the environment are given by Eq. (97).

In terms of total genetic selection

Using the expression for the evolutionary dynamics of the phenotype (Eq. 92 for $\boldsymbol{\zeta} = \mathbf{z}$) in that for the environment (Eq. 97) yields

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}}{\mathrm{d}\tau} = \left[\frac{\partial (\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{z}^\intercal} \left(\mathbf{H}_{\mathbf{zy}} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right) + \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (87) for $\boldsymbol{\zeta} = \mathbf{z}$ yields

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}}{\mathrm{d}\tau} = \left[\frac{\partial (\boldsymbol{\epsilon} + \check{\boldsymbol{\epsilon}})}{\partial \mathbf{z}^\intercal} \left(\frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{z}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right) + \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Collecting for $\partial\boldsymbol{\epsilon}/\partial\tau$ and using Eq. (71) yields

$$\frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}}{\mathrm{d}\tau} = \left(\frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \boldsymbol{\epsilon}}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (87) yields Eq. (92) for $\boldsymbol{\zeta} = \boldsymbol{\epsilon}$. Using the third line of Eq. (64) and Eq. (85) yields Eq. (91) for $\boldsymbol{\zeta} = \boldsymbol{\epsilon}$, whereas using the fourth line of Eq. (64) and Eq. (86) yields Eq. (88a) for $\boldsymbol{\zeta} = \boldsymbol{\epsilon}$.

Appendix 12: evolutionary dynamics of the metaphenotype

In terms of total genetic selection

Here we obtain an equation describing the evolutionary dynamics of the resident metaphenotype, that is, $\mathrm{d}\bar{\mathbf{m}}/\mathrm{d}\tau$. In this section, we write such an equation in terms of total genetic selection. Since $\mathrm{d}\bar{\mathbf{m}}/\mathrm{d}\tau = (\mathrm{d}\bar{\mathbf{x}}/\mathrm{d}\tau; \mathrm{d}\bar{\mathbf{y}}/\mathrm{d}\tau; \mathrm{d}\bar{\boldsymbol{\epsilon}}/\mathrm{d}\tau)$, from Eqs. (A82), (14a), and (92) for $\boldsymbol{\zeta} = \boldsymbol{\epsilon}$, we can write the evolutionary dynamics of the resident metaphenotype $\bar{\mathbf{m}}$ as

$$\frac{\mathrm{d}\bar{\mathbf{m}}}{\mathrm{d}\tau} = \left[\begin{pmatrix} \mathbf{H}_{\mathbf{xy}} \\ \mathbf{G}_\mathbf{y} \\ \mathbf{H}_{\boldsymbol{\epsilon}\mathbf{y}} \end{pmatrix} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \\ \mathbf{0} \\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \end{pmatrix} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A91}$$

Using Eqs. (84) and (70), this is

$$\frac{\mathrm{d}\bar{\mathbf{m}}}{\mathrm{d}\tau} = \left[\begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^\intercal} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^\intercal} \\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^\intercal} \end{pmatrix} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \begin{pmatrix} \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \end{pmatrix} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right]\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (74), this reduces to

$$\frac{\mathrm{d}\bar{\mathbf{m}}}{\mathrm{d}\tau} = \left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{y}^\intercal} \mathbf{G}_\mathbf{y} \frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}} + \frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\boldsymbol{\epsilon}^\intercal} \frac{\partial \bar{\boldsymbol{\epsilon}}}{\partial \tau} \right)\Bigg|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (87) yields Eq. (92) for $\boldsymbol{\zeta} = \mathbf{m}$.. Using the third line of Eq. (64) and Eq. (85) yields Eq. (91) for $\boldsymbol{\zeta} = \mathbf{m}$, whereas using the fourth line of Eq. (64) and Eq. (86) yields Eq. (88a) for $\boldsymbol{\zeta} = \mathbf{m}$.

In contrast to other arrangements, the premultiplying matrix $\mathbf{H}_{\mathbf{my}}$ is non-singular if $\mathbf{G}_{\mathbf{y}}$ is non-singular. Indeed, if

$$\left.\frac{s\mathbf{m}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} = \mathbf{0}$$

for some vector $\mathbf{r}$, then from Eqs. (74a) and (70b) we have

$$\left.\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{y}^\intercal} \\ \mathbf{I} \\ \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} = \mathbf{0}.$$

Doing the multiplication yields

$$\begin{pmatrix} \left.\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} \\ \mathbf{r} \\ \left.\frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \mathbf{r} \end{pmatrix} = \mathbf{0},$$

which implies that $\mathbf{r} = \mathbf{0}$, so $s\mathbf{m}/s\mathbf{y}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ is non-singular. Thus, $\mathbf{H}_{\mathbf{my}}$ is non-singular if $\mathbf{G}_{\mathbf{y}}$ is non-singular.

In terms of total selection on the metaphenotype

Here we write the evolutionary dynamics of the metaphenotype in terms of the total selection gradient of the metaphenotype.

First, using Eq. (77), we define the *additive genetic covariance matrix of the undeveloped metaphenotype* $\hat{\mathbf{m}} = (\bar{\mathbf{x}}; \mathbf{y}; \bar{\boldsymbol{\epsilon}})$ as

$$\mathbf{G}_{\hat{\mathbf{m}}} \equiv \mathrm{cov}[\mathbf{a}_{\hat{\mathbf{m}}}, \mathbf{a}_{\hat{\mathbf{m}}}] = \left.\left(\frac{d\hat{\mathbf{m}}}{d\mathbf{y}^\intercal} \mathbf{G}_{\mathbf{y}} \frac{d\hat{\mathbf{m}}^\intercal}{d\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_a(N_s+N_c+N_e)\times N_a(N_s+N_c+N_e)}.$$

By definition of $\hat{\mathbf{m}}$, we have

$$\mathbf{G}_{\hat{\mathbf{m}}} = \left.\left[\begin{pmatrix} \frac{d\bar{\mathbf{x}}}{d\mathbf{y}^\intercal} \\ \frac{d\mathbf{y}}{d\mathbf{y}^\intercal} \\ \frac{d\bar{\boldsymbol{\epsilon}}}{d\mathbf{y}^\intercal} \end{pmatrix} \mathbf{G}_{\mathbf{y}} \begin{pmatrix} \frac{d\bar{\mathbf{x}}^\intercal}{d\mathbf{y}} & \frac{d\mathbf{y}^\intercal}{d\mathbf{y}} & \frac{d\bar{\boldsymbol{\epsilon}}^\intercal}{d\mathbf{y}} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

From Eqs. (2) and (1), resident states and environment are independent of mutant controls, so

$$\mathbf{G}_{\hat{\mathbf{m}}} = \left.\left[\begin{pmatrix} \mathbf{0} \\ \mathbf{I} \\ \mathbf{0} \end{pmatrix} \mathbf{G}_{\mathbf{y}} \begin{pmatrix} \mathbf{0} & \mathbf{I} & \mathbf{0} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Doing the matrix multiplication yields

$$\mathbf{G}_{\hat{\mathbf{m}}} = \left.\left[\begin{pmatrix} \mathbf{0} \\ \mathbf{I} \\ \mathbf{0} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{G}_{\mathbf{y}} & \mathbf{0} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_{\mathbf{y}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}. \tag{A92}$$

The matrix $\mathbf{G}_{\hat{\mathbf{m}}}$ is singular because the undeveloped metaphenotype includes controls (i.e., $d\hat{\mathbf{m}}^\intercal/d\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has fewer rows than columns). For this reason, the matrix $\mathbf{G}_{\hat{\mathbf{m}}}$ would still be singular even if the zero block entries in Eq. (A92) were non-zero (i.e., if $d\bar{\mathbf{x}}^\intercal/d\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$ and $d\bar{\boldsymbol{\epsilon}}^\intercal/d\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$).

Now, we write an alternative factorization of $\mathbf{H}_{\mathbf{m}}$ in terms of $\mathbf{G}_{\hat{\mathbf{m}}}$. Using Eqs. (60) and (75), we have

$$\left.\left(\frac{s\mathbf{m}}{s\mathbf{m}^\intercal} \mathbf{G}_{\hat{\mathbf{m}}} \frac{d\mathbf{m}^\intercal}{d\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left[\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{x}^\intercal} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal} & \frac{s\mathbf{x}}{s\boldsymbol{\epsilon}^\intercal} \\ \mathbf{0} & \mathbf{I} & \mathbf{0} \\ \frac{s\boldsymbol{\epsilon}}{s\mathbf{x}^\intercal} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal} & \frac{s\boldsymbol{\epsilon}}{s\boldsymbol{\epsilon}^\intercal} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_{\mathbf{y}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix} \begin{pmatrix} \frac{d\mathbf{x}^\intercal}{d\mathbf{x}} & \mathbf{0} & \frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{x}} \\ \frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \mathbf{I} & \frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \frac{d\mathbf{x}^\intercal}{d\boldsymbol{\epsilon}} & \mathbf{0} & \frac{d\boldsymbol{\epsilon}^\intercal}{d\boldsymbol{\epsilon}} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Doing the matrix multiplication yields

$$\begin{aligned} &\left.\left(\frac{s\mathbf{m}}{s\mathbf{m}^\intercal} \mathbf{G}_{\hat{\mathbf{m}}} \frac{d\mathbf{m}^\intercal}{d\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\left[\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{x}^\intercal} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal} & \frac{s\mathbf{x}}{s\boldsymbol{\epsilon}^\intercal} \\ \mathbf{0} & \mathbf{I} & \mathbf{0} \\ \frac{s\boldsymbol{\epsilon}}{s\mathbf{x}^\intercal} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal} & \frac{s\boldsymbol{\epsilon}}{s\boldsymbol{\epsilon}^\intercal} \end{pmatrix} \begin{pmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \mathbf{G}_{\mathbf{y}} & \mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \mathbf{G}_{\mathbf{y}} & \mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \end{aligned}$$

Using Eq. (70b), we have

$$\begin{aligned} &\left.\left(\frac{s\mathbf{m}}{s\mathbf{m}^\intercal} \mathbf{G}_{\hat{\mathbf{m}}} \frac{d\mathbf{m}^\intercal}{d\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ &= \left.\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{y}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \frac{s\mathbf{y}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{y}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{y}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{y}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \\ \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\mathbf{y}^\intercal}{d\mathbf{y}} & \frac{s\boldsymbol{\epsilon}}{s\mathbf{y}^\intercal}\mathbf{G}_{\mathbf{y}}\frac{d\boldsymbol{\epsilon}^\intercal}{d\mathbf{y}} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \end{aligned}$$

Notice that the matrix on the right-hand side is

$$\left.\left(\frac{s\mathbf{m}}{s\mathbf{y}^\intercal} \mathbf{G}_{\mathbf{y}} \frac{d\mathbf{m}^\intercal}{d\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{H}_{\mathbf{m}}.$$

Hence, we obtain an alternative factorization for $\mathbf{H}_{\mathbf{m}}$ as

$$\mathbf{H}_{\mathbf{m}} = \left.\left(\frac{s\mathbf{m}}{s\mathbf{m}^\intercal} \mathbf{G}_{\hat{\mathbf{m}}} \frac{d\mathbf{m}^\intercal}{d\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

We can now write the selection response of the metaphenotype (in the form of Eq. 88a) as

$$\mathbf{H}_{\mathbf{m}} \left.\frac{\partial w}{\partial \mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{m}^{\intercal}}\mathbf{G}_{\hat{\mathbf{m}}}\frac{\mathrm{d}\mathbf{m}^{\intercal}}{\mathrm{d}\mathbf{m}}\frac{\partial w}{\partial \mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using the relationship between the total and partial selection gradients of the metaphenotype (Eq. 67), this becomes

$$\mathbf{H}_{\mathbf{m}} \left.\frac{\partial w}{\partial \mathbf{m}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{m}^{\intercal}}\mathbf{G}_{\hat{\mathbf{m}}}\frac{\mathrm{d}w}{\mathrm{d}\mathbf{m}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

We can further simplify this equation by noticing the following. Using Eq. (84) and $\hat{\mathbf{m}} = (\bar{\mathbf{x}};\mathbf{y};\bar{\boldsymbol{\epsilon}})$, we have that the *additive socio-genetic cross-covariance matrix of the metaphenotype and the undeveloped metaphenotype* is

$$\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}} = \left.\left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{y}^{\intercal}}\mathbf{G}_{\mathbf{y}}\frac{\mathrm{d}\hat{\mathbf{m}}^{\intercal}}{\mathrm{d}\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} \in \mathbb{R}^{N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})\times N_\mathrm{a}(N_\mathrm{s}+N_\mathrm{c}+N_\mathrm{e})}. \tag{A93}$$

Expanding, we have

$$\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}} = \left.\left[\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^{\intercal}}\\ \frac{\mathrm{s}\mathbf{y}}{\mathrm{s}\mathbf{y}^{\intercal}}\\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^{\intercal}}\end{pmatrix}\mathbf{G}_{\mathbf{y}}\begin{pmatrix}\frac{\mathrm{d}\bar{\mathbf{x}}^{\intercal}}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\mathbf{y}^{\intercal}}{\mathrm{d}\mathbf{y}} & \frac{\mathrm{d}\bar{\boldsymbol{\epsilon}}^{\intercal}}{\mathrm{d}\mathbf{y}}\end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (70b) and since resident states and environment do not depend on mutant controls, then

$$\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}} = \left.\left[\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^{\intercal}}\\ \mathbf{I}\\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^{\intercal}}\end{pmatrix}\mathbf{G}_{\mathbf{y}}\begin{pmatrix}\mathbf{0} & \mathbf{I} & \mathbf{0}\end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Doing the matrix multiplication yields

$$\begin{aligned}\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}} &= \left.\left[\begin{pmatrix}\frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^{\intercal}}\\ \mathbf{I}\\ \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^{\intercal}}\end{pmatrix}\begin{pmatrix}\mathbf{0} & \mathbf{G}_{\mathbf{y}} & \mathbf{0}\end{pmatrix}\right]\right|_{\mathbf{y}=\bar{\mathbf{y}}}\\ &= \left.\begin{pmatrix}\mathbf{0} & \frac{\mathrm{s}\mathbf{x}}{\mathrm{s}\mathbf{y}^{\intercal}}\mathbf{G}_{\mathbf{y}} & \mathbf{0}\\ \mathbf{0} & \mathbf{G}_{\mathbf{y}} & \mathbf{0}\\ \mathbf{0} & \frac{\mathrm{s}\boldsymbol{\epsilon}}{\mathrm{s}\mathbf{y}^{\intercal}}\mathbf{G}_{\mathbf{y}} & \mathbf{0}\end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}}.\end{aligned}$$

Notice that the last matrix equals

$$\left.\left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{m}^{\intercal}}\mathbf{G}_{\hat{\mathbf{m}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Thus,

$$\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}} = \left.\left(\frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\mathbf{m}^{\intercal}}\mathbf{G}_{\hat{\mathbf{m}}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

We can then write the evolutionary dynamics of the resident metaphenotype $\bar{\mathbf{m}}$ in terms of the total selection gradient of the metaphenotype as

$$\frac{\mathrm{d}\bar{\mathbf{m}}}{\mathrm{d}\tau} = \left.\left(\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}}\frac{\mathrm{d}w}{\mathrm{d}\mathbf{m}} + \frac{\mathrm{s}\mathbf{m}}{\mathrm{s}\boldsymbol{\epsilon}^{\intercal}}\frac{\partial\bar{\boldsymbol{\epsilon}}}{\partial\tau}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}. \tag{A94}$$

The cross-covariance matrix $\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}}$ is singular because $\mathrm{d}\hat{\mathbf{m}}^{\intercal}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}}$ has fewer rows than columns since the undeveloped metaphenotype includes controls. For this reason, $\mathbf{H}_{\mathbf{m}\hat{\mathbf{m}}}$ would still be singular even if the zero block entries in Eq. (A93) were non-zero (i.e., if $\mathrm{d}\bar{\mathbf{x}}^{\intercal}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$ and $\mathrm{d}\bar{\boldsymbol{\epsilon}}^{\intercal}/\mathrm{d}\mathbf{y}|_{\mathbf{y}=\bar{\mathbf{y}}} \neq \mathbf{0}$). Then, evolutionary equilibria of the metaphenotype do not imply absence of total selection on the metaphenotype, even if exogenous plastic response is absent.

Appendix 13: connection to dynamic optimization

Life-history models often consider traits that depend on an underlying variable (e.g., age) together with developmental (or dynamic) constraints. When such a model is simple enough, analytical solution (i.e., identification of evolutionarily stable strategies) is possible using optimal control or dynamic programming methods (Sydsæter *et al.* 2008). A key tool from optimal control theory that enables finding such analytical solutions (i.e., optimal controls) is Pontryagin's maximum principle. The maximum principle is a theorem that essentially transforms the dynamic optimization problem into a simpler problem of maximizing a function called the Hamiltonian, which depends on control, state, and costate (or adjoint) variables. The problem is then to maximize the Hamiltonian with respect to the controls, while state and costate variables can be found from associated dynamic equations. We now show that our results recover the maximization of the Hamiltonian.

First, we identify what the costate variables are and show that they are proportional to the total selection gradient of states, for which we have obtained general formulas, provided that the problem is a standard life-history model of R_0 maximization. Let us write $R_0(\mathbf{z},\bar{\mathbf{z}})$ for the expected lifetime number of offspring of a mutant with phenotype $\mathbf{z} = (\mathbf{x};\mathbf{y})$ in the context of a resident with phenotype $\bar{\mathbf{z}} = (\bar{\mathbf{x}};\bar{\mathbf{y}})$. Let $\mathbf{z}^* = (\mathbf{x}^*;\mathbf{y}^*)$ be such that

$$\mathbf{y}^* \in \arg\max_{\mathbf{y}} R_0(\mathbf{z},\mathbf{z}^*),$$

subject to the dynamic constraint (8)

$$\mathbf{x}_{a+1} = \mathbf{g}_a(\mathbf{z}_a,\bar{\mathbf{z}},\mathbf{h}_a(\mathbf{z}_a,\bar{\mathbf{z}},\tau)).$$

Such $\mathbf{z}^*$ is a best response to itself under the best response function R_0, where $\mathbf{y}^*$ is an optimal control and $\mathbf{x}^*$ is its associated optimal state. From Eq. (92) for $\boldsymbol{\zeta} = \mathbf{z}$ and Eq. (29b), it follows that if there is no exogenous environmental change, then such $\mathbf{z}^*$ is an admissible locally stable evolutionary equilibrium. Moreover, the costate for the i-th state variable at age a is defined as

$$k_{x_{ia}} \equiv \left.\frac{\mathrm{d}R_0}{\mathrm{d}x_{ia}}\right|_{\mathbf{z}=\bar{\mathbf{z}}=\mathbf{z}^*} \tag{A95}$$

(section 9.6 of Sydsæter *et al.* 2008). Hence, from Eq. (29b), we have that the costate for the i-th state variable at age a is

$$k_{x_{ia}} = T \left.\frac{\mathrm{d}w}{\mathrm{d}x_{ia}}\right|_{\mathbf{z}=\bar{\mathbf{z}}=\mathbf{z}^*}. \tag{A96}$$

That is, costate variables are proportional to the total selection gradient of state variables at an admissible evolutionary equilibrium $\mathbf{z}^*$. The total selection gradient of states thus generalizes the costate notion to outside of evolutionary equilibrium for the life-history problem of R_0 maximization. The fifth line of Eq. (64) shows how such generalized costates affect the evolutionary process, namely, indirectly by being transformed by the semi-total effects of controls on states, $\delta\mathbf{x}^\top/\delta\mathbf{y}$. Additionally, we have obtained various equations (63) that enable calculation of such generalized costates in age structured models with R_0 maximization.

Second, we show that the total selection gradient of controls is proportional to the semi-total effects of controls on the Hamiltonian when both are evaluated at optimal controls. We have that the total selection gradient of controls can be written in terms of the total selection gradients of states (fifth line of Eq. 64), so for the controls at age a we have

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{\delta\mathbf{x}^\top}{\delta\mathbf{y}_a}\frac{\mathrm{d}w}{\mathrm{d}\mathbf{x}} + \frac{\delta w}{\delta\mathbf{y}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eq. (29) yields

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{1}{T}\left.\left(\frac{\delta\mathbf{x}^\top}{\delta\mathbf{y}_a}\frac{\mathrm{d}R_0}{\mathrm{d}\mathbf{x}} + \frac{\delta R_0}{\delta\mathbf{y}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

From Eqs. (A48) and (28) given that the semi-total derivative only considers the environmental constraint (9) but ignores the developmental constraint (8), it follows that

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \frac{1}{T}\left.\left(\frac{\delta\mathbf{x}_{a+1}^\top}{\delta\mathbf{y}_a}\frac{\mathrm{d}R_0}{\mathrm{d}\mathbf{x}_{a+1}} + \frac{\delta(\ell_a f_a)}{\delta\mathbf{y}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Using Eqs. (A95) and (8) yields

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}=\mathbf{y}^*} = \frac{1}{T}\left.\left(\frac{\delta\mathbf{g}_a^\top}{\delta\mathbf{y}_a}\mathbf{k}_{\mathbf{x}_{a+1}} + \frac{\delta(\ell_a f_a)}{\delta\mathbf{y}_a}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}=\mathbf{y}^*} = \mathbf{0}.$$

This suggests to define

$$H_a \equiv \mathbf{g}_a^\top\mathbf{k}_{\mathbf{x}_{a+1}} + \ell_a f_a,$$

which recovers the Hamiltonian of Pontryagin's maximum principle in discrete time (section 12.5 of Sydsæter *et al.* 2008). Then, the total selection gradient of controls at a given age is proportional to the semi-total effects of such controls on the Hamiltonian when both gradients are evaluated at optimal controls:

$$\left.\frac{\mathrm{d}w}{\mathrm{d}\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}=\mathbf{y}^*} = \frac{1}{T}\left.\frac{\delta H_a}{\delta\mathbf{y}_a}\right|_{\mathbf{y}=\bar{\mathbf{y}}=\mathbf{y}^*} = \mathbf{0}.$$

Appendix 14: matrix calculus notation

For vectors $\mathbf{a} \in \mathbb{R}^{n\times 1}$ and $\mathbf{b} \in \mathbb{R}^{m\times 1}$, we denote

$$\frac{\partial\mathbf{a}}{\partial\mathbf{b}^\top} = \begin{pmatrix} \frac{\partial a_1}{\partial b_1} & \cdots & \frac{\partial a_1}{\partial b_m} \\ \vdots & \ddots & \vdots \\ \frac{\partial a_n}{\partial b_1} & \cdots & \frac{\partial a_n}{\partial b_m} \end{pmatrix} \in \mathbb{R}^{n\times m},$$

so $(\partial\mathbf{a}/\partial\mathbf{b}^\top)^\top = \partial\mathbf{a}^\top/\partial\mathbf{b}$.

Appendix 15: matrix of socio-devo stability

To see why the matrix

$$\left.\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

is sufficient to determine socio-devo stability, consider the following. Let $\bar{\mathbf{x}}(\theta+1) = \tilde{\mathbf{g}}(\bar{\mathbf{x}}(\theta))$ denote the solution of iterating Eq. (4) over a, where we highlight only the argument corresponding to the states of social partners. An equilibrium $\bar{\mathbf{x}}^{**}$ of the socio-devo stabilization dynamics satisfies $\bar{\mathbf{x}}^{**} = \tilde{\mathbf{g}}(\bar{\mathbf{x}}^{**})$. Taylor-expanding $\bar{\mathbf{x}}(\theta+1)$ to first-order around $\bar{\mathbf{x}}^{**}$, we have

$$\bar{\mathbf{x}}(\theta+1) = \tilde{\mathbf{g}}(\bar{\mathbf{x}}^{**}) + \left.\frac{\mathrm{d}\tilde{\mathbf{g}}}{\mathrm{d}\bar{\mathbf{x}}^\top}\right|_{\bar{\mathbf{x}}=\bar{\mathbf{x}}^{**}}(\bar{\mathbf{x}}(\theta)-\bar{\mathbf{x}}^{**}) + O(||\bar{\mathbf{x}}(\theta)-\bar{\mathbf{x}}^{**}||^2),$$

where the operator $\mathrm{d}/\mathrm{d}\bar{\mathbf{x}}^\top$ takes the total derivative to take into account developmental and environmental constraints. Noting that $\mathrm{d}\tilde{\mathbf{g}}/\mathrm{d}\bar{\mathbf{x}}^\top|_{\bar{\mathbf{x}}=\bar{\mathbf{x}}^{**}} = \mathrm{d}\mathbf{x}/\mathrm{d}\bar{\mathbf{x}}^\top|_{\mathbf{y}=\bar{\mathbf{y}}}$ since the resident is a socio-devo equilibrium, we have that a perturbation from a socio-devo equilibrium is approximately

$$\bar{\mathbf{x}}(\theta+1) - \tilde{\mathbf{g}}(\bar{\mathbf{x}}^{**}) \approx \left.\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}}(\bar{\mathbf{x}}(\theta)-\bar{\mathbf{x}}^{**}),$$

which asymptotically converges to $\mathbf{0}$ (i.e., $\bar{\mathbf{x}}^{**}$ is locally stable) if all the eigenvalues of the matrix

$$\left.\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}\bar{\mathbf{x}}^\top}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$$

have absolute value strictly less than one.

Appendix 16: Total and semi-total derivatives

Consider a function $f(a,\mathbf{b},\mathbf{c}) \in \mathbb{R}$ where the vectors $\mathbf{b} \in \mathbb{R}^{n\times 1}$ and $\mathbf{c} \in \mathbb{R}^{m\times 1}$ satisfy the (equality) constraints

$$\begin{aligned}\mathbf{b} &= \mathbf{d}(a)\\ \mathbf{c} &= \mathbf{e}(a),\end{aligned}$$

for some differentiable functions $\mathbf{d}(a) \in \mathbb{R}^{n\times 1}$ and $\mathbf{e}(a) \in \mathbb{R}^{m\times 1}$. From the chain rule, the total derivative of $f(a,\mathbf{b},\mathbf{c})$ with respect to a is

$$\begin{aligned}\frac{\mathrm{d}f}{\mathrm{d}a} &= \frac{\mathrm{d}f(a,\mathbf{d}(a),\mathbf{e}(a))}{\mathrm{d}a} = \frac{\partial f}{\partial a} + \sum_{i=1}^{n}\frac{\partial f}{\partial b_i}\frac{\mathrm{d}b_i}{\mathrm{d}a} + \sum_{i=1}^{m}\frac{\partial f}{\partial c_i}\frac{\mathrm{d}c_i}{\mathrm{d}a}\\ &= \frac{\partial f}{\partial a} + \frac{\partial f}{\partial\mathbf{b}^\top}\frac{\mathrm{d}\mathbf{b}}{\mathrm{d}a} + \frac{\partial f}{\partial\mathbf{c}^\top}\frac{\mathrm{d}\mathbf{c}}{\mathrm{d}a}.\end{aligned}$$

We call the semi-total derivative of $f(a,\mathbf{b},\mathbf{c})$ with respect to a, considering the constraints on $\mathbf{b}$ without considering the constraints on $\mathbf{c}$, the quantity

$$\frac{\delta f}{\delta a} = \frac{\mathrm{d}f(a,\mathbf{d}(a),\mathbf{c})}{\mathrm{d}a} = \frac{\partial f}{\partial a} + \frac{\partial f}{\partial\mathbf{b}^\top}\frac{\mathrm{d}\mathbf{b}}{\mathrm{d}a}.$$

We use "derivative-like" notation like this one for various differential operators, motivated by some analogous use by Caswell (2019) (his Eqs. 1.2 and 2.21, which he based on a suggestion by Samuelson 1947).

Appendix 17: Selection response and genetic lines of least resistance

Lande's equation ($\Delta\bar{\mathbf{z}} = \mathbf{G}\boldsymbol{\beta}$) describes evolutionary change in terms of the direction of selection ($\boldsymbol{\beta}$) modified by genetic covariation ($\mathbf{G}$). Evolutionary change is thus thought to occur along "genetic lines of least resistance" (Schluter 1996), that is, on trajectories that are parallel to a leading eigenvector of $\mathbf{G}$. We now show that selection response occurs along genetic lines of least resistance if only one control at one age evolves (it might also be the case when an arbitrary number of controls evolve at an arbitrary number of ages, but we do not prove it).

Recall that selection response of the phenotype is $\mathbf{H_z}\delta w/\delta\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$, which reduces to Lande's equation $\mathbf{G_z}\partial w/\partial\mathbf{z}|_{\mathbf{y}=\bar{\mathbf{y}}}$ if there are no exogenous environmental effects on states, no social development, and no niche construction. We now characterize the eigensystem of $\mathbf{H_z}$, and thus the eigensystem of $\mathbf{G_z}$ as a particular case. The eigenvalues ρ and eigenvectors $\mathbf{q}$ of $\mathbf{H_z}$ are given by the equation

$$\mathbf{H_z q} = \rho\mathbf{q}. \tag{A97}$$

Using Eq. (83), this is

$$\left.\begin{pmatrix} \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G_y}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G_y} \\ \mathbf{G_y}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}} & \mathbf{G_y} \end{pmatrix}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \begin{pmatrix} \mathbf{q_x} \\ \mathbf{q_y} \end{pmatrix} = \rho \begin{pmatrix} \mathbf{q_x} \\ \mathbf{q_y} \end{pmatrix},$$

for some vectors $\mathbf{q_x} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{s}}$ and $\mathbf{q_y} \in \mathbb{R}^{N_\mathrm{a}N_\mathrm{c}}$. Doing the matrix multiplication yields the two equations

$$\left.\left(\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G_y}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\mathbf{q_x} + \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G_y}\mathbf{q_y}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \rho\mathbf{q_x} \tag{A98a}$$

$$\left.\left(\mathbf{G_y}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\mathbf{q_x} + \mathbf{G_y}\mathbf{q_y}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \rho\mathbf{q_y}. \tag{A98b}$$

Collecting for $\mathbf{q_y}$ in Eq. (A98b) yields

$$\mathbf{G_y}\left.\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\mathbf{q_x} = (\rho\mathbf{I} - \mathbf{G_y})\mathbf{q_y},$$

which substituted in Eq. (A98a) yields

$$\left.\left(\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}(\rho\mathbf{I} - \mathbf{G_y})\mathbf{q_y} + \frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{G_y}\mathbf{q_y}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \rho\mathbf{q_x}.$$

Factorizing the left-hand side and simplifying yields

$$\rho\left.\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\mathbf{q_y} = \rho\mathbf{q_x}.$$

Then, for any non-trivial eigenvector $\mathbf{q} = (\mathbf{q_x};\mathbf{q_y})$ of $\mathbf{H_z}$, that is, one whose eigenvalue is $\rho \neq 0$, we have

$$\left.\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\mathbf{q_y} = \mathbf{q_x}, \tag{A99}$$

which substituted in Eq. (A98b) yields

$$\left.\left(\mathbf{G_y}\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\mathbf{q_y} + \mathbf{G_y}\mathbf{q_y}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \rho\mathbf{q_y},$$

and factorizing the left-hand side we obtain

$$\mathbf{G_y}\left.\left(\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\frac{s\mathbf{x}}{s\mathbf{y}^\intercal} + \mathbf{I}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}\mathbf{q_y} = \rho\mathbf{q_y}.$$

Therefore, from Eq. (A99), we have that any non-trivial eigenvector of $\mathbf{H_z}$ is given by

$$\mathbf{q} = \begin{pmatrix} \left.\frac{s\mathbf{x}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}} \\ \mathbf{I} \end{pmatrix}\mathbf{q_y} = \left.\frac{s\mathbf{z}}{s\mathbf{y}^\intercal}\right|_{\mathbf{y}=\bar{\mathbf{y}}}\mathbf{q_y}, \tag{A100}$$

where $\mathbf{q_y}$ is a non-trivial eigenvector of $\mathbf{G_y}\left.\left(\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\frac{s\mathbf{x}}{s\mathbf{y}^\intercal} + \mathbf{I}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}$. Eq. (A100) shows that the matrix $s\mathbf{z}/s\mathbf{y}^\intercal|_{\mathbf{y}=\bar{\mathbf{y}}}$ transforms any such non-trivial eigenvector in control space into a non-trivial eigenvector of $\mathbf{H_z}$.

Now, recall that we have that selection response of the phenotype is

$$\mathbf{H_z}\left.\frac{\delta w}{\delta\mathbf{z}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \mathbf{H_{zy}}\left.\frac{dw}{d\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}} = \left.\left(\frac{s\mathbf{z}}{s\mathbf{y}^\intercal}\mathbf{G_y}\frac{dw}{d\mathbf{y}}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}.$$

Hence, from Eq. (A100) we have that selection response of the phenotype is a non-trivial eigenvector of $\mathbf{H_z}$ if and only if $\mathbf{G_y}\left.\frac{dw}{d\mathbf{y}}\right|_{\mathbf{y}=\bar{\mathbf{y}}}$ is a non-trivial eigenvector of $\mathbf{G_y}\left.\left(\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\frac{s\mathbf{x}}{s\mathbf{y}^\intercal} + \mathbf{I}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}$. In particular, if there is a single control ($N_\mathrm{c} = 1$) and it evolves at a single age, the matrix $\mathbf{G_y}\left.\left(\frac{d\mathbf{x}^\intercal}{d\mathbf{y}}\frac{s\mathbf{x}}{s\mathbf{y}^\intercal} + \mathbf{I}\right)\right|_{\mathbf{y}=\bar{\mathbf{y}}}$ is effectively a scalar and selection-led-evolution is necessarily a non-trivial and leading eigenvector of $\mathbf{H_z}$; that is, with a single control evolving at a single age, selection response of the phenotype occurs along genetic lines of least resistance.