Frequency-dependence favors social plasticity and facilitates socio-eco-evolutionary feedback in fluctuating environments

Jordan S. Martin*[1,2], David F. Westneat[3], Alastair J. Wilson[4],
Niels J. Dingemanse[5], Yimen Araya-Ajoy[6]

*jordanscott.martin@eawag.ch

[1]*Fish Ecology and Evolution, Eawag,*
Swiss Federal Institute of Aquatic Science and Technology, Switzerland

[2]*Human Ecology Group, Institute of Evolutionary Medicine,*
University of Zurich, Switzerland

[3]*Department of Biology,*
University of Kentucky, United States of America

[4]*Evolution Group, Centre for Biosciences,*
University of Exeter, United Kingdom

[5]*Behavioral Ecology Unit, Department of Biology,*
Ludwig Maximilian University of Munich, Germany

[6]*Department of Biology,*
Norwegian University of Science and Technology, Norway

Abstract

1. Increasing attention is being devoted to the study of phenotypic plasticity in social environments. However, much remains unknown about the selection pressures driving the evolution of social plasticity, as well as the pathways by which social plasticity may facilitate or constrain feedback between ecological and evolutionary dynamics. Here we explore these questions using quantitative genetic models, providing general results regarding the causes of selection on social reaction norms, as well as their consequences for adaptive microevolution in fluctuating environments.

2. We model the fitness effects of character states expressed across spatially heterogeneous microhabitats, with variation in the degree to which trait expression and selection are affected by the local social environment. We find that when selection on character states is frequency-dependent within microhabitats, stochastic fluctuations in the social environment cause selection for reversible social plasticity across microhabitats, as quantified by the interaction coefficient ψ. When the phenotype is heritable, fluctuating frequency-dependent selection further promotes the adaptive evolution of indirect genetic effects (IGEs).

3. Ecological factors can shape the frequency-dependent costs and benefits of social interactions, such as through density-dependence. Fluctuations in the ecological state of the social environment cause selection for multidimensional social plasticity and context dependent IGEs, as well as quadratic selection on the phenotypic (co)variance generated by social plasticity within and across microhabitats.

4. We demonstrate how pathways of socio-eco-evolutionary feedback can arise across microevolutionary timescales during the adaptation of socially plastic traits. Our findings provide testable predictions for future comparative research and suggest that mechanisms of social plasticity likely play a key functional role in linking ecological and evolutionary dynamics across contemporary timescales.

Keywords: eco evo, social evolution, social ecology, adaptation, indirect genetic effect, interacting phenotype, quantitative genetics, social behavior

Introduction

The fitness consequences of organisms' phenotypes often vary across space and time in response to environmental heterogeneity and the many conflicting demands individuals face throughout their lifespans. Such fluctuating selection can promote the evolution of phenotypic plasticity (de Jong, 1995; Gavrilets & Scheiner, 1993a; Gomulkiewicz & Kirkpatrick, 1992), allowing genes and the individuals carrying them to change their trait expression and better maintain fitness (survival and reproduction) across environments. Extensive work has established the eco-evolutionary consequences of phenotypic plasticity, such as in promoting colonization of and persistence in novel habitats (Bilandžija et al., 2020; Ghalambor et al., 2007; Hendry, 2016; Wang & Althoff, 2019; Wund et al., 2008), as well as in accelerating or inhibiting adaptation to climate change and other stressors (Crowther et al., 2024; Kelly, 2019; Oostra et al., 2018; Vinton et al., 2022). Experimental research has also revealed elements of the genetic, physiological, and cognitive mechanisms regulating plasticity across taxa (Ledón-Rettig & Ragsdale, 2021; Sommer, 2020; Westneat et al., 2019; Zhang et al., 2024). Most of this research has focused on responses to non-social components of the environment, such as temperature and chemical gradients or resource availability and density. However, increasing attention is also being given to the importance of phenotypic plasticity in response to the traits, activities, and organization of other individuals in an organism's social environment, phenomena we collectively refer to as social plasticity.

The study of social plasticity has a long and productive history in evolutionary ecology. Animal behaviorists, for instance, have been studying the ecological drivers of plasticity in primate social behavior for over half a century (Washburn et al., 1965). Evolutionary game theorists have also long been interested in and extensively investigated the evolutionary consequences of social plasticity in ecological contexts with repeated interactions and mixed-strategy equilibria (McNamara & Leimar, 2020; Van Cleve & Akçay, 2014). Yet it is only in recent decades that focus has turned to the interplay between social plasticity and heritable variation in phenotypes. These developments have principally come through theory of indirect genetic effects (IGEs) in evolutionary quantitative genetics (Bijma, 2011; Bijma & Wade, 2008; McGlothlin et al., 2010; Moore et al., 1997). When the trait under consideration is not a fitness component, IGEs capture the heritable component of phenotypic expression that is caused by social plasticity toward the traits of con- or heterospecifics (De Lisle et al., 2022; Dingemanse & Araya-Ajoy, 2015; Kirkpatrick & Lande, 1989; Martin & Jaeggi, 2022; Martin et al., 2022; McGlothlin et al., 2022; Moore et al., 1997). In other words, genes that directly affect the expression of an individual's phenotype may also indirectly affect the expression of others' phenotypes in their social environment. These direct and indirect effects are important for understanding evolutionary dynamics because they can feedback on and (co)evolve with one another across time, magnifying or reducing the heritable variation available to selection (Bijma, 2011; Moore et al., 1997), modifying selection gradients (Araya-Ajoy et al., 2020; Martin et al., 2022; McGlothlin et al., 2022), and potentially constraining or accelerating phenotypic adaptation (Fisher, 2024; McGlothlin & Fisher, 2022; Moorad & Wade, 2013; Wade et al., 2010; Wilson et al., 2011). Despite the fundamental connection between the study of social plasticity in and IGEs on phenotypes, with the former being the mechanistic cause of the latter, much of the research on these topics has been and remains theoretically disconnected, though recent work in behavioral ecology is beginning to bridge this divide (Bailey et al., 2017; Dingemanse & Araya-Ajoy, 2015; Martin et al., 2022; Santostefano et al., 2017). Most theory and empirical research on IGEs has also ignored ecological effects on social plasticity as well as the evolutionary consequences of genetic variation in social plasticity (see Hunt et al., 2019; Kazancioğlu et al., 2012; Martin & Jaeggi, 2022 for important exceptions). This leaves much to be learned about the fundamental questions of when and why social plasticity will evolve in the first place.

Social interactions such as resource competition, reproductive cooperation, and mating behavior are central determinants of populations' fates in response to rapid environmental change, yet little is currently known about the role that social plasticity in these interactions plays in broader eco-evolutionary dynamics. Extensive theory and empirical study have investigated how environmental conditions shape the expression and selection of plasticity in antagonism and mutualism among species (Fordyce, 2006), as well as its evolutionary consequences (De Lisle et al., 2022). Work on transgenerational plasticity and parental effects has demonstrated the importance of interactions between social, genetic, and environmental factors in shaping the pace and direction of contemporary microevolution in many species (Lind et al., 2020; Pettersen et al., 2024; Sturiale & Bailey, 2023). Comparative phylogenetic studies have shown how social learning, a specific form of social plasticity, tends to coevolve with brain size and rates of behavioral innovation (Reader & Laland, 2002); these traits in turn appear to be linked to species' success in colonizing novel habitats and tolerating habitat degradation, while also reducing their probability of extinction (Ducatez et al., 2020; Sol et al., 2005). In field crickets *Teleogryllus oceanicus*, an allele promoting silencing of wings also increases social plasticity of neural responses to the acoustic environment (Pascoal et al., 2018). This suggests that recent adaptation of the silent morph in response to an acoustically orienting parasitoid has been accompanied by rapid evolution of social plasticity in gene expression. Recent work in humans has also shown how IGEs generated by social plasticity and selection among neighbors can feed back with fluctuations in the social environment to accelerate adaptive population growth (Martin et al., 2025). These and many other studies demonstrate that social plasticity may be an important mechanism promoting eco-evolutionary feedback in complex traits, but general predictions from formal models explicitly linking these phenomena remain an important and open target for contemporary research.

To address these gaps in the current literature, we used evolutionary quantitative genetic theory to develop general insights into two closely related questions. Firstly, *what ecological factors drive the selection and adaptation of social plasticity, and thus IGEs, in complex phenotypes* (**selection for social plasticity** section)? We aimed to discover the conditions under which selection will specifically favor mechanisms of social plasticity, rather than conditions where social plasticity evolves as a correlated response to selection on mean phenotypic expression (Gavrilets & Scheiner, 1993b). We focused on understanding the role of fluctuating social environments in the evolution of social plasticity, with specific interest in the phenotypes organisms encounter in their social environments, as well as the environmental factors that influence the fitness consequences of these phenotypes. We expected that fluctuations in the social environment would play a key role both in generating selection on socially plastic traits, as well as in shaping their adaptive evolution via IGEs. Using these results, we then asked, *what are the consequences of social plasticity for eco-evolutionary dynamics in response to persistent environmental fluctuation and change* (**adaptation of social plasticity and its eco-evolutionary consequences** section)*?* We addressed this question with respect to microevolutionary timescales more amenable to direct empirical study of contemporary environmental processes. Our aim was to develop general heuristics about the conditions under which feedback between the ecological causes and evolutionary consequences of social plasticity may accelerate or inhibit the adaptation of fitness-relevant phenotypes. Throughout the paper, we also consider the insights our results provide with respect to the evolution of context dependent IGEs, demonstrating how predictions regarding heritable variation and evolutionary change can be greatly affected by genetic variation in and ecological effects on social plasticity.

Selection for social plasticity

In this section, we aim to identify key ecological factors driving the selection and adaptation of social plasticity and attendant IGEs. We begin with a brief overview of our general **analytic approach**, building on standard quantitative genetic models of plasticity in complex phenotypes. We introduce a simple **social reaction norm** model of a single phenotype that accounts for individual variation in social, ecological, and socioecological plasticity. This model is used for subsequent analysis and allows us to explore how variation in the genetic and environmental components shaping the phenotype influence the total heritable variation available to selection via **context dependent IGEs**. We then introduce this phenotype model into a broader model of **fluctuating selection across social environments** that is then used to derive key results.

Analytic approach

Quantitative genetics provides a flexible toolkit for investigating gene-by-environment interactions and phenotypic plasticity through a broad class of models referred to as reaction norms (RN). In the most general sense, a RN describes how an organism or genotype changes its expressed phenotype in response to variation in the environment. This is accomplished through a set of RN parameters capturing different properties of the response function, such as intercepts determining the expected phenotype in the absence of an environmental exposure (or in an average environment), and slopes determining the magnitude and direction of phenotypic change across different levels of the environment. While it has been historically debated whether RN parameters should be conceptualized as separately evolving traits (Futuyma, 2021; Nicoglou, 2015), quantitative genetic theory has long emphasized that under a broad range of plausible scenarios, selection and microevolutionary change can be equivalently expressed with respect to context-specific phenotypes—i.e. *character states* (Via & Lande, 1985)—and the RN parameters predicting these trait values across contexts and developmental environments (de Jong, 1995; Gavrilets & Scheiner, 1993b).This provides a general mathematical framework for understanding how patterns of fluctuating selection on expressed phenotypes shape the adaptation of plasticity mechanisms in heterogeneous environments. These models are also particularly attractive for theory building in evolutionary ecology because they can be readily estimated with standard statistical methods and empirical datasets (Kruuk, 2004), facilitating more direct tests of model predictions on contemporary timescales.

In the present study, we used this basic analytic approach to investigate the adaptive evolution of social plasticity in complex (i.e. polygenic and environmentally responsive) phenotypes, such as morphology, behavior, and physiology, whose expression and microevolution are well described by standard assumptions of quantitative genetic models (Bulmer, 1971; Fisher, 1930; Turelli & Barton, 1994). As discussed further below, previous work has extensively explored the evolution of developmental plasticity in response to spatial and temporal variation in the environment (Gavrilets & Scheiner, 1993a; King & Hadfield, 2019; Moran, 1992; Tufto, 2000). Here we focus attention on the evolution of labile plasticity, where expression of the phenotype remains reversible and flexible even after the organism has reached developmental maturation (Scheiner, 1993), considering how fluctuations in social environments that shape both phenotypic expression and selection influence the adaptive evolution of labile social plasticity. The conditions under which such labile social plasticity evolves as a direct consequence of natural selection are poorly understood (McGlothlin et al., 2022).

Social reaction norm

We begin by developing a so-called *social reaction norm* (SRN) model describing a complex phenotype expressed as a function of parameters (mechanisms) regulating responses toward the social environment (**Fig. 1**), which may vary genetically among individuals and thus be subject to selection and adaptive evolution. Broadly, an SRN refers to any formal model with parameters determining how the expression of a phenotype changes in response to the phenotypes expressed by other organisms in the social environment, as well as in response to ecological properties of the social environment that are not individual phenotypes per se, such as group size or density, sex ratios, age structure, etc. (de Groot et al., 2023; Martin & Jaeggi, 2022; Martin et al., 2022; Moore et al., 1997; Strickland et al., 2021). The functional relationships captured by an SRN can vary widely based on the biological system under consideration, the mechanistic resolution of the analysis, and the temporal scale of interactions. For instance, previous models have explored feedback caused by SRNs expressed in instantaneous, finite or infinite interactions, within groups of various size, structure, and composition, demonstrating distinct effects on phenotypic expression and the response to selection as a consequence of social plasticity (Araya-Ajoy et al., 2020; Kazancioğlu et al., 2012; J. S. Martin & Jaeggi, 2022; McGlothlin et al., 2022, 2010; Trubenová et al., 2015). Given that our goal is to capture general conditions under which selection will directly target social plasticity, we avoid making specific assumptions and instead introduce a model that remains agnostic about the functional pathways of social interactions. Our SRN simply parameterizes social plasticity as the expected phenotypic change caused by the social environment, which may or may not reflect the cumulative or aggregate effects of complex iterative feedback processes. This allowed us to model social plasticity in a conceptually analogous way to non-social plasticity, making symmetries between theoretical results for the (co)variance components of both processes clear. Readers are encouraged to see (Bijma, 2014; Martin & Jaeggi, 2022) for details on appropriate statistical methods to empirically estimate SRNs across a variety of scenarios.

We focus herein on a single phenotype linearly responding to simple environmental gradients for theoretical clarity and accessibility, as our results can be straightforwardly generalized to more complex scenarios. We begin with an SRN determining the character state η that individual *j* expresses in discrete state *e* of the social environment

$$\eta_{je} = \mu_j + \psi_j \, {\mu'}_e + \delta_j x_e \qquad (\textbf{Eq. 1})$$

The phenotype is expressed a function of an intrinsic trait value μ_j, reflecting the individual's expected character state independently of variation in the social environment, as well as two SRN slopes: a *social plasticity* parameter ψ_j, often termed an interaction coefficient in quantitative genetics (Bailey & Desjonquères, 2022; Moore et al., 1997), which determines how the individual changes their character state in response to the expected intrinsic trait value μ'_e expressed by conspecifics in their social environment, such as the level of parental investment from a mate, the aggressiveness of a competitor, or the mean body size of neighbors; and *ecological plasticity* parameter δ, which determines how the individual changes their character state as a function of an ecological quantity x_e affecting the social environment and the fitness effects of social interactions, such as the density of conspecifics, the size and composition of social groups, or the availability of local resources (Fisher & McAdam, 2019; Gardner et al., 2007; Hammerstein & Noë, 2016; Henshaw et al., 2019; Martin et al., 2025; Powers & Lehmann, 2017; West et al., 2002; Wright et al., 2019). The value μ'_e can be conceptualized as a generalized representation of the social trait value arising from any specific model of interactions in social environment *e*, e.g. dyadic interactions where $\mu'_e = \mu'_k$ is the trait value of social partner *k* or for interactions in larger groups where $\mu'_e = \bar{\mu}'_K n$ is the summed trait value across *n* partners in social group *K*.

The SRN within a population is defined by vectors of individual trait values $\boldsymbol{\mu}$, $\boldsymbol{\psi}$ and $\boldsymbol{\delta}$, and the social environments $\boldsymbol{e}$ experienced by individuals within that population are defined by vectors $\boldsymbol{\mu}'$ and $\boldsymbol{x}$ (**Fig. 1a**). Throughout the manuscript, we focus on the simple case where the focal $\boldsymbol{\mu}$ and partner $\boldsymbol{\mu}'$ vectors reference trait values for the same phenotype η, though our findings for selection gradients do not rely on this assumption. Stochastic residual variation due to factors such as unmeasured environments, developmental noise, or measurement error were irrelevant for our theoretical purposes here and were, therefore, ignored to focus attention on the repeatable and potentially heritable component of phenotype. While empirically quantified RNs are often nonlinear on the original scale of measurement (Gomulkiewicz et al., 2018; Oomen & Hutchings, 2022), linearity can generally be achieved on a latent scale under appropriate statistical transformation (Bolker et al., 2009; de Villemereuil et al., 2016; Martin, Araya-ajoy, et al., 2024). Gaussian approximations for quantitative genetic inference are also highly robust to deviations (Turelli & Barton, 1994), and theory predicts that stochastic fluctuations in selection tend to facilitate the evolution of linear RNs (Gavrilets & Scheiner, 1993a). Therefore, we focused attention on the simple linear case, noting that our results can be straightforwardly extended to investigate more complex RN shapes of interest (see **data availability** for R code using numeric methods).

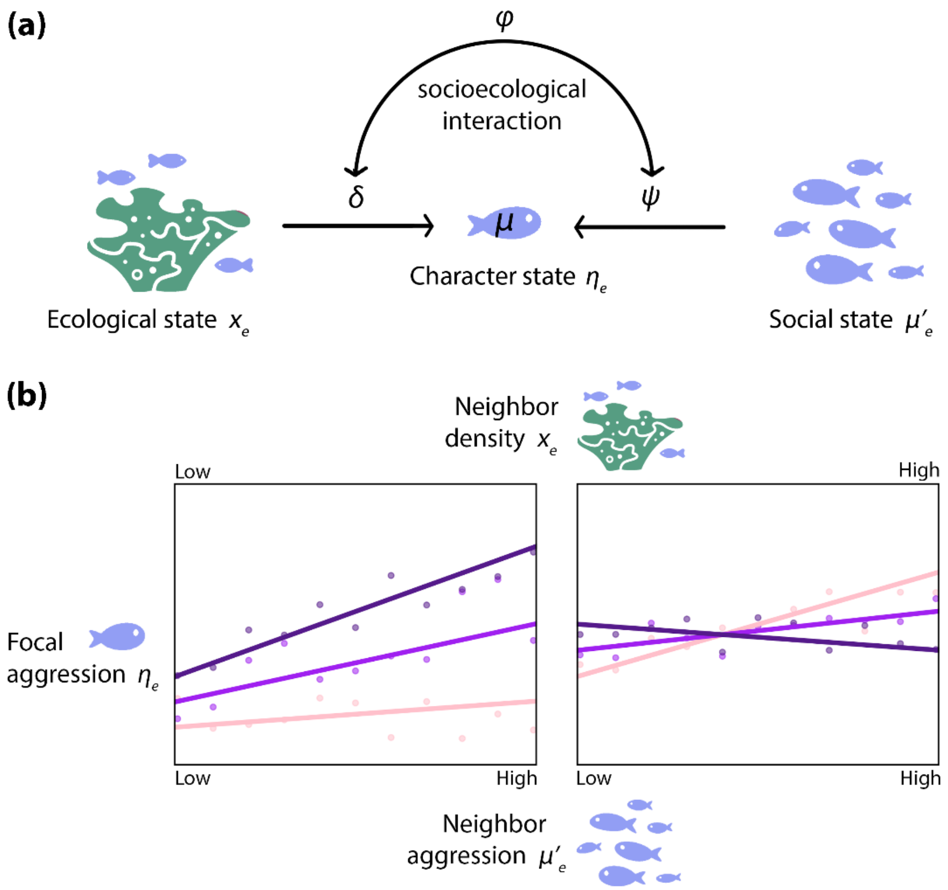
Socioecological plasticity

The SRN in **Eq. 1** assumes that responses toward different components of the social environment ($\boldsymbol{\mu}'$ and $\boldsymbol{x}$) are independent and can effectively be considered in isolation as unidimensional causes of plasticity. Thus, how one responds to conspecifics ψ is not affected by the non-phenotypic, ecological state x of the social environment, and how one responds δ to the ecological state is independent of the expected conspecific phenotype μ'. This will often be an unrealistic assumption, as the costs and benefits of social interactions are inherently tied to the structure of the environment in which they take place, and interactions with conspecifics tend to shape how ecological factors influence organismal phenotypes. For example, individuals may be plastic toward the aggression of conspecifics in low density habitats, but relatively canalized at high density due to prohibitive energetic costs in highly competitive environments, as has been found in field crickets *Gryllus bimaculatus* (Han et al., 2018). Ecological factors shaping the costs and benefits of cooperation within social groups can also modulate levels of social plasticity, such as in many non-industrialized human societies, where reciprocal food sharing, alloparenting, and other cooperative behaviors have been shown to predictably change as a function of variation in kinship, nutritional status, spatial distance among social partners, resource predictability, quality, and availability, and the local risk of environmental hazards such as natural disasters and famine, among other factors (Dirks et al., 1980; Ember et al., 2018; Gurven, 2004; Jaeggi et al., 2016; Kaplan et al., 1985). To explore how such socioecological interactions shape selection on social plasticity, we extend the basic SRN to capture multidimensional plasticity.

$$\eta_{je} = \mu_j + \psi_j \mu'_e + \delta_j x_e + \varphi_j \mu'_e x_e \qquad (\mathbf{Eq.\ 2})$$

The *socioecological plasticity* parameter φ_j regulates how the effects of ψ_j and δ_j change in response to the interaction between social phenotypes and ecological conditions $\mu'_e x_e$ (**Fig. 1a**). Accounting for multidimensional plasticity brings attention to the fact that individuals often face complex and multifaceted environments that can place contingent, fluctuating and potentially conflicting selection pressures on their phenotypes across space and time (Chapin et al., 1987; Fordyce, 2006; Michel, 2012; Stillwell et al., 2007). Despite likely being ubiquitous in nature, such multidimensional plasticity remains poorly understood for both social and non-social components of the environment (Westneat et al., 2019).

Fig 1. Social reaction norm accounting for socioecological plasticity.

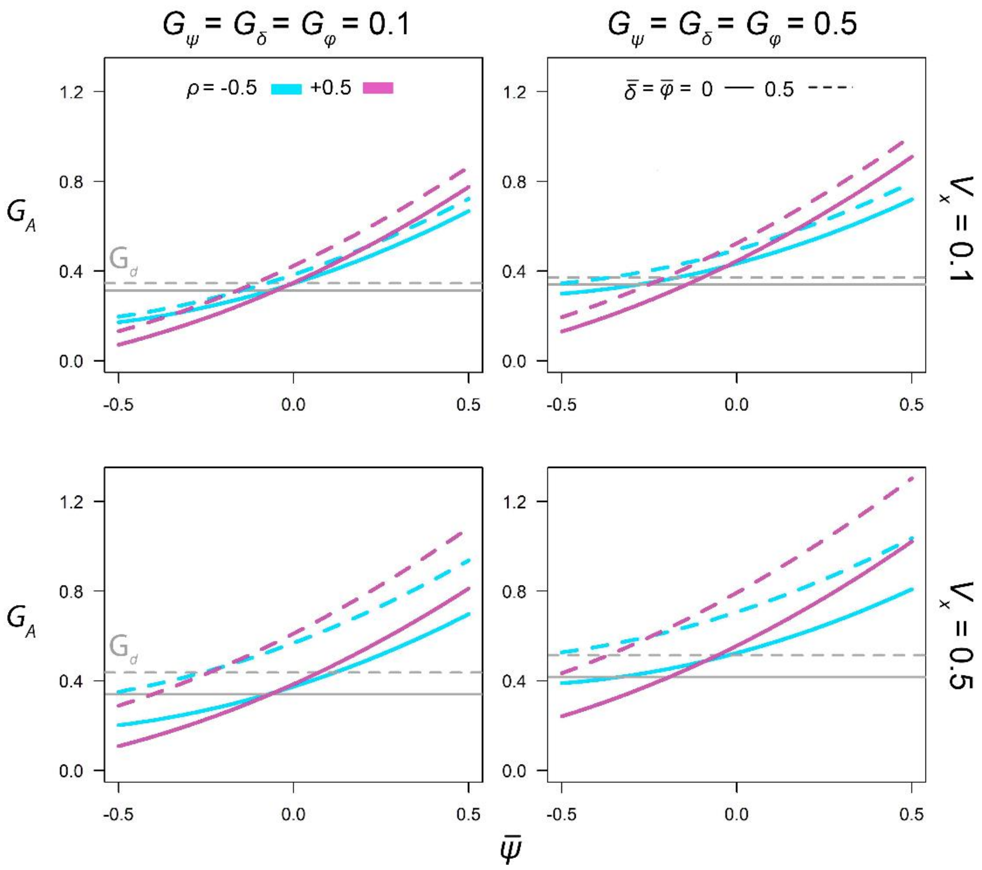


Footnote. A conceptual visualization of the SRN model with socioecological plasticity (**Eq. 2**). (**a**) An individual's expressed character state η_e in social environment e is determined by their expected trait value μ as well as their plasticity toward the social state μ' and ecological state x of this environment. The additive main effects of social and ecological plasticity are quantified by ψ and δ parameters, respectively. Multiplicative effects can also arise when the expression of social plasticity is contingent on the ecological state (and vice versa), i.e. socioecological interaction, which is quantified by the φ parameter. (**b**) An example describing the aggression (y-axis) of three individuals (color-coded), where dots indicate raw empirical observations with stochastic variation and lines indicate underlying deterministic expectations from individuals' SRN functions. The expression of aggression is contingent on the degree of aggression among local neighbors (the social state; x-axis) as well as the density of neighbors in the social environment (ecological state; panels, left = low density, right = high density). The changing of individuals' slopes across panels reflects socioecological plasticity due to the interactive effect of the ecological state. At low density, the dark purple individual is expected to be the most aggressive (largest μ) and to exhibit the greatest escalating response to neighbor aggression (largest ψ); however, because they are also the most sensitive to the costs of increasing neighbor density (negative φ), they express the lowest aggression in the most dense and aggressive social environments. The pink individual instead becomes more likely to escalate aggression in denser social environments (positive φ).

Context dependent IGEs

As described above, social plasticity and IGEs are fundamentally connected as cause and consequence when the phenotypes responding and being responded to are heritable. This implies that genetic variation in social partners' trait values and individuals' responsiveness toward these trait values will determine the magnitude of IGEs on the phenotype. In the **supplementary material**, we delineate analytic relationships between ψ and IGEs under a linear SRN to demonstrate how the direct and indirect components of genetic variation change across socioecological contexts (**Eq. S17-31**). **Fig. 2** shows that the total additive genetic variance available to selection on a socially plastic trait G_A is contingent on standing genetic variances $G_\psi, G_\delta, G_\varphi$ and genetic correlations ρ of SRN parameters, as well as stochastic ecological fluctuations V_x across the population. The magnitude of heritable variation is constrained in the presence of negative social plasticity $\bar{\psi} < 0$ (e.g. when aggressive social environments reduce individuals' aggression), while it can be dramatically magnified in the presence of positive social plasticity $\bar{\psi} > 0$ (e.g. when aggressive social environments escalate aggression, as in **Fig. 1**). Importantly, the magnitude of G_A contributing to the realized phenotypic response to selection is contingent on relatedness among social interactants as well as the strength of social selection (Bijma, 2010; Martin et al., 2025; McGlothlin & Fisher, 2022). This suggests that if environmental change affects population structure and viscosity, it can potentially reveal a large magnitude of cryptic heritable variation in SRNs due to IGEs among genetically assorted individuals.

Fig 2. Total heritable variation of a socially plastic phenotype in a fluctuating environment.



Footnote. The total additive genetic variance G_A available for response to selection on a phenotype is shown (y-axes) as a function of the average level of social plasticity $\bar{\psi}$ in the population (x-axes) across different levels of genetic and socioecological variation, where $G_A = G_d + G_i n^2 + 2nG_{d,i}$ with components defined as in **Eq. S17-31**. Results assume that social interactions are on average dyadic ($\bar{n}$ = 1). Plots vary from top (0.1) to bottom (0.5) rows in the variance of ecological states V_x across microhabitats; Plots vary from left (0.1) to right (0.5) columns in the genetic variance of social G_ψ, ecological G_δ, and socioecological G_φ plasticity. Colored lines demonstrate the effect of genetic covariance between SRN parameters on G_A, with blue lines showing results for constrained SRNs with negative correlations among parameters ($\rho = G_{p,q}\sqrt{V_p}\sqrt{V_q} = -0.5$ for parameters p and q) and dark pink lines showing integrated SRNs with positive correlations among all parameters ($+0.5$). Differing line types show the effect of the population average ecological $\bar{\delta}$ and socioecological plasticity $\bar{\varphi}$ parameters, indicating whether ecological states tend to increase (+0.5, dashed) or have no effect (0, solid) on phenotypic expression. The horizontal grey line indicates the magnitude of direct genetic effects on the phenotype (G_d), which varies as a function of $\bar{\delta}$ and $\bar{\varphi}$. Regions where colors lines are above/below the corresponding grey lines indicate that IGEs are magnifying/constraining the evolvability of the phenotype.

Fluctuating selection across social environments

Using the phenotype model (**Eq. 2**), we now consider how fluctuating selection on the character states produced by SRNs relates to selection on SRN parameters across social environments. Extensive theoretical work has established a causal relationship between fluctuating selection on character states and the adaptation of reaction norms (de Jong, 1995; Gavrilets & Scheiner, 1993a; Gomulkiewicz & Kirkpatrick, 1992), but to our knowledge, prior research has not directly considered how fluctuations in social environments affect the adaptation of social plasticity and IGEs. The evolution of plasticity is affected both by the predictability and reliability of fitness-relevant environmental cues across space and time, which shape the potential costs and limits of plastic responses to environmental fluctuations throughout the lifespan (Botero et al., 2015; De Jong, 1999; Dewitt et al., 1998; Moran, 1992; Tufto, 2000). For instance, adaptive developmental plasticity is likely to evolve when phenotypic changes made in response to early life environments remain predictive of the direction of adaptive response in adulthood (Michel et al., 2014; Tufto, 2015). The same considerations apply more generally to any form of predictive error in organismal responses to the environment, due to a weak or potentially negative correlation between the environmental cues generating plasticity and the environmental states causing selection on the phenotype. Associations between spatial and temporal fluctuations in selection also shape the evolution of plasticity. In some systems, for example, spatial fluctuations may be cancelled out by opposing (countergradient) temporal fluctuations, reducing selection for plasticity in response to spatial variation (King & Hadfield, 2019). These findings are well established and highly generalizable across models. Therefore, we do not address these contingencies to avoid recapitulating prior work. Instead, we focus on the adaptive evolution of labile social plasticity, considering spatial fluctuations in fitness effects, where the same social environmental states affect the expression and selection of individuals' phenotypes.

Model structure

The basic structure of our fluctuating selection model is outlined in **Fig. 3** and mathematical details can be found in the **supplementary material (Eq. S1-5)**. Key parameters and notation are described in **Table 1**. In the model, individuals can be conceptualized as randomly and independently dispersing into microhabitats across a spatially heterogeneous, continuously varying landscape (**Fig. 3a**). Within a given microhabitat, an individual's SRN (**Eq. 2**) determines the character state they express in response to social environment $e = (\mu'_e, x_e)$. Social environments were sampled from a zero-centered multivariate normal distribution with variances $V_{\mu'}$ and V_x and covariance $C_{\mu' x} = 0$, such that $\bar{e} = (0,0)$. This allowed us to readily distinguish between selection occurring directly on the plasticity parameters ψ, δ, φ versus indirectly as a correlated response to selection for increasing or decreasing the mean phenotype μ. See the **supplementary material** for a detailed discussion of the consequences of and motivation for zero-centering in our analysis. Selection then took place on the microhabitat-specific character state, also as a function of the local social environment.

Our model is based on prior work by (de Jong, 1995), who demonstrated the symmetry between microevolutionary models of character states and RNs for continuously varying phenotypes in spatially heterogeneous environments. In **Eq. S1-5**, we modify and simplify the Taylor series approximations used in their model to analyze quadratic fitness functions and linear SRNs in stochastically fluctuating social environments. Individuals' relative fitness in a given microhabitat is expressed as a function of standardly measured linear $\boldsymbol{\beta}$ and quadratic selection $\boldsymbol{\gamma}$ gradients on their character states, expanding the well-known (Lande, 1980; Lande & Arnold, 1983) model. Quadratic approximation is sufficient for our purposes to demonstrate key theoretical relationships, and we expect that under weak selection, quadratic functions will often do a good job of approximating curvature in the local adaptive landscape over microevolutionary timescales (Arnold et al., 2001). This approach also connects predictions directly to commonly estimated selection gradients, providing clear targets for future research.

To allow for fluctuating selection, microhabitat-specific selection gradients were additively partitioned into average directional β_η and stabilizing/disruptive γ_η selection gradients on character states across social environments, as well as deviations $\boldsymbol{\Delta\beta}$ and $\boldsymbol{\Delta\gamma}$ in selection gradients across microhabitats as a function of variation across social environments. See **Eq. S3-5** for details. Given that social environments were randomly distributed and zero-centered across microhabitats, average selection gradients β_η and γ_η specified the magnitude of selection expected on the average character state expressed across social environments. In turn, the interactive fitness effects $\boldsymbol{\Delta\beta}$ and $\boldsymbol{\Delta\gamma}$ (**Table 1**) described how the respective magnitudes of directional and quadratic selection on character states changed additively as a function of variation in the social environment (**Fig. 3b**), i.e. the degree to which the causal effect of phenotype on fitness fluctuated in response to the expected partner trait value μ'_e and the ecological state x_e in the local microhabitat.

Fluctuating directional selection on character states $\boldsymbol{\Delta\beta}$ was captured by three parameters $\Delta\beta_x, \Delta\beta_{\mu'}, \Delta\beta_{\mu'x}$ describing changes in the linear effect of phenotype on fitness as a function of the local ecological x_e, social μ'_e, and socioecological state $\mu'_e x_e$ in a microhabitat. If, for instance, directional selection on η is reduced in denser microhabitats, then $\Delta\beta_x < 0$ such that the expected selection gradient $\beta_\eta + \beta_x x_e$ in microhabitat *e* will be smaller as group density x increases; similarly, if directional selection on η increases as the expected trait value of social partners increases, then $\Delta\beta_{\mu'} > 0$ so that $\beta_\eta + \beta_{\mu'}\mu'_e$ will be greater in *e* with higher μ'. Importantly, this implies that $\Delta\beta_{\mu'}$ *quantifies frequency-dependent selection across microhabitats*, i.e. the degree to which selection on the focal individual's phenotype changes as a function of the trait value exhibited by others in their social environment. This frequency-dependent contribution to the selection gradient can be equivalently conceptualized as a form of correlational selection between focal and partner trait values (McGlothlin et al., 2022), as well as a multiplicative selection effect caused by the interaction between the phenotypes of focal individuals and their social partners (Araya-Ajoy et al., 2020; Westneat, 2012). The term $\beta_{\mu'x}$ allowed the strength of frequency-dependent selection to also vary in response to the ecological state.

For theoretical clarity, we separate fluctuations in the strength of quadratic selection caused by frequency-dependence and any forms of (socio)ecological-dependence into two sets of terms: parameters $\Delta\gamma_{\mu'}, \Delta\gamma_x, \Delta\gamma_{\mu'x}$ capturing effects due to the social state μ' and ecological state x, as well as parameters $\Delta\gamma_{\mu'^2}, \Delta\gamma_{x^2}, \Delta\gamma_{\mu'^2x}, \Delta\gamma_{\mu'x^2}, \Delta\gamma_{\mu'^2x^2}$ capturing effects due to the squared values μ'^2 and x^2.

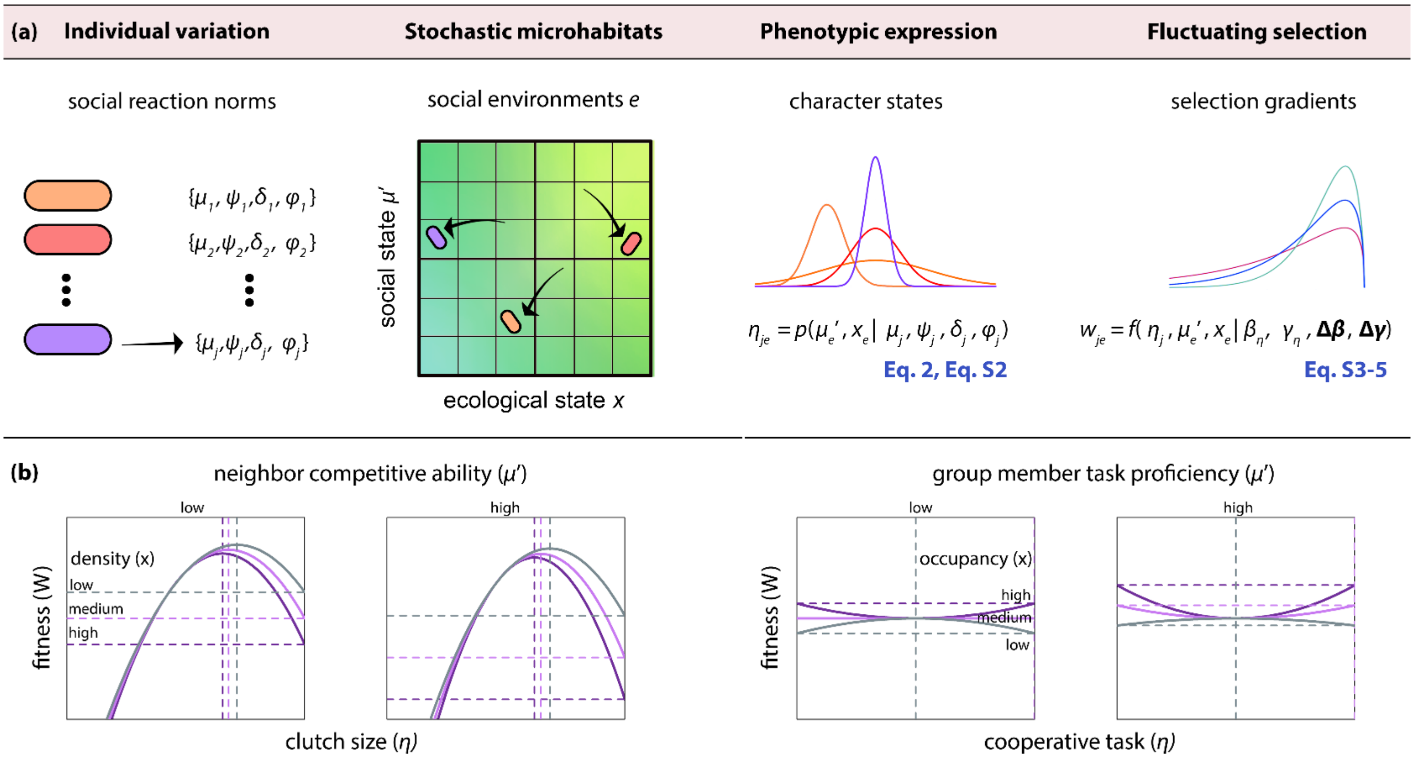
These terms all describe how the curvature of the adaptive landscape relating fitness and phenotype changes as a function of the social environment (**Fig. 3b**). For instance, when $\Delta\gamma_{\mu'} < 0$, $\Delta\gamma_{x} < 0$, and/or $\Delta\gamma_{\mu' x} < 0$, the relative concavity of the fitness function is expected to increase as μ', x , and/or $\mu' x$ increases. Negative deviations due to squared environmental effects $\Delta\gamma_{\mu'^2} < 0$, $\Delta\gamma_{x^2} < 0$, $\Delta\gamma_{\mu'^2 x} < 0$, $\Delta\gamma_{\mu' x^2} < 0$, and/or $\Delta\gamma_{\mu'^2 x^2} < 0$ similarly indicate that relative concavity of the function is expected to accelerate at larger absolute values (herein more 'extreme' values) of the social environment. In **Fig. 3b**, an example is shown for clutch size, where increasing competitive ability among and density of neighbors leads to stronger stabilizing selection, with accelerating declines in fitness for larger clutch sizes. Conversely, when these quadratic terms are positive, the relative convexity of the fitness function increases with μ', x , and/or $\mu' x$. **Fig. 3b** provides another example for performance of a cooperative task within a social group, where increasing occupancy of and proficiency in tasks among group members magnifies the convexity of the fitness function, switching from stabilizing selection for a generalist phenotype toward increasingly disruptive selection for task specialization.

Using our fitness model (**Eq. S5**), selection gradients on character states $\boldsymbol{\eta}$ across social environments could then be related to population-level selection gradients on components of social, ecological, and socioecological plasticity using multiple methods. Selection gradients were calculated through partial differentiation of the fitness function with respect to the SRN parameters (Lande & Arnold, 1983), under varying levels of state-dependency and magnitudes of fluctuating selection across microhabitats. State-dependency was determined by $\boldsymbol{\Delta\beta}$ and $\boldsymbol{\Delta\gamma}$. The causal effects represented by these coefficients were fixed, so that the magnitude of fluctuating selection on character states could be varied as a function of variances V_{μ}' and V_x for social environments across microhabitats. Given the assumptions of the SRN (**Eq. 2**) and fitness models (**Eq. S5**), analytic results could also be derived using covariance mathematics for multivariate Gaussian variables following the Robertson-Price identity (Price, 1972; Robertson, 1966), of which the multivariate breeder's equation is a special case (Queller, 2017). We begin by ignoring the effects of imperfect inheritance and bias in genetic transmission to focus attention on selection gradients, i.e. we take the phenotypic gambit (Grafen, 1984). Therefore, the model can be conceptualized as investigating how a haploid genotype directly encoding an SRN will experience selection as a function of its phenotypically expressed character states across social environments. We consider quantitative genetic effects on the phenotype again in the following section to investigate the consequences of selection for microevolutionary adaptation.

Table 1. Overview of key terminology and notation.

Term	**Notation**	**Interpretation**
Social reaction norm (SRN)	$\mu, \psi, \delta, \varphi$	A function or 'strategy' (**Eq. 1-2**) describing how an individual changes their expressed character state across social environments. Parameters of an individuals' SRN regulate their expected trait value μ, as well as their social ψ, ecological δ, and socioecological plasticity φ toward the social environment
Character state	η_e	The trait value η_e an individual expresses in social environment *e* as a function of their SRN parameters (**Fig. 1**)
Social environment	e, μ', x , $V_{\mu'}, V_x, V_{\mu' x}$	A multivariate environment described by social and ecological states $e = (\mu'_e, x_e)$, where μ' is the expected conspecific trait value and x is an ecological factor influencing social interactions (**Fig. 3a**). These states fluctuate stochastically and independently with variances $V_{\mu'}, V_x, V_{\mu' x}$ across social environments.
Directional selection	$\beta_\eta, \boldsymbol{\beta_p}$	Gradients describing how selection is shaping the average character state β_η expressed in a social environment, as well as average SRN parameters $\boldsymbol{\beta_p}$ across social environments (**Eq. 3, Fig. 4**)
Fluctuating directional selection on character states	$\Delta\beta_{\mu'}, \Delta\beta_x, \Delta\beta_{\mu' x}$	Changes in the magnitude of directional selection on character states as a function of changes in the social $\Delta\beta_{\mu'}$, ecological $\Delta\beta_x$, and socioecological $\Delta\beta_{\mu' x}$ state of the social environment (**Eq. S5**, **Fig. 3a**). Parameters including μ' quantify the strength of frequency-dependent directional selection on character states.
Quadratic selection	$\gamma_\eta, \boldsymbol{\gamma_p}$	Gradients describing how selection is shaping the average variance of character states γ_η expressed in a social environment, as well as the (co)variance of SRN parameters $\boldsymbol{\gamma_p}$ across social environments (**Eq. 4, Fig. 4**).
Fluctuating quadratic selection on character states	$\Delta\gamma_{\mu'}, \Delta\gamma_x, \Delta\gamma_{\mu' x}$ $\Delta\gamma_{\mu'^2}, \Delta\gamma_{x^2}, \Delta\gamma_{\mu'^2 x}$ $\Delta\gamma_{\mu' x^2}, \Delta\gamma_{\mu'^2 x^2}$	Changes in the magnitude of quadratic selection on character states as a function of changes in the social $\Delta\gamma_{\mu'}$, $\Delta\gamma_{\mu'^2}$, ecological $\Delta\gamma_x$, $\Delta\gamma_{x^2}$ and socioecological $\Delta\gamma_{\mu' x}, \Delta\gamma_{\mu'^2 x}, \Delta\gamma_{\mu' x^2}, \Delta\gamma_{\mu'^2 x^2}$ state of the social environment (**Eq. S5**, **Fig. 3a**). Parameters including μ' quantify the strength of frequency-dependent quadratic selection on character states.
Additive genetic (co)variance	$G_A, \boldsymbol{G}_p, G_\eta$	The magnitude of heritable genetic variance in a trait can magnified or constrained by indirect genetic effects (IGEs), as quantified by the total additive genetic variance available to selection G_A (**Fig. 2**, **Eq. S17-31**). The contribution of direct genetic effects across social environments can be quantified by the matrix $\boldsymbol{G}_p$ containing additive genetic (co)variances of SRN parameters (**Eq. 5**), as well as the additive genetic variance G_η of character states (**Eq. 9-10**).

Fig 3. Overview of the fluctuating selection model.



Footnote. A conceptual visualization of the fluctuating selection model used to investigate the causes of selection on SRNs. **(a)** The basic model structure**.** Individuals / haploid genotypes have a fixed social strategy, described by their SRN parameters, that determines how they their phenotype responds to the social environment. Individuals randomly and independently disperse to discrete but continuously varying microhabitats, in which they experience a social environment characterized by a given social state (phenotypic trait value of conspecifics) and ecological state (non-phenotypic value that affects social interactions). In a microhabitat, the social environment interfaces with the individual's social reaction norm to determine their expressed character state, represented by phenotype function *p*(), and selection in turn occurs as a consequence of the expressed character state and local social environment, represented by fitness function *f*() (**Eq. S1-5**). **(b)** Examples of local adaptive landscapes described by the fitness model. Horizontal dashed lines indicate fitness at the maximum trait value, while vertical lines indicate the trait value that maximizes fitness. On the left is a fitness function for clutch size, where individual fitness changes quadratically with respect to the density (ecological state) and competitive ability (social state) of neighbors. The concavity of the fitness function, and thus the strength of stabilizing selection on clutch size, increases as both conspecific density and competitive ability increase, with accelerating declines in fitness for large clutches laid in more extreme social environments (lower horizontal lines). The right plot shows a fitness function for a cooperative task, with quadratic changes in fitness in response to the proficiency and occupancy of group members for the given task. For conditions of low task occupancy and proficiency, stabilizing selection acts to maintain a generalist phenotype (grey vertical line). The convexity of the fitness function, and thus the strength of disruptive selection, increases as more group members engage and exhibit higher proficiency in the task, with accelerating increases in fitness for specialized phenotypes (very high or very low task expression) in more extreme social environments.

Results

For directional selection on character states, the corresponding vector $\boldsymbol{\beta_p}$ of directional selection gradients on SRN parameters is given by

$$\boldsymbol{\beta_p} = \begin{bmatrix} \beta_\mu \\ \beta_\psi \\ \beta_\delta \\ \beta_\varphi \end{bmatrix} = \begin{bmatrix} \beta_\eta \\ \Delta\beta_{\mu'} V_{\mu'} \\ \Delta\beta_x V_x \\ \Delta\beta_{\mu' x} V_{\mu'} V_x \end{bmatrix} \qquad (\textbf{Eq. 3})$$

See **Eq. S1-5**, **Eq. S8-16**, and **Table S1** for mathematical details and **Eq. S13** for selection differentials. The corresponding matrix $\boldsymbol{\gamma_p}$ of quadratic selection gradients on SRN parameters is given by

$$\boldsymbol{\gamma_p} = \begin{bmatrix} \gamma_\mu & \gamma_{\mu,\psi} & \gamma_{\mu,\delta} & \gamma_{\mu,\varphi} \\ & \gamma_\psi & \gamma_{\psi,\delta} & \gamma_{\psi,\varphi} \\ & & \gamma_\delta & \gamma_{\delta,\varphi} \\ & & & \gamma_\varphi \end{bmatrix} \qquad (\textbf{Eq. 4})$$

$$= \begin{bmatrix} \gamma_\eta & \Delta\gamma_{\mu'} V_{\mu'} & \Delta\gamma_x V_x & \Delta\gamma_{\mu' x} V_{\mu'} V_x \\ & \Delta\gamma_{\mu'^2} V_{\mu'}^2 & \Delta\gamma_{\mu' x} V_{\mu'} V_x & \Delta\gamma_{\mu'^2 x} V_{\mu'}^2 V_x + \Delta\gamma_x V_x V_{\mu'} \\ & & \Delta\gamma_{x^2} V_x^2 & \Delta\gamma_{\mu' x^2} V_{\mu'} V_x^2 + \Delta\gamma_{\mu'} V_{\mu'} V_x \\ & & & \Delta\gamma_{\mu'^2} V_{\mu'}^2 V_x + \Delta\gamma_{x^2} V_{\mu'} V_x^2 + \Delta\gamma_{\mu'^2 x^2} V_{\mu'}^2 V_x^2 \end{bmatrix}$$

where the symmetric lower-triangular elements are suppressed for clarity. **Fig. 4** visualizes these relationships in greater detail. We unpack findings below in a stepwise fashion to highlight important results.

Average directional selection

The magnitude of directional selection on the character state in the average social environment β_η causes directional selection β_μ on the SRN intercept μ (**Fig. 4a**). Intuitively, this implies that selection will act to move the mean level of phenotypic expression toward the optimal trait value in the average social environment (Gavrilets & Hastings, 1994).

Fluctuating directional selection

The directional selection gradient β_{ψ} on the SRN parameter ψ is determined by the product $\Delta\beta_{\mu'}V_{\mu'}$ of the variance in the expected trait value of the social environment $V_{\mu'}$ and the degree to which selection changes $\Delta\beta_{\mu'}$ as a function of this trait value. Therefore, selection directly targets social plasticity when (i) selection on character states is frequency-dependent, such that $\Delta\beta_{\mu'} \neq 0$, and (ii) the magnitude of frequency-dependent selection fluctuates across microhabitats, such that $V_{\mu'} \neq 0$ (**Fig. 4a**). Conversely, selection for social plasticity is not expected when there is frequency-dependence without fluctuations in the phenotype of the social environment, or when such fluctuations occur but in the absence of frequency-dependence. Moreover, given a fixed magnitude of frequency-dependence, we expect that increasing variability in the social states experienced across microhabitats will generate stronger selection for social plasticity (**Fig. 4a**). The same considerations apply with respect to the corresponding components of ecological plasticity, consistent with prior theory (de Jong, 1995). The magnitude of directional selection on the SRN slope δ is determined by the product $\Delta\beta_x V_x$ of the variance in the ecological state of the social environment and the degree to which selection changes as a function of this ecological state. Fluctuations in density-dependent selection, for example, are expected to select for plasticity toward the local density of conspecifics within a given microhabitat, while the absence of local density-dependence in fitness and fluctuations in local density will not generate direct selection for such plasticity.

Multidimensional social plasticity

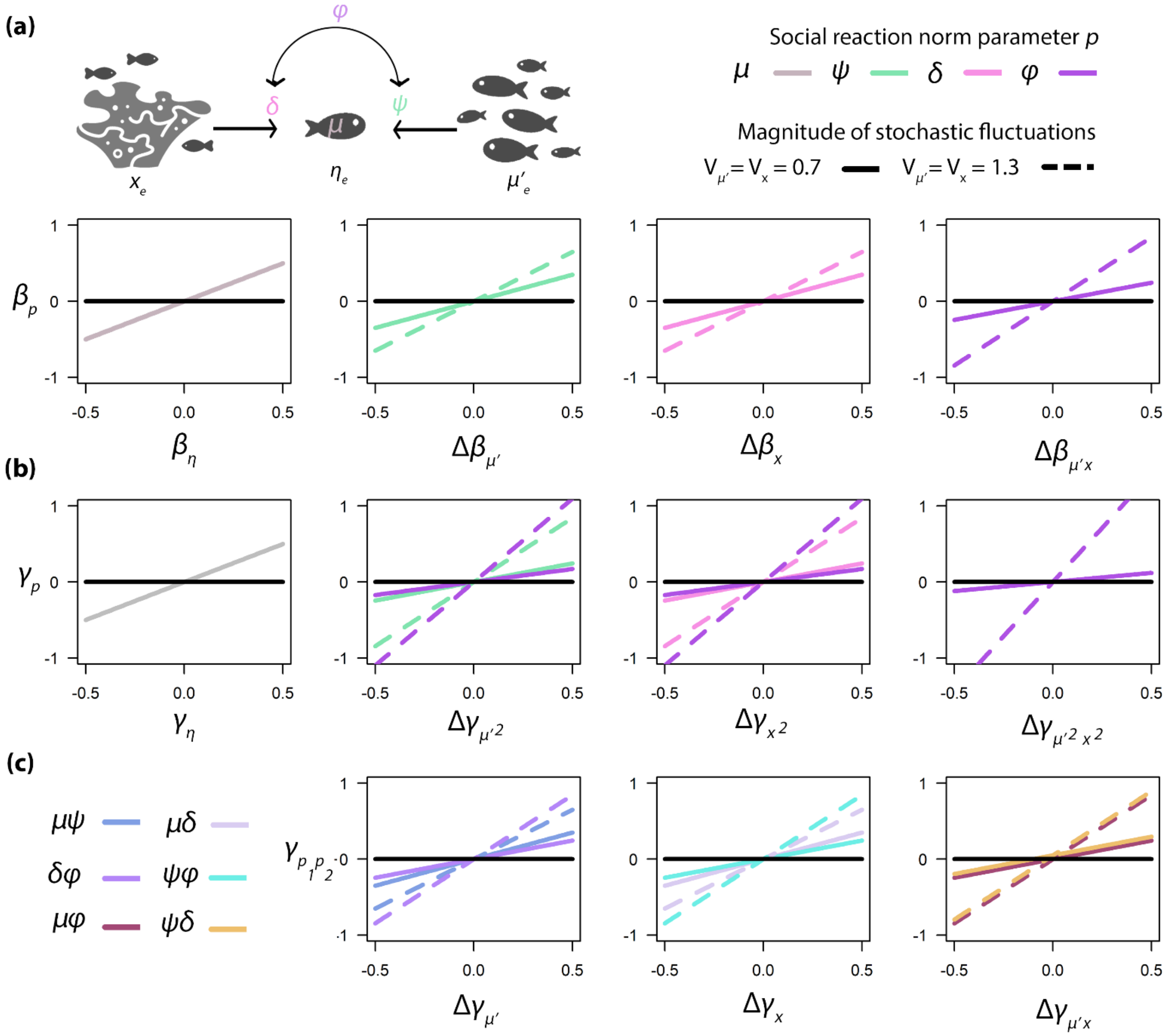
The directional selection gradient β_{φ} on socioecological plasticity parameter φ is similarly determined by the product $\Delta\beta_{\mu'x}V_{\mu'}V_x$, which combines two components: (i) the variances of the social $V_{\mu'}$ and ecological states V_x and (ii) the magnitude $\Delta\beta_{\mu'x}$ indicating the degree to which frequency-dependent selection is contingent on ecological variation. This implies that selection for socioecological plasticity φ will occur when there is both variation in the components of the social environment across microhabitats $V_{\mu'}V_x \neq 0$ and ecologically contingent frequency-dependent selection on the phenotype $\Delta\beta_{\mu'x} \neq 0$ (**Fig. 3b, 4a**). If, for example, the antagonistic effects of competitors on fitness are increased in denser microhabitats, then the degree of negative frequency-dependent selection will be greater at higher densities, and the degree of negative-density dependence will be greater in more competitive microhabitats. If both frequency and density vary across microhabitats, we expect for this to generate population-level selection for multidimensional socioecological plasticity.

Average and fluctuating quadratic selection

After appropriate centering (**Eq. S5**), we find that average quadratic selection γ_{η} on character states only causes direct quadratic selection on the SRN intercept γ_{μ} (**Fig. 4b**). Direct quadratic selection on the SRN slopes thus only occurs because of fluctuations in quadratic selection across social environments. When quadratic selection changes as a function of the social environment, this indicates that the width of the fitness function, and thus the curvature of the adaptive landscape, is shifting across microhabitats in response to socioecological conditions. The degree to which these shifts occur linearly or nonlinearly across extreme environmental values will determine the degree to which fluctuating quadratic selection on the character state induces disruptive/stabilizing selection or correlational selection on SRN parameters. Specifically, disruptive/stabilizing selection on social plasticity γ_{ψ} resulted from fluctuating, frequency-dependent quadratic selection $\Delta\gamma_{\mu'^2}V_{\mu'}^2$ driven by variation in the squared social state μ'^2. This suggests that quadratic selection will directly target among-individual variance in social plasticity V_{ψ} when (i) extreme conspecific trait values have accelerating or decelerating effects on the curvature of the fitness function $\Delta\gamma_{\mu'^2} \neq 0$, and when variation in those extreme trait values fluctuates across social environments $V_{\mu'}^2 \neq 0$ (**Fig. 4b**). The same results apply for the slope δ regulating ecological plasticity, with quadratic selection γ_{δ} directly targeting V_{δ} being determined by the product $\Delta\gamma_{x^2}V_x^2$ of variation in extreme ecological values V_x^2 and the magnitude $\Delta\gamma_{x^2}$ by which these values influence the curvature of the fitness function. Disruptive or stabilizing selection on the socioecological coefficient γ_{φ} combines these effects and their interaction $\Delta\gamma_{\mu'^2}V_{\mu'}^2V_x + \Delta\gamma_{x^2}V_{\mu'}V_x^2 + \Delta\gamma_{\mu'^2x^2}2V_x^2V_{\mu'}^2$.

Correlational selection among SRN parameters is in turn generated by fluctuating quadratic selection on the character state driven by the linear rather than squared effects of the social environment (**Fig. 4c**). Correlational selection among the SRN intercept and the SRN slopes results from the linear effects of socioecological fluctuations proportional to their magnitude of variation, such that for $\gamma_{\mu,\psi} = \Delta\gamma_{\mu'}V_{\mu'}$, $\gamma_{\mu,\delta} = \Delta\gamma_{x}V_{x}$, and $\gamma_{\mu,\varphi} = \Delta\gamma_{\mu' x}V_{\mu'}V_{x}$. Linear and nonlinear effects induce correlational selection among the SRN slopes, proportional to the product of their variances, with $\gamma_{\psi,\delta} = \Delta\gamma_{\mu' x}V_{\mu'}V_{x}$, $\gamma_{\psi,\varphi} = \Delta\gamma_{x}V_{\mu'}V_{x} + \Delta\gamma_{\mu'^2 x}V_{\mu'}^{2}V_{x}$, and $\gamma_{\delta,\varphi} = \Delta\gamma_{\mu'}V_{\mu'}V_{x} + \gamma_{\mu' x^2}V_{\mu'}V_{x}^{2}$. Therefore, when quadratic selection exhibits linear fluctuations in response to the social environment, selection directly targets the integration among individuals' average character states and socioecological plasticity across microhabitats. For example, if there is positive frequency-dependent directional $\Delta\beta_{\mu'} > 0$ and quadratic selection $\Delta\gamma_{\mu'} > 0$, the upward slope of the fitness surface with respect to the phenotype will become increasingly convex and accelerating with higher trait values in the social environment, e.g. because of synergy among cooperative phenotypes. If social environments fluctuate, this will generate selection on the integration of SRN intercepts and social plasticity slopes $\gamma_{\mu,\psi}$, pushing individuals with higher trait values to also take greater advantage of the multiplicative benefits arising from interactions with similar social partners. To the degree that fluctuations also occur in the ecological state of the social environment $V_{x} > 0$, we expect for such effects to further generate selection for integration $\gamma_{\delta,\varphi} > 0$ between ecological δ and socioecological φ slopes of the SRN, further modulating the expression of ψ. When the interaction between social and ecological variation contributes to fluctuations in the strength of quadratic selection $\Delta\gamma_{\mu' x} \neq 0$, we in turn expect for correlational selection to occur on the social and ecological slopes $\gamma_{\psi,\delta}$, proportional to the product of their variation $V_{\mu'}V_{x}$ across microhabitats.

Fig 4. Relating selection gradients on character states and social reaction norms.



Footnote. (a) Plots show how the magnitude of selection on each parameter *p* (colored lines) of the SRN evolving in the population relates to the strength of microhabitat-specific selection on character states η (**Eq. 3-4**). The solid (0.7) and dotted (1.3) lines show how these relationships change as a function of the degree of social $V_{\mu'}$ and ecological V_x variability across microhabitats. The first row shows how directional selection on SRN parameters β_p across social environments (y-axes) is related to average directional selection β_η on character states and fluctuations in directional selection due to the social $\Delta\beta_{\mu'}$, ecological $\Delta\beta_x$, and socioecological $\Delta\beta_{\mu' x}$ state of the microhabitat (x-axes). (b) The middle and bottom rows show relationships for quadratic selection on SRN parameters γ_p. The middle plot shows stabilizing and disruptive selection on SRNs due to average quadratic selection on character states γ_η and fluctuations $\Delta\gamma_{\mu'^2}, \Delta\gamma_{x^2}, \Delta\gamma_{\mu'^2 x^2}$ caused by squared values of the social environment. (c) The bottom plot shows correlational selection on parameters p_1 and p_2 due to fluctuations $\Delta\gamma_{\mu'}, \Delta\gamma_x, \Delta\gamma_{\mu' x}$ caused by the main effects of the social environment. We assume $\Delta\gamma_{\mu' x^2} = \Delta\gamma_{\mu'^2 x} = 0$ for simplicity (see **Table S1** for full results). Note that fluctuations attributable to μ' reflect frequency-dependent selection.

Adaptation of social plasticity and its eco-evolutionary consequences

To understand the implications of our findings for adaptive evolution of the phenotype, we first express the evolutionary response in the mean SRN parameters across a single generation, expanding on previous quantitative genetic theory for the adaptation of social plasticity (Kazancioğlu et al., 2012; Martin & Jaeggi, 2022). To do so, we use the vector $\boldsymbol{\beta}_\mathbf{p} = \left[\beta_\mu, \beta_\psi, \beta_\delta, \beta_\varphi\right]^\mathrm{T}$ of directional selection gradients for each of the *p* SRN parameters (**Eq. 3**) and incorporate a $\boldsymbol{G_p}$ matrix describing among-individual genetic (co)variance across SRN parameters. Using the multivariate breeder's equation (Lande, 1979), adaptation of the average SRN parameters in the population is determined by

$$\begin{bmatrix} \Delta\bar{\mu} \\ \Delta\bar{\psi} \\ \Delta\bar{\delta} \\ \Delta\bar{\varphi} \end{bmatrix} = \boldsymbol{G_p \beta_p} \qquad (\textbf{Eq. 5})$$

under the standard quantitative genetic assumptions that genetic and environmental values are independent, the phenotype is well described by an infinitesimal or continuum-of-alleles model (Fisher, 1930; Hill, 2010; Kimura, 1965), where phenotypic trait values are determined by many alleles of small additive effect, and there are no systematic changes in the effects of migration, mutation, and drift on mean trait values between generations.

We can then determine the magnitude of adaptive change in the average character state in the next generation following an episode of selection on the first generation ($t = 1$). Assuming that expected trait values (SRN intercepts) for individuals and their social partners are drawn from the same population distribution ($\bar{\mu} = \bar{\mu}'$), then

$$\bar{\eta}_{t=2} = (\bar{\mu} + \Delta\bar{\mu}) + (\bar{\psi} + \Delta\bar{\psi})(\bar{\mu}' + \Delta\bar{\mu}\bar{n}) + (\bar{\delta} + \Delta\bar{\delta})\bar{x} + (\bar{\varphi} + \Delta\bar{\varphi})(\bar{\mu}' + \Delta\bar{\mu}\bar{n})\bar{x} \qquad (\mathbf{Eq.\,6})$$

for the change in the average character state due to genetic adaptation. While the selection analyses above were agnostic about the structure of social interactions, so that results were independent of group size, the response to selection in the mean phenotype will be contingent on the average number of conspecifics $\bar{n}$ encountered by individuals in their social environment. We assume that variation in group size is random with respect to the phenotype. Given that social plasticity occurs in response to the same trait that is undergoing adaptation, the expected trait value of the social environment $\bar{\mu}' + \Delta\bar{\mu}\bar{n}$ and its effects via $\bar{\psi}$ will also evolve alongside the phenotype, a central result from IGE theory (Bijma et al., 2007; McGlothlin et al., 2010; Moore et al., 1997). Moreover, because ψ can also evolve in response to selection, the rate of phenotypic evolution will be further magnified as a function of IGEs generated by $\Delta\bar{\psi}\bar{\mu}'$ and $\Delta\bar{\psi}\Delta\bar{\mu}$ (Kazancioğlu et al., 2012; Martin & Jaeggi, 2022), as well as through $\Delta\bar{\varphi}(\bar{\mu}' + \Delta\bar{\mu})\bar{x}$ due to the effects of multidimensional plasticity and socioecological interactions whenever $\bar{x}_{t=2} \neq 0$, i.e. when ecological change occurs between generations.

Therefore, in comparison to standard models that focus on selection of the character state in an average environment, where the adaptive response is solely determined by $\beta_{\eta} = \beta_{\mu}$, our model predicts that the rate of adaptation in the average character state will be further accelerated or constrained because of stochastic fluctuations in frequency-dependence, proportional to

$$\boldsymbol{G}_{(\boldsymbol{\psi}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\left(\bar{\mu}' + \boldsymbol{G}_{(\boldsymbol{\mu}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\bar{n}\right) + \boldsymbol{G}_{(\boldsymbol{\varphi}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\left(\bar{\mu}' + \boldsymbol{G}_{(\boldsymbol{\mu}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\bar{n}\right)\bar{x} \qquad (\mathbf{Eq.\,7.1})$$

Here $\boldsymbol{G}_{(\boldsymbol{p}.\boldsymbol{\psi}\boldsymbol{\varphi})}$ is the 1 x 2 submatrix of $\boldsymbol{G}_{\boldsymbol{p}}$ describing the (co)variance of *p* with ψ and φ and $\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}$ is the 2 x 1 submatrix of $\boldsymbol{\beta}_{\boldsymbol{p}}$ for the fluctuating frequency dependent effects that determine β_ψ and β_φ (**Eq. 3-4**). This reduces to

$$\boldsymbol{G}_{(\boldsymbol{\psi}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\boldsymbol{G}_{(\boldsymbol{\mu}.\boldsymbol{\psi}\boldsymbol{\varphi})}\boldsymbol{\beta}_{(\boldsymbol{\psi},\boldsymbol{\varphi})}\bar{n} \qquad (\textbf{Eq. 7.2})$$

under the assumptions that $\bar{\mu}'_{t=1} = \bar{x}_{t=1} = 0$ and the ecological state of the social environment remains static $\bar{x}_{t=2} = 0$. Our results imply that when frequency-dependence is aligned with average directional selection on the phenotype $\mathrm{sign}(\beta_\eta) = \mathrm{sign}(\Delta\beta_{\mu'} + \Delta\beta_{\mu' x})$ and there are no tradeoffs generating negative genetic covariances in $\boldsymbol{G}_{(\boldsymbol{\mu}.\boldsymbol{\psi}\boldsymbol{\varphi})}$, stochastic fluctuations in the composition of the social environment will tend to facilitate more rapid adaptation of the phenotype in comparison to homogenous social environments (**Fig. 5**). Conversely, if frequency-dependence opposes average directional selection $\mathrm{sign}(\beta_\eta) \neq \mathrm{sign}(\Delta\beta_{\mu'} + \Delta\beta_{\mu' x})$, adaptation of the average character state can be more constrained in fluctuating versus homogeneous social environments (**Fig. 5a**).

Our findings also expand understanding of the adaptive consequences of nonlinear selection on SRNs. We can predict the adaptive change in $\boldsymbol{G}_{\boldsymbol{p}}$ due to changes in the frequency of pleiotropic alleles and/or linkage disequilibrium (Lande, 1980; Phillips & Arnold, 1989) as a consequence of the SRN quadratic selection gradients, such that

$$\Delta\boldsymbol{G}_{\boldsymbol{p}} = \boldsymbol{G}_{\boldsymbol{p}}\left(\boldsymbol{\gamma}_{\boldsymbol{p}} - \boldsymbol{\beta}_{\boldsymbol{p}}\boldsymbol{\beta}_{\boldsymbol{p}}^{\mathrm{T}}\right)\boldsymbol{G}_{\boldsymbol{p}} \qquad (\textbf{Eq. 8})$$

where $\boldsymbol{\gamma}_{\boldsymbol{p}}$ is the matrix defined above (**Eq. 4**) with stabilizing / disruptive selection effects on the diagonals and correlational selection effects on the off-diagonals. Subtraction of $\boldsymbol{\beta}_{\boldsymbol{p}}\boldsymbol{\beta}_{\boldsymbol{p}}^{\mathrm{T}}$ captures the additional reduction in genetic variance expected under directional selection, which may further reduce genetic variance if multiplicative tradeoffs in directional selection occur between life history components or episodes of selection (McGlothlin, 2010). In the absence of directional selection $\boldsymbol{\beta}_{\boldsymbol{p}} = \boldsymbol{0}$, environmental change $V_{xt=1} = V_{xt=2}$, or assortment, assuming zero-centered trait values and environmental states, adaptive change in the variance of character states is given by

$$\mathrm{G}_{\eta_{t=2}} = V_\mu + \Delta G_\mu + \left(G_\psi + \Delta G_\psi\right)\left(G_{\mu'} + \frac{\Delta G_\mu}{\bar{n}}\right) + \qquad (\mathbf{Eq.\,9})$$

$$+\left[G_\delta + \Delta G_\delta + \left(G_\varphi + \Delta G_\varphi\right)\left(G_{\mu'} + \frac{\Delta G_\mu}{\bar{n}}\right)\right] V_x$$

The response to selection in the genetic variance of character states is then

$$\begin{gathered} \Delta \mathrm{G}_\eta = \Delta G_\mu + \Delta G_\psi G_{\mu'} + \left(G_\psi + \Delta G_\psi\right)\frac{\Delta G_\mu}{\bar{n}} \\ + \left[\Delta G_\delta + \Delta G_\varphi G_{\mu'} + \left(G_\varphi + \Delta G_\varphi\right)\frac{\Delta G_\mu}{\bar{n}}\right] V_x \end{gathered} \qquad (\mathbf{Eq.\,10})$$

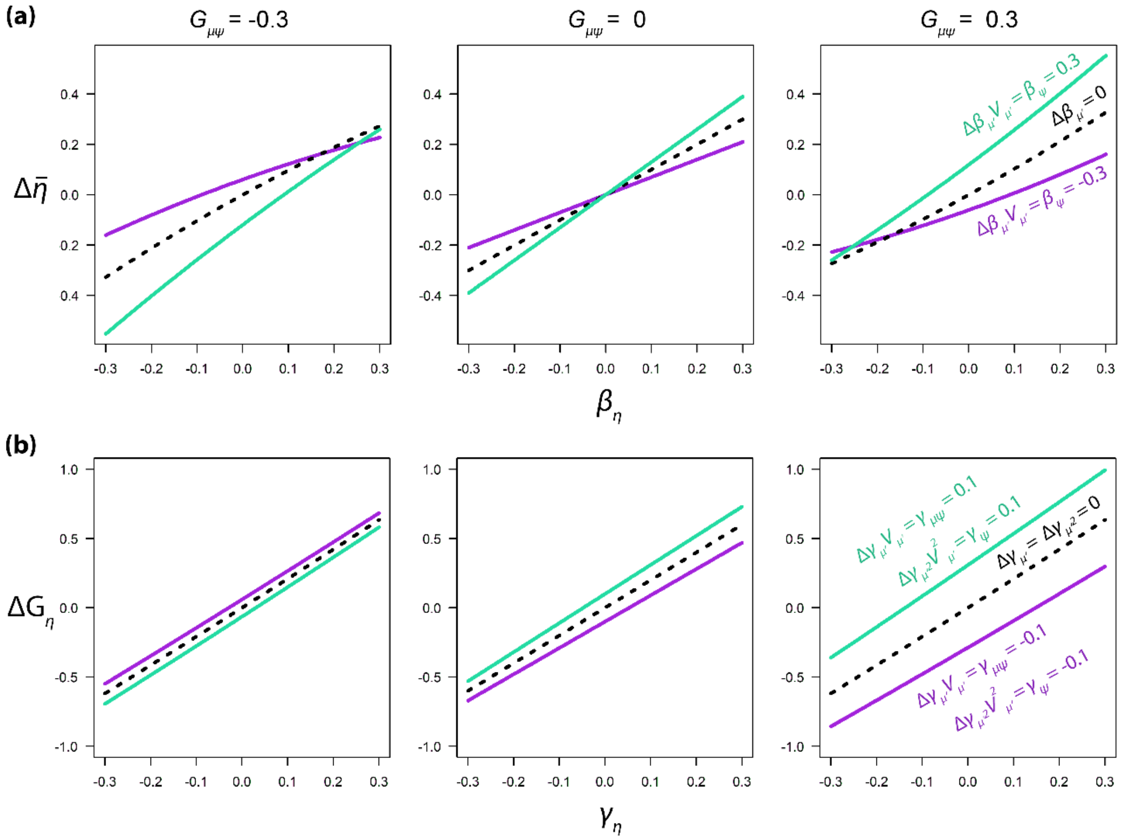
See **Eq. S32-33** for further details and more general results relaxing assumptions and explicitly incorporating IGEs.

As with directional selection, our results for quadratic selection indicate that, depending on the structure of the adaptive landscape, stabilizing or disruptive selection on distinct parameters of the SRN can magnify or constrain the evolution of phenotypic variance to a greater degree than expected in the absence of fluctuating selection (**Fig. 5**). For instance, if there is on average stabilizing negative quadratic selection across social environments (e.g. if the population is near the optimum for reproductive behavior in the average environment), but this quadratic selection is subject to fluctuations in positive frequency-dependent selection (e.g. due to interactions with cooperative social partners increasing offspring survival), we generally expect less genetic variance in the phenotype to be lost than predicted in the absence of fluctuating selection across social environments (**Fig. 5b**). Conversely, under fluctuating negative frequency-dependent quadratic selection, the evolutionary potential of the phenotype may be more greatly constrained than expected due to additional stabilizing selection acting to reduce genetic variance attributable to SRN slopes (**Fig. 5b**). When fluctuations in directional and quadratic selection co-occur, these processes can act multiplicatively to magnify or constrain adaptive responses in more complex ways (**Eq. S32**).

Socio-eco-evolutionary feedback

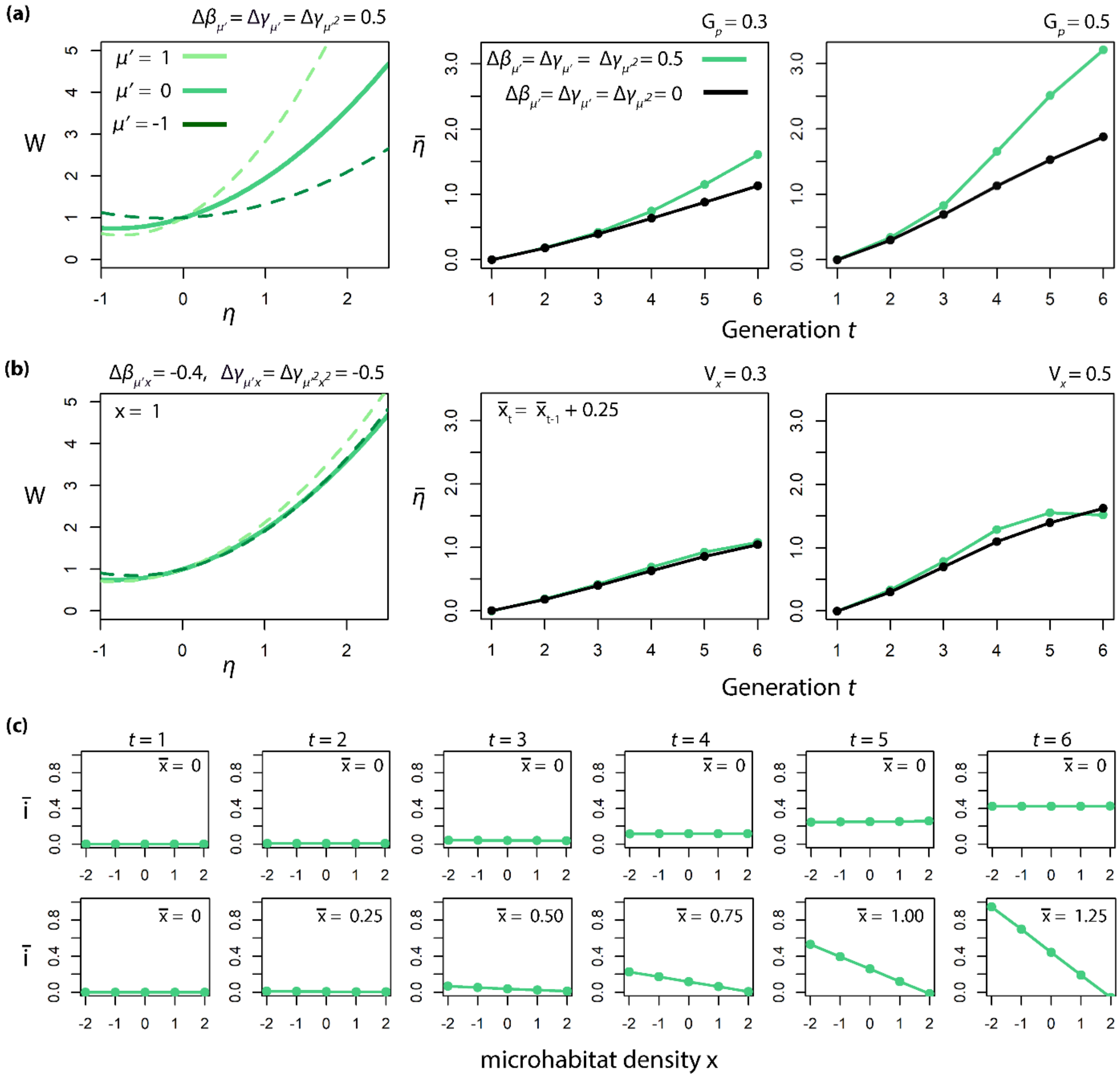
When social plasticity occurs in response to the same phenotype experiencing selection, any fluctuating frequency-dependence in the current generation is expected to feedback on the strength of selection in the next generation due to its effects on the mean and variance of trait values in the social environment (**Eq. 7**), which will in turn determine the strength of selection on the SRN in the subsequent generation (**Eq. 3-4, Table S1**). The same phenomena can also occur when two or more distinct interacting phenotypes are (co)evolving. These conditions potentiate feedback loops when a population is evolving on the slopes of an adaptive landscape—social plasticity can accelerate or decelerate the response to selection (**Eq. 7, 10**) and in turn shape the magnitude of selection on SRNs in the subsequent generation through its effects on the distribution of social environments. In **Fig. 6**, we show an example of such *socio-eco-evolutionary feedback*, where the adaptation of social plasticity in a single trait under positive frequency-dependent selection accelerates a population's climb toward the local fitness peak in the presence of fluctuating social environments (**Fig. 6a**). This feedback can be amplified or dampened as a function of ecological change, such as through increasing microhabitat density caused by habitat fragmentation, due to the coevolution of socioecological plasticity (**Fig. 5b**). Our results also clarify how fluctuating frequency-dependent selection can shape the adaptation of IGEs across contexts and generations. As emphasized above, IGEs on phenotypes are fundamentally determined by the distribution of SRN parameters in a population (**Fig. 2, Eq. S17-30**). Therefore, any adaptive change in the means and genetic (co)variances of these parameters (**Eq. 5, 8**) will necessarily cause adaptive evolution of IGEs and thus the total additive genetic variance in the phenotype. Analytic results for adaptive change in IGEs are cumbersome (**Eq. S32**) and are, therefore, demonstrated in **Fig. 6c** using simulation.

Figure 5. Adaptation in the presence of fluctuating frequency-dependent selection.



Footnote. Adaptive change in the phenotype in the presence of fluctuating social environments and frequency-dependent selection. For simplicity, interactions are dyadic ($\bar{n} = 1$), ecological variability is ignored $V_x = 0$, and there are no permanent environmental effects on the phenotype. (a) The top row shows adaptation of the mean character state $\Delta\bar{\eta}$ (y-axis) as a function of average directional selection across social environments β_{η} (x-axis) and the genetic correlation $G_{\mu\psi}$ between SRN intercepts ($G_{\mu} = V_{\mu'} = 1$) and social plasticity slopes ($G_{\psi} = 1$). Black dashed lines indicate the response in the absence of fluctuating frequency-dependent selection across microhabitats ($\Delta\beta_{\mu'} = 0$), while colors indicate the response in the presence of fluctuating social environments under positive (green; $\Delta\beta_{\mu'}V_{\mu'} = 0.3$) or negative (purple; $\Delta\beta_{\mu'}V_{\mu'} = -0.3$) frequency-dependent directional selection. (b) The bottom row shows the adaptive response to selection in the genetic variance of character states ΔG_{η} (y-axis) in the absence of directional selection, as a function of the strength of average disruptive (+) / stabilizing (-) selection across social environments γ_{η} (x-axis). Black dashed lines indicate the absence of fluctuating frequency-dependent selection ($\Delta\gamma_{\mu'} = \Delta\gamma_{\mu'^2} = 0$), while colors indicate the response in the presence of fluctuating positive (green; $\Delta\gamma_{\mu'}V_{\mu'} = \Delta\gamma_{\mu'^2}V_{\mu'}^2 = \gamma_{\psi} = 0.10$) or negative (purple; $\Delta\gamma_{\mu'}V_{\mu'} = \Delta\gamma_{\mu'^2}V_{\mu'}^2 = \gamma_{\psi} = -0.10$) frequency-dependent quadratic selection. Note that because of heterogeneity in microhabitats, change in the variance of expected trait values $\Delta G_{\mu} = \Delta V_{\mu'}$ still interacts with standing genetic variance in social plasticity ($G_{\psi} = 1$) to change ΔG_{η} even in the absence of fluctuating selection (black lines).

Figure 6. Socio-eco-evolutionary feedback in fluctuating social environments.



Footnote. Feedback in phenotypic evolution across generations in the presence or absence of fluctuating frequency-dependent selection. Results consider a single phenotype that is plastic in response to the same phenotype being expressed in the social environment, such that genetic variance is equivalent for the expected trait values $G_{\mu} = G_{\mu'}$ of individuals and their social partners. For simplicity, there are no permanent environmental effects on the phenotype.

(**a**) The left plot shows the local shape of the adaptive landscape relating individuals' character state η (x-axis) to their fitness W (y-axis). Ecological states do not change across time. The shape of the landscape can stochastically fluctuate relative to the average social environment ($\mu' = 0$) as a function of variation in the social state of an individual's microhabitat. Positive frequency-dependence increases/decreases the slope ($\Delta\beta_{\mu'} = 0.5$) and convexity ($\Delta\gamma_{\mu'} = 0.5$) of the landscape when social partners have higher/lower expected trait values μ' relative to the average value across microhabitats. The right plots show the pace of adaptation in the phenotype $\bar{\eta}$ as the population moves toward its local fitness peak across generations (t = 1 – 6), depending on whether stochastic fluctuations in frequency-dependent selection are present (green line) or absent (black line). The two plots show different magnitudes (0.3 or 0.5) of standing genetic variation in SRN parameters G_p in the first generation ($t = 1$), assuming no genetic correlations ($G_{p_1,p_2} = 0$). The model initializes with an expected trait value of 0 and no plasticity on average ($\bar{\mu} = \bar{\psi} = \bar{\delta} = \bar{\varphi} = 0$), such that the difference in the rate of adaptation at each generation (the slope connecting adjacent points) changes as a function of the evolution of social plasticity ($\Delta\bar{\psi}$ and $\Delta \mathrm{G}_{\psi}$), the expected trait value ($\Delta\bar{\mu}$ and $\Delta \mathrm{G}_{\mu}$), and their genetic integration ($\Delta \mathrm{G}_{\mu\psi}$). Results assume that interactions are dyadic ($\bar{n} = 1$).

(**b**) The same plots as in (**a**), but now with additional fluctuations in frequency-dependence due to ecological change and negative density-dependent effects ($\Delta\beta_{\mu' x} = -0.4$, $\Delta\gamma_{\mu' x} = \Delta\gamma_{\mu'^2 x^2} = -0.5$), which generate selection on the socioecological plasticity parameter φ. The fitness plot shows how higher density (x = 1) dampens the magnitude of frequency-dependent selection. The right plots show how phenotypic evolution proceeds under ecological change at varying magnitudes (0.3 or 0.5) of ecological fluctuation V_x as the average density of local microhabitats increases from 0 by 0.25 per generation ($\bar{x}_t = \bar{x}_{t-1} + 0.25$).

(**c**) Plots show how average context dependent IGEs ($\bar{\iota}$; y-axis; **Eq. S17**) change across microhabitat densities (x-axis) and adaptively evolve across generations $t_1 - t_6$ (left to right plots). The top and bottom rows show how context-dependence in IGEs evolves as a function of whether ecological change is absent (top; $\bar{x} = 0$) or present (bottom; $\bar{x}_t = \bar{x}_{t-1} + 0.25$), assuming a constant ecological variance $V_x = 0.3$ and genetic variances of $G_p = 0.3$ and covariances $G_{p_1,p_2} = 0$ at the start of the simulation.

Discussion

Using a relatively simple model for the evolution of a complex phenotype in a heterogeneous environment (**Eq. 1-2, Eq. S1-5, Fig. 3**), our results demonstrate that when the fitness effects of organisms' phenotypes are frequency-dependent, fluctuations in the composition of the social environment play a central role in facilitating the adaptative evolution of social plasticity (**Eq. 3-4, Fig. 4, Table S1**). In many cases, we expect that social plasticity will be contingent on ecological conditions (**Eq. 2, Fig. 1**), and as we show, this can further potentiate the evolution of multivariate SRNs characterized by socioecological plasticity (**Eq. 3-4, Fig. 4, Table S1**). Once evolved, social plasticity in turn fundamentally shapes the expression of heritable genetic variation in the phenotype through IGEs (**Fig. 2, 6, Eq. S17-30**). Consistent with predictions from prior IGE models (Araya-Ajoy et al., 2020; Bailey et al., 2021; Bijma & Wade, 2008; Kazancioğlu et al., 2012; Martin et al., 2022; Martin et al., 2025; McGlothlin et al., 2010) and niche construction models of ecological inheritance (Fogarty & Wade, 2022), we find that social plasticity and genetic variation in social plasticity can greatly modify the rate of adaptive microevolution in the phenotype (**Eq. 6-10**; **Fig. 5**). Our findings also show how the adaptation of social plasticity and IGEs can feed forward across generations, further modifying the strength of selection and rates of ongoing phenotypic evolution in fluctuating environments, a process we refer to as socio-eco-evolutionary feedback (**Fig. 6-7**). Taken together, our results demonstrate the importance of linking the ecological causes and evolutionary consequences of social plasticity to better understand the pace of phenotypic adaptation in complex and rapidly changing environments (**Fig. 7**).

There are many scenarios where plasticity may reduce rather than amplify rates of genetic evolution by shielding heritable variation from selection (Ancel, 2000; Ghalambor et al., 2007; Price et al., 2003). In general, the diversity of functional mechanisms underpinning phenotypic plasticity across taxa, as well as the complex dynamics of environmental change across space and time, make it challenging to generate simple predictions about the effects of plasticity on adaptive evolution (Vinton et al., 2022). For example, evolutionary simulations have shown that while adaptive plasticity reduces rates of molecular genetic evolution in novel environments, it also increases the rate at which adaptive and maladaptive mutations are respectively retained and removed from the population (Lalejini et al., 2021). Life history evolution and demographic processes shaping dispersal also have importance influences on the likelihood of adaptive developmental plasticity evolving in response to fluctuating selection pressures (Scheiner & Holt, 2012; Tufto, 2015). Notwithstanding such nuances, theory indicates that plasticity will generally accelerate/diminish evolutionary change when it is aligned with the direction of selection and a population is moving up a convex/concave slope on the local adaptive landscape (Paenke et al., 2007). Our findings are consistent with this general result while also extending it to the specific case of fluctuating frequency-dependent selection, which generates multiplicative payoffs across social environments (**Fig. 6A**) that either tend to magnify (convex, positive frequency-dependence) or constrain (concave, negative frequency-dependence) the evolutionary response in the phenotype. Multidimensional plasticity also further nuances predictions by showing how the alignment of plasticity and selection may be highly sensitive to ongoing socioecological change, quickly shifting from facilitating to inhibiting phenotypic evolution across space and time (**Fig. 6B**). These results motivate greater attention to the understudied but likely ubiquitous phenomenon (Westneat et al., 2019) of multidimensional, socioecological plasticity in future empirical research, which our results suggest is likely to play a key role in shaping socio-eco-evolutionary dynamics (**Fig. 7**).

Game theoretic models have also provided key insights into the evolutionary causes and consequences of social plasticity, such as its central role in sustaining cooperation in repeated interactions (Avila et al., 2021; Van Cleve & Akçay, 2014), as well as in maximizing fitness across ecological scenarios when individuals benefit from adjusting to and coordinating with their social partners (Akçay et al., 2009; Yamaguchi & Iwasa, 2015). While these models often assume perfect inheritance of phenotypes to focus attention on evolutionary stability and convergence, our findings emphasize the importance of genetic variance in social G_{ψ} and socioecological plasticity G_{φ} as determinants of the rate of adaptive microevolution (**Eq. 5-10**, **Fig. 2, 5**) as well as the potential magnitude of socio-eco-evolutionary feedback (**Fig. 6**). In this regard, while our findings highlight fluctuating state-dependent selection as a fundamental driver of both social and ecological plasticity (**Eq. 3-4**, **Fig. 4**), they also demonstrate why the effects of social plasticity on genetic adaptation are unique in comparison to other forms of plasticity and require distinct theoretical consideration. Due to the influence of IGEs, selection on socially plastic traits causes coevolutionary responses in the traits of organisms as well as the traits expressed in their social environment (**Eq. 6-10**), further modifying the phenotypic consequences of genetic evolution in social environments (**Fig. 5-6**). Our findings extend prior IGE theory by identifying fluctuating frequency-dependent selection as the central driver of the evolution of social plasticity and adaptive IGEs (**Eq. 3-4, Fig. 4, Table S1**), as well as by demonstrating how ecological change shapes the expression of context dependent IGEs and their consequences for ongoing phenotypic change (**Fig. 2, 6C, Eq. S17-32**). Greater integration of social plasticity and IGEs into preexisting frameworks for the study of eco-evolutionary feedback (Lion, 2018) is a clear target for future research (**Fig. 7**).

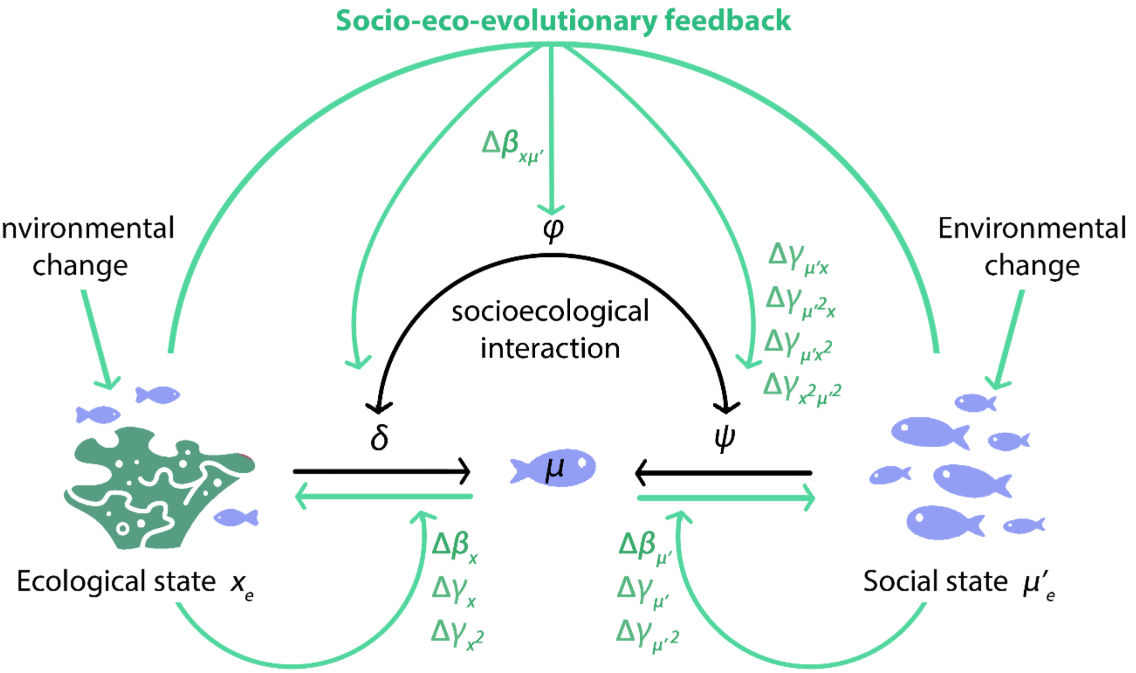
There are important limitations to our analysis that should be considered before extrapolating theoretical predictions for empirical study. To focus attention on the evolution of labile social plasticity in spatially heterogeneous environments, we ignored the well-established effects of imperfect cues and temporal fluctuations in the social environment (King & Hadfield, 2019). These factors will inevitably play a role in the eco-evolutionary dynamics of plasticity in natural populations, potentially driving populations toward distinct developmental strategies (Michel et al., 2014; Price et al., 2003; Tufto, 2015). Prior theory can be combined with nuanced consideration of a population's ecology and life history to extrapolate our general findings for social plasticity and generate more targeted empirical predictions. Relatedly, we took a rather "black box" analytic approach to modeling the expression and selection of plasticity, focusing on net selection of character states and SRNs irrespective of the details underlying the mechanistic pathways causing these effects. We did not consider the mechanistic basis of plasticity in detail beyond the weak constraints of a polygenic genetic architecture and continuous reaction norm, nor did we model the functional consequences of plasticity for distinct components of organismal performance, both of which will determine the proximal costs of producing and maintaining plastic responses across environments (Auld et al., 2010; Bergmann & McElroy, 2014; Dewitt et al., 1998; Haaland et al., 2021). While fitness costs of plasticity have not been consistently supported by prior research, most studies have also not accounted for condition-dependent fitness effects (De Lisle & Rowe, 2023).

This further emphasizes the importance of incorporating the (co)evolution of life history into future empirical and theoretical research on adaptive social plasticity. Relatedly, while we conceptualize SRN parameters as distinctly evolving complex traits for theoretical utility, the empirical value of this perspective will be contingent on the independence of the mechanisms determining parameter values within a given system (Futuyma, 2021). Plastic responses across complex environments will often be caused by common physiological and neurobiological pathways, such as hormonal signaling or generalized cognitive processes, that are generally regulated by highly pleiotropic genetic architectures and tend to develop and evolve in a modular fashion (Charvet et al., 2011; Heyland et al., 2005; McNamara & Houston, 2009; Watanabe et al., 2019; Wittman et al., 2021). Our results indicate a key role for fluctuating quadratic selection on character states, and thus correlational selection on SRN parameters, in the genetic integration of multiple dimensions of plasticity across multivariate social environments (**Eq. 4**, **Fig. 4**). However, recent work suggests that the genetic integration of quantitative traits in many clades is unlikely to be principally driven by a history of correlational selection (Dochtermann et al., 2023). Whether the mechanistic basis of socioecological plasticity is more likely to be a consequence of or rather a constraint on adaptive responses to correlational selection of SRNs thus remains unclear. Our quantitative genetic approach also relies on the convenient but oversimplifying assumption of a linear mapping between additive genetic and phenotypic variation. This linear mapping may lead to biased predictions about the microevolutionary trajectories of complex phenotypes regulated by highly nonlinear developmental dynamics (Milocco & Salazar-Ciudad, 2022).

While our results provide useful heuristic predictions for the effects of social plasticity on phenotypic adaptation and socio-eco-evolutionary feedback over microevolutionary timescales, they do not address the conditions under which social plasticity is expected to persist across macroevolutionary timescales. Prior theory provides clear hypotheses for time course of plasticity-led evolution during environmental change, predicting that plasticity is likely to be initially favored and subsequently disfavored while evolving toward an adaptive peak in a new environment (Kelly, 2019; Lande, 2009), contingent on the persistence of environmental change (Scheiner et al., 2017). The persistence of fluctuating frequency-dependent selection across generations is also expected to play a central role in determining the macroevolutionary trajectory of social plasticity, as well as the potential for socio-eco-evolutionary feedback to be sustained during environmental change, with stronger fluctuations expected to produce more chaotic dynamics (Chevin et al., 2022). Comparative evidence suggests that weak to moderate frequency-dependent selection is common in natural populations (Gómez-Llano et al., 2024), but the typical scale and regularity of spatiotemporal fluctuations in frequency-dependent selection is currently unknown. Therefore, as with phenotypic plasticity more generally, future studies aiming to explain and accurately predict variation in social plasticity across taxa will require closer attention to the interaction between mechanisms of social plasticity, the magnitude and timescale of frequency-dependent fluctuations in contemporary social environments, as well as the multigenerational dynamics of these fluctuations across early and later stages of environmental adaptation.

In our rapidly changing world, organisms increasingly face complex environmental challenges arising from a host of intersecting ecological and anthropogenic factors such as resource depletion, habitat fragmentation, and climate warming, among others, which are collectively accelerating rates of species extinction and biodiversity loss across the globe (Eberle et al., 2023). Social interactions play a central role in determining how populations respond to such challenges. Cooperation in reproduction, for example, can buffer against habitat degradation, promote colonization of harsh environments, and generate evolutionary rescue (Griesser et al., 2017; Henriques & Osmond, 2020; Martin et al., 2020); the adaptation of conflict and competition can in turn deteriorate the environment and precipitate ecological tipping points that drive rapid population collapse (Matsuda & Abrams, 1994; Parvinen & Dieckmann, 2013; Ratzke et al., 2018). Our findings demonstrate the importance of plasticity in shaping the evolutionary consequences of such social interactions, motivating greater attention to social plasticity as a functional mechanism channeling the rate and direction of adaptive social evolutionary processes on observable timescales in response to environmental change. Due to the dual effects of socioecological states on the expression and adaptation of phenotypes, selection on SRNs may be a potent but underappreciated driver of rapid contemporary adaptation and socio-eco-evolutionary feedback in heterogeneous environments (**Fig. 7**).

Fig 7. Pathways of socio-eco-evolutionary feedback.



Footnote. Black arrows indicate causal effects on phenotypic expression, while green arrows indicate potential pathways of socio-eco-evolutionary feedback due to the dual consequences of the social environment for phenotypic expression and selection (**Fig. 3-4**). Social environments can generate feedback effects on trait expression via social plasticity ψ, enhancing or diminishing the total additive genetic variance in the phenotype (**Fig. 2**), while also determining the magnitude of selection on the SRN parameters ψ and φ via fluctuating frequency-dependent selection on character states (**Eq. 3-4**, **Fig. 4**), changing the rate of phenotypic adaptation (**Fig. 5**) and potentiating intergenerational feedback cycles between social ecological and evolutionary processes (**Fig. 6a**). Ecological states can also modify the evolution of social plasticity through effects on δ and φ that change the magnitude of heritable variation in the phenotype (**Fig. 2, 6c**) and the direction of fluctuating selection on character states (**Fig. 6b**). Any exogeneous causes of environmental change can also accelerate or dampen these processes by affecting the state of and magnitude of fluctuations in the social environment.

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Supplementary materials for:

Frequency-dependence favors social plasticity and facilitates socio-eco-evolutionary feedback in fluctuating environments

Jordan S. Martin, David F. Westneat, Alastair J. Wilson,
Niels J. Dingemanse, Yimen Araya-Ajoy

Contents

Phenotype and fitness models

Our social reaction norm (SRN) model builds on prior work by de Jong (1995), who explored symmetries between character state and reaction models of phenotypic plasticity across spatially heterogeneous environments. A Taylor series can be used to effectively approximate how the continuous output of a function changes in response to a set $\boldsymbol{e}$ of state variables. Here the variables of interest characterize the social and ecological states of the social environment (**Fig. 1, 3**). For some function *g*, the general form is

$$g(\boldsymbol{e}) = g_0 + \nabla \boldsymbol{g}^{\top} \boldsymbol{e} + \frac{1}{2} \boldsymbol{e}^{\top} \boldsymbol{H} \boldsymbol{e}_i + \cdots \frac{1}{n!} \boldsymbol{e}^{\top} \boldsymbol{N} \boldsymbol{e} \qquad (\textbf{Eq. S1})$$

The series involves partial derivatives specified from the first to the *n*th polynomial order required for effectively approximating the underlying function. As explained in the main text, we simplify the full series to focus attention on linear phenotype functions of the form

$$p(\boldsymbol{e}) = p_0 + \nabla \boldsymbol{p}^{\top} \boldsymbol{e} \qquad (\textbf{Eq. S2. 1})$$

Where the output $p(\boldsymbol{e})$ corresponds to the character state η_e in social environment $\boldsymbol{e}$, p_0 is the expected character state at $\boldsymbol{e} = \boldsymbol{0}$, and $\nabla \boldsymbol{p}$ is the gradient operator describing how the first partial derivative of the output changes in response to variation in each state composing $\mathbf{e}$. For a Gaussian response with zero-centered, multivariate normal environmental effects and SRN parameters, the phenotype model can be expressed as a linear function of constant coefficients, giving the SRN model (**Eq. 2**) in the main text.

$$\eta_e = p(\boldsymbol{e}) = \mu + \psi \mu_e' + \delta x_e + \varphi \mu_e' x_e \qquad (\textbf{Eq. S2. 2})$$

For fitness, we consider quadratic functions of the form

$$f(\boldsymbol{e}) = f_0 + \nabla \boldsymbol{f}^{\top} \boldsymbol{e} + \frac{1}{2} \boldsymbol{e}^{\top} \boldsymbol{H} \boldsymbol{e} \qquad (\textbf{Eq. S3. 1})$$

where $\boldsymbol{H}$ is the Hessian matrix. Expanding to linear notation to clearly distinguish first- and second-order fitness effects clarifies the connection between different components of state-dependent selection

$$f(\boldsymbol{e}) = f_0 + \begin{pmatrix} \frac{\partial f}{\partial \mu'} & \frac{\partial f}{\partial x} & \frac{\partial f}{\partial \mu' x} \end{pmatrix} \begin{pmatrix} \Delta\mu' \\ \Delta x \\ \Delta\mu' x \end{pmatrix} \qquad (\mathbf{Eq. S3.2})$$

$$+\frac{1}{2}\begin{pmatrix} \Delta\mu' & \Delta x & \Delta\mu' x \end{pmatrix} \begin{pmatrix} \frac{\partial^2 f}{\partial \mu'^2} & \frac{\partial^2 f}{\partial \mu' \partial x} & \frac{\partial^2 f}{\partial \mu' \partial \mu' x} \\ \frac{\partial^2 f}{\partial \mu' \partial x} & \frac{\partial^2 f}{\partial x^2} & \frac{\partial^2 f}{\partial x \partial \mu' x} \\ \frac{\partial^2 f}{\partial \mu' \partial \mu' x} & \frac{\partial^2 f}{\partial x \partial \mu' x} & \frac{\partial^2 f}{\partial \mu'^2 x^2} \end{pmatrix} \begin{pmatrix} \Delta\mu' \\ \Delta x \\ \Delta\mu' x \end{pmatrix}$$

$$= f_0 + \frac{\partial f}{\partial \mu'}\Delta\mu' + \frac{\partial f}{\partial x}\Delta x + \frac{\partial f}{\partial \mu\, x}\Delta\mu' x +$$

$$\frac{1}{2}\left(\frac{\partial^2 f}{\partial \mu'^2}\Delta\mu'^2 + \frac{\partial^2 f}{\partial x^2}\Delta x^2 + \frac{\partial^2 f}{\partial \mu' x}[\Delta\mu' x]^2\right.$$

$$\left. + 2\left[\frac{\partial^2 f}{\partial \mu' \partial x}\Delta\mu' \Delta x + \frac{\partial^2 f}{\partial \mu' \partial \mu' x}\Delta\mu' \Delta\mu' x + \frac{\partial^2 f}{\partial x \partial \mu' x}\Delta x \Delta\mu' x\right]\right)$$

Terms containing $\Delta\mu'$ reflect changes in selection due to the social state, Δx terms capture changes in selection due to the ecological state, and $\Delta\mu' x$ terms describe changing selection due to the interactive effects of the socioecological state.

As with the phenotype model (**Eq. S2.2**), assuming zero-centered, multivariate normal environmental effects and SRN parameters allows for translating the fitness model into a linear function with directional and quadratic selection gradients replacing partial derivatives (Lande & Arnold, 1983). Dropping delta notation from **Eq. S3** because we assume that social environments are zero-centered $\bar{\bar{\boldsymbol{e}}} = \mathbf{0}$ (see below), fitness across social environments can be expressed by

$$f(\boldsymbol{e}) = \beta_0 + \Delta\beta_{\mu'}\mu' + \Delta\beta_x x + \Delta\beta_{\mu' x}\mu' x \qquad (\mathbf{Eq. S4.1})$$

$$+\Delta\gamma_{\mu' x}\mu' x + \Delta\gamma_{\mu'^2 x}\mu'^2 x + \Delta\gamma_{\mu' x^2}\mu' x^2$$

$$+\frac{1}{2}\left(\gamma_0 + \Delta\gamma_{\mu'^2}\mu'^2 + \Delta\gamma_{x^2}x^2 + \Delta\gamma_{\mu'^2 x^2}\mu'^2 x^2\right)$$

For clarity, f_0 is now partitioned into expected directional β_0 and quadratic γ_0 selection effects in the average, zero-centered social environment. The $\Delta\beta$ terms quantify changes in linear selection (∂) due to environmental states $\mu', x, \mu' x$, while $\Delta\gamma$ terms quantify changes in quadratic selection (∂^2) due to squared environmental states $\mu'^2, x^2, \mu'^2 x\ \mu' x^2$, $\mu'^2 x^2$. We expand beyond the standard order of the Taylor series to also include $\Delta\gamma_{\mu'}\mu', \Delta\gamma_x x$ terms capturing the effects of μ', x on quadratic selection

$$f(\boldsymbol{e}) = \beta_0 + \Delta\beta_{\mu'}\mu' + \Delta\beta\, x\ + \Delta\beta_{\mu' x}\mu' x \qquad (\textbf{Eq. S4.2})$$

$$+\Delta\gamma_{\mu' x}\mu' x + \Delta\gamma_{\mu'^2 x}\mu'^2 x + \Delta\gamma_{\mu' x^2}\mu' x^2$$

$$+\frac{1}{2}\left(\gamma_0 + \Delta\gamma_{\mu'}\mu' +\ \Delta\gamma_x x + \Delta\gamma_{\mu'^2}\mu'^2 + \Delta\gamma_{x^2}x^2 + \Delta\gamma_{\mu'^2 x^2}\mu'^2 x^2\right)$$

Mean-scaling by average fitness and centering on second moments of the Gaussian variables $\mathrm{E}(z^2) = V_z$ gives the individual fitness model used for analysis, which predicts relative fitness w_e in social environment *e* as a function of average β_η, γ_η selection gradients and deviations in selection $\boldsymbol{\Delta\beta}, \boldsymbol{\Delta\gamma}$ on character state η_e

$$w_e = 1 + \left(\beta_\eta + \Delta\beta_{\mu'}\mu'_e + \Delta\beta_x x_e + \Delta\beta_{\mu' x}\mu'_e x_e\right)\eta_e \qquad (\textbf{Eq. S5})$$

$$+\ \frac{1}{2}(\gamma_\eta + \Delta\gamma_{\mu'}\mu'_e + \Delta\gamma_x x_e + \Delta\gamma_{\mu' x}\mu'_e x_e)\left(\eta_e^2 - V_\eta\ \right)$$

$$+\frac{1}{4}\left(\Delta\gamma_{\mu'^2}\left[\mu_e'^2 - V_{\mu'}\right] + \Delta\gamma_{x^2}[x_e^2 - V_x] + \Delta\gamma_{\mu'^2 x}\left[\mu_e'^2 - V_{\mu'}\right]x_e + \Delta\gamma_{\mu' x^2}[x_e^2 - V_x]\mu'\right)\left(\eta_e^2 - V_\eta\ \right)$$

$$+\frac{1}{8}\left(\Delta\gamma_{\mu'^2 x^2}\left[\mu_e'^2 - V_{\mu'}\right][x_e^2 - V_x]\right)\left(\eta_e^2 - V_\eta\ \right)$$

Fractions $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}$ scale the expanded **Eq S4.2** to account for the multiplicative powers $\eta_e^2, \mu_e'^2, x_e^2$ involved in each selection effect. Now β_η quantifies average linear selection on the character state η_e, while γ_η quantifies average quadratic selection on the squared character state η_e^2. Additive deviations across social environments are captured by $\boldsymbol{\Delta\beta}, \boldsymbol{\Delta\gamma}$. Relationships (**Table S1**) between partial derivatives of the fitness function and selection gradients on character states and SRNs are derived from **Eq. S5** by partial differentiation of the fitness function with respect to the SRN parameters, as well as using covariance mathematics (see below). Demographic stochasticity, missing variables, and measurement error were not relevant for our theoretical goals and so were ignored as sources of residual variation in individual fitness.

Table S1. Analytic relationships between partial derivates and selection gradients.

Partial derivative of fitness function	Selection gradient on character state	Selection gradient on social reaction norm
f_0	β_η, γ_η	$\beta_\mu = \beta_\eta, \gamma_\mu = \gamma_\eta$
$\frac{\partial f}{\partial \mu'} \Delta\mu'$	$\Delta\beta_{\mu'}$	$\beta_\psi = \Delta\beta_{\mu'} V_{\mu'}$
$\frac{\partial f}{\partial x} \Delta x$	$\Delta\beta_x$	$\beta_\delta = \Delta\beta_x V_x$
$\frac{\partial f}{\partial \mu\, x} \Delta\mu' x$	$\Delta\beta_{\mu' x}$	$\beta_\varphi = \Delta\beta_{\mu' x} V_{\mu'} V_x$
$\frac{\partial^2 f}{\partial \mu'^2} \Delta\mu'^2$	$\Delta\gamma_{\mu'^2}$	$\gamma_\psi = \Delta\gamma_{\mu'^2} V_{\mu'}^2$
$\frac{\partial^2 f}{\partial x^2} \Delta x^2$	$\Delta\gamma_{x^2}$	$\gamma_\delta = \Delta\gamma_{x^2} V_x^2$
$\frac{\partial^2 f}{\partial \mu' x} [\Delta\mu' x]^2$	$\Delta\gamma_{\mu'^2 x^2}$	$\gamma_\varphi = \Delta\gamma_{\mu'^2 x^2} V_{\mu'}^2 V_x^2 +$ $\Delta\gamma_{\mu'^2} V_{\mu'}^2 V_x + \Delta\gamma_{x^2} V_{\mu'} V_x^2$
$\frac{\partial^2 f}{\partial \mu'} \Delta\mu'$	$\Delta\gamma_{\mu'}$	$\gamma_{\mu\psi} = \Delta\gamma_{\mu'} V_{\mu'}$
$\frac{\partial^2 f}{\partial x} \Delta x$	$\Delta\gamma_x$	$\gamma_{\mu\delta} = \Delta\gamma_x V_x$
$\frac{\partial^2 f}{\partial \mu' \partial x} \Delta\mu' \Delta x$	$\Delta\gamma_{\mu' x}$	$\gamma_{\psi\delta} = \gamma_{\mu\varphi} = \Delta\gamma_{\mu' x} V_{\mu'} V_x$
$\frac{\partial^2 f}{\partial \mu' \partial \mu' x} \Delta\mu' \Delta\mu' x$	$\Delta\gamma_{\mu'^2 x}$	$\gamma_{\psi\varphi} = \Delta\gamma_{\mu'^2 x} V_{\mu'}^2 V_x + \Delta\gamma_x V_{\mu'} V_x$
$\frac{\partial^2 f}{\partial x \partial \mu' x} \Delta x \Delta\mu' x$	$\Delta\gamma_{\mu' x^2}$	$\gamma_{\delta\varphi} = \Delta\gamma_{\mu' x^2} V_{\mu'} V_x^2 + \Delta\gamma_{\mu'} V_{\mu'} V_x$

Note. Light grey rows mark partial derivatives containing μ' that shape the distribution of ψ and thus average social plasticity across ecological states. Dark grey rows mark partial derivatives containing $\mu' x$ that shape the distribution of φ and thus changes in social plasticity across ecological states. Relationships hold under the linear SRN (**Eq. 1-2, S2**) and quadratic fitness (**Eq. S5**) functions explored in the present study.

Centering the social environment

Throughout the analysis, we assume that the average ecological $\bar{x} = 0$ and social state $\bar{\mu}' = 0$ are zero. If the mean social environment was not zero-centered in this way, any source of average directional selection on the character state across social environments would cause directional selection on all linear SRN parameters. This is a consequence of the character state being a composite phenotype determined by the linear sum of SRN parameter effects (**Eq. 1-2, S2**), so that if $\bar{\mu}' \neq 0$ and $\bar{x} \neq 0$, selection acting to increase the expected phenotype in the average environment $\bar{e}$ would affect any parameters contributing to the average character state $\eta_{\bar{e}}$. This is a classic result from quantitative genetic theory (Gavrilets & Scheiner, 1993), which tells us that the evolution of social plasticity can be promoted as a correlated response to directional selection on the character state. Here we are primarily interested in establishing the general conditions under which selection will directly target the component of character states attributable to SRN plasticity parameters ψ, δ, and φ. Therefore, we fixed $\bar{\mu}' = \bar{x} = 0$ for the analysis to eliminate correlative effects caused by directional selection on the phenotype, and to in turn isolate the specific conditions under which selection directly favors the adaptive evolution of social plasticity per se. This leads to interpretation of μ in the SRN function (**Eq. 2**) as the focal individual's intrinsic trait value independent of variation in the social environment, which may nonetheless include mean environmental effects that do not vary among individuals or within microhabitats. The same considerations apply with respect to quadratic selection in the average environment, motivating centering of the squared character state on its expectation $E(\eta^2) = V_\eta$ (i.e. the phenotypic variance of character states) as well as the squared social environmental values on their expectations $E(\mu'^2) = V_{\mu'}$ and $E(x^2) = V_x$ (**Eq. S5**). Doing so similarly isolates the conditions under which quadratic selection will directly target the (co)variances of the SRN parameters regulating social and ecological plasticity, independently of average quadratic effects that cause selection on all SRN parameters influencing phenotypic variance. Finally, we also ignored assortment in social environments $C_{\mu,\mu'} = 0$ to explore selection on social plasticity irrespective of population structure. Analytic results below provide the means for straightforwardly extrapolating our findings to more complex scenarios.

Analytic results

Under multivariate normality, results presented in **Table S1** and **Eq. 3-10** can be derived analytically by applying covariance mathematics to **Eq. 2** and **Eq. S5**, following the Roberts-Price identity (Robertson, 1966; Price, 1972). For a single phenotype, the adaptive response in the mean trait value $\bar{\eta}_{\mathrm{e}}$ within a given social environment *e* is determined by the magnitude of selection on the phenotype $\beta_{\eta|e}$ expected in *e* and the additive genetic variance η_α of the phenotype in *e*

$$\Delta\bar{\eta}_{\mathrm{e}} = \mathrm{cov}\left(w_e, \eta_{a|e}\right) = s_{|e}\frac{\mathrm{var}(\eta_{\alpha|e})}{\mathrm{var}(\eta_{|e})} = \beta_{\eta|e}\mathrm{var}\left(\eta_{a|e}\right) \qquad (\textbf{Eq. S6})$$

Where *w* is relative individual fitness, *s* is the selection differential, and | indicates that the magnitudes of total additive genetic variance and selection are conditional on the population under consideration being in *e*. Note that we switch $\mathrm{cov}(\,)$ and $\mathrm{var}(\,)$ notation interchangeably with C_{p_1,p_2} and V_p (or G_{p_1,p_2} and G_p for genetic (co)variances) throughout this supplement to enhance the clarity or efficiency of mathematical expressions.

For a multivariate phenotype such as the SRN expressed across social environments (**Fig. 1**), the adaptive response in the mean trait value is determined both by direct selection on each SRN parameter across environments as well as any indirect selection caused by genetic covariance among SRN parameters. For example, plugging the SRN intercept μ into the Price-Roberts identity, we find

$$\Delta\bar{\mu} = \mathrm{cov}(w, \mu_a) = \beta_\mu \mathrm{var}(\mu_a) + \beta_\psi \mathrm{cov}(\mu_\alpha, \psi_\alpha) + \beta_\delta \mathrm{cov}(\mu_\alpha, \delta_\alpha) + \beta_\varphi \mathrm{cov}(\mu_\alpha, \varphi_\alpha) \quad (\textbf{Eq. S7})$$

As explained in **Eq. 5**, This result can be written more succinctly for all SRN parameters using the multivariate breeders' equation (Lande & Arnold, 1983), where $\boldsymbol{G_p}$ is a matrix of genetic (co)variances for SRN parameters

$$\begin{bmatrix}\Delta\bar{\mu}\\ \Delta\bar{\psi}\\ \Delta\bar{\delta}\\ \Delta\bar{\varphi}\end{bmatrix} = \boldsymbol{G_p}\boldsymbol{\beta_p}$$

Our goal is then to understand how variation in character state selection within a given social environment (**Eq. S6**) relates to expected patterns of multivariate selection on and adaptation of a population's SRN parameters across fluctuating microhabitats composed of heterogeneous social environments (**Eq. 5**), using the phenotype (**Eq. 2, S2**) and fitness models (**Eq. S5**) determining state-dependent expression and selection of individuals' character states. We treated deviations in selection due to the local social environment $\boldsymbol{\Delta\beta}, \boldsymbol{\Delta\gamma}$ as population constants, reflecting the biologically motivated assumption that causal effects of phenotype on fitness are fixed under a given socioecological scenario. In turn, we modeled fluctuations in the phenotype and ecology of the social environment as independent random variables $\boldsymbol{\mu}' \sim N(0, V_{\mu'})$ and $\boldsymbol{x} \sim N(0, V_x)$. We then used covariance mathematics to derive and validate the analytic relationships of interest. These results can be independently derived and validated using numeric methods. See https://github.com/Jordan-Scott-Martin/SRNselection for relevant R code.

Deriving selection gradients

The directional selection differential on character states across social environments can also be expressed in terms of the SRN parameters determining these values. Ignoring quadratic effects on fitness, the selection differential is given by

$$\mathrm{s}_{|\boldsymbol{\gamma}=0} = \mathrm{cov}\left(\boldsymbol{w}_{|\boldsymbol{\gamma}=0}, \boldsymbol{\eta}\right) \qquad (\mathbf{Eq.\,S8})$$

$$= \mathrm{cov}\begin{pmatrix} 1 + \left(\beta_\eta + \Delta\beta_{\mu'}\boldsymbol{\mu}' + \Delta\beta_x\boldsymbol{x} + \Delta\beta_x\boldsymbol{\mu}' \circ \boldsymbol{x}\right) \circ \boldsymbol{\eta}, \\ \boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x} \end{pmatrix}$$

$$= \mathrm{cov}\begin{pmatrix} \beta_\eta(\boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}) \\ +\Delta\beta_{\mu'}\boldsymbol{\mu}' \circ (\boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}) \\ +\Delta\beta_x\boldsymbol{x} \circ (\boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}) \\ +\Delta\beta_{\mu'x}\boldsymbol{\mu}' \circ \boldsymbol{x} \circ (\boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}), \\ \boldsymbol{\mu} + \boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x} \end{pmatrix}$$

Bold font is used to distinguish population vectors for random variables (individual phenotypes and social environmental values) from scalar constants (selection gradients), and $\circ$ is used to indicate element-wise multiplication of these vectors (Hadamard products). Note that *e* subscripts are now removed from the character states and environmental variables because the vectors $\boldsymbol{\eta}, \boldsymbol{\mu}', \boldsymbol{x}$ contains all values across all social environments. Assuming that $\bar{\mu} = \bar{\psi} = \bar{\delta} = \bar{\varphi} = \bar{\mu}' = \bar{x} = 0$ and $\mathrm{cov}(\boldsymbol{\mu}', \boldsymbol{x}) = \mathrm{cov}(\boldsymbol{\mu}, \boldsymbol{\mu}') = 0$ simplifies results and is biologically motivated by our interest in isolating conditions under which selection directly targets each parameter, independently of population structure or mean effects generating selection on SRN parameters as a correlated response to selection on the character state (see previous section). As is clear from **Eq. S8**, without centering, all SRN parameters experience selection when there is directional selection on the phenotype

$$\beta_\eta \eta_{\bar{e}} = \beta_\eta(\mu + \psi\,\bar{\mu}' + \delta\,\bar{x} + \varphi\,\bar{\mu}'\bar{x}) = \beta_\eta\mu + \beta_\eta\psi\,\bar{\mu}' + \beta_\eta\delta\,\bar{x} + \beta_\eta\varphi\,\bar{\mu}'\bar{x} \qquad (\mathbf{Eq. S9})$$

because of the correlated response generated by non-zero means. As previously noted, the same considerations apply to squared character and environmental states, focusing attention on stochastic fluctuations around the mean social environment.

We can first consider independently distributed SRN parameters to isolate direct from indirect selection gradients on fitness, which produces covariance relationships that are conditional forms of the simple univariate case of the Roberts-Price identity (**Eq. S6**). We start with the SRN intercept μ conditionally independent of the SRN slopes, deriving the directional selection gradient β_μ from the fitness model (**Eq. S5**), the definition of covariance $\mathrm{cov}(\boldsymbol{w},\boldsymbol{\mu}) = E(\boldsymbol{w} \circ \boldsymbol{\mu}) - E(\boldsymbol{w})E(\boldsymbol{\mu})$, and the assumptions $\mathrm{cov}(\boldsymbol{\mu},\boldsymbol{\mu}') = \mathrm{cov}(\boldsymbol{\mu},\boldsymbol{x}) = \mathrm{cov}(\boldsymbol{\mu},\boldsymbol{\mu}'\boldsymbol{x}) = 0$, such that

$$\mathrm{cov}(\boldsymbol{w},\boldsymbol{\mu})_{|\boldsymbol{\psi},\boldsymbol{\delta},\boldsymbol{\varphi}} = E\big(\beta_\eta[\boldsymbol{\mu} \circ \boldsymbol{\mu}]\big) = \beta_n \mathrm{E}(\boldsymbol{\mu}^{\mathbf{2}}) = \beta_\eta \mathrm{var}(\boldsymbol{\mu}) = \beta_\mu \mathrm{var}(\boldsymbol{\mu}) \qquad (\mathbf{Eq. S10})$$

where all other terms besides $\mathrm{E}(\boldsymbol{\mu}^{\mathbf{2}})$ are eliminated from $E(\boldsymbol{w} \circ \boldsymbol{\mu}) - E(\boldsymbol{w})E(\boldsymbol{\mu})$ due to being conditionally independent and multiplied by $E(\boldsymbol{\mu}) = 0$. It follows from **Eq. S6-7** that $\beta_\eta = \beta_\mu$, i.e., the SRN intercept directional selection gradient is equivalent to the average directional selection gradient on character states across social environments. Similarly, for social plasticity conditional on the other SRN parameters

$$\mathrm{cov}(\boldsymbol{w},\boldsymbol{\psi})_{|\boldsymbol{\mu},\boldsymbol{\delta},\boldsymbol{\varphi}} = E\big(\Delta\beta_\eta \boldsymbol{\mu}' \circ [\boldsymbol{\psi} \circ \boldsymbol{\psi} \circ \boldsymbol{\mu}']\big) \qquad (\mathbf{Eq. S11})$$

$$= \Delta\beta_{\mu'} \mathrm{E}(\boldsymbol{\mu}'^{\mathbf{2}})\mathrm{E}(\boldsymbol{\psi}^{\mathbf{2}}) = \Delta\beta_{\mu'} \mathrm{var}(\boldsymbol{\mu}')\mathrm{var}(\boldsymbol{\psi}) = \beta_\psi \mathrm{var}(\boldsymbol{\psi})$$

which again follows from the assumptions that $\mathrm{cov}(\boldsymbol{\psi},\boldsymbol{\mu}') = \mathrm{cov}(\boldsymbol{\mu}',\boldsymbol{x}) = \mathrm{cov}(\boldsymbol{\mu}',\boldsymbol{\mu}'\boldsymbol{x}) = \mathrm{cov}(\boldsymbol{\mu}',\boldsymbol{\mu}'\boldsymbol{x}) = 0$ and $\bar{\psi} = \bar{\mu}' = 0$, which cause other terms in $E(\boldsymbol{w} \circ \boldsymbol{\psi}) - E(\boldsymbol{\psi})E(\boldsymbol{w})$ multiplied by $E(\boldsymbol{\psi}) = 0$ to be eliminated, showing that $\beta_\psi = \Delta\beta_{\mu'}\mathrm{var}(\boldsymbol{\mu}')$. This general approach can be used to derive directional selection gradients for all SRN parameters.

Incorporating covariance among traits allows for predicting within and among generation responses to selection that account for indirect selection effects. For instance, Using **Eq. S6-8**, consider the effects of phenotypic association among SRN intercepts and social plasticity on the selection differential for intercepts s_μ, conditional on ecological δ and socioecological φ plasticity.

$$\mathrm{cov}(\boldsymbol{w},\boldsymbol{\mu})_{|\boldsymbol{\delta},\boldsymbol{\varphi}} = s_{\mu|\boldsymbol{\delta},\boldsymbol{\varphi}} = \beta_\eta \mathrm{var}(\boldsymbol{\mu}) + \beta_\psi \mathrm{var}(\boldsymbol{\mu}')\mathrm{cov}(\boldsymbol{\mu},\boldsymbol{\psi}) \qquad (\mathbf{Eq.\,S12})$$

Assumptions such as the independent distribution of focal and partner trait values can be relaxed here to further consider how assortment and relatedness influence the adaptive response in SRN parameters (Martin & Jaeggi, 2022; McGlothlin et al., 2010). Full results for selection differentials on all SRN parameters can be calculated in this way by expanding **Eq. 3-4** in the main text, substituting in results from **Table S1** and the matrix $\boldsymbol{P_p}$ of phenotypic (co)variances among SRN parameters.

$$\begin{bmatrix} \mathrm{s}_{\overline{\mu}} \\ \mathrm{s}_{\psi} \\ \mathrm{s}_{\overline{\delta}} \\ \mathrm{s}_{\overline{\phi}} \end{bmatrix} = \boldsymbol{P_p}\boldsymbol{\beta}_{\mathbf{p}} = \begin{bmatrix} \beta_\mu V_\mu + \beta_\psi C_{\mu,\psi} + \beta_\delta C_{\mu,\delta} + \beta_\varphi C_{\mu,\varphi} \\ \beta_\mu C_{\psi,\mu} + \beta_\psi V_\psi + \beta_\delta C_{\psi,\delta} + \beta_\varphi C_{\psi,\varphi} \\ \beta_\mu C_{\delta,\mu} + \beta_\psi C_{\delta,\psi} + \beta_\delta V_\delta + \beta_\varphi C_{\delta,\varphi} \\ \beta_\mu C_{\varphi,\mu} + \beta_\psi C_{\varphi,\psi} + \beta_\delta C_{\varphi,\delta} + \beta_\varphi V_\varphi \end{bmatrix} \qquad (\mathbf{Eq.\,S13})$$
$$= \begin{bmatrix} \beta_\eta V_\mu + \Delta\beta_{\mu'} V_{\mu'} C_{\mu,\psi} + \Delta\beta_{x'} V_x C_{\mu,\delta} + \Delta\beta_{\mu' x} V_{\mu'} V_x C_{\mu,\varphi} \\ \beta_\eta C_{\psi,\mu} + \Delta\beta_{\mu'} V_{\mu'} V_\psi + \Delta\beta_{x'} V_x C_{\psi,\delta} + \Delta\beta_{\mu' x} V_{\mu'} V_x C_{\psi,\varphi} \\ \beta_\eta C_{\delta,\mu} + \Delta\beta_{\mu'} V_{\mu'} C_{\delta,\psi} + \Delta\beta_{x'} V_x V_\delta + \Delta\beta_{\mu' x} V_{\mu'} V_x C_{\delta,\varphi} \\ \beta_\eta C_{\varphi,\mu} + \Delta\beta_{\mu'} V_{\mu'} C_{\varphi,\psi} + \Delta\beta_{x'} V_x C_{\varphi,\delta} + \Delta\beta_{\mu' x} V_{\mu'} V_x V_\varphi \end{bmatrix}$$

Equivalent considerations apply for deriving the quadratic selection gradients with respect to the vector of squared character states across social environments.

$$\begin{gathered} \boldsymbol{\eta}^2 = \boldsymbol{\eta} \circ \boldsymbol{\eta} \qquad (\mathbf{Eq.\,S14}) \\ = \boldsymbol{\mu}^2 + \boldsymbol{\psi}^2 \circ \boldsymbol{\mu}'^2 + \boldsymbol{\delta}^2 \circ \boldsymbol{x}^2 + \boldsymbol{\varphi}^2 \circ \boldsymbol{\mu}'^2 \circ \boldsymbol{x}^2 \\ +2\boldsymbol{\mu} \circ (\boldsymbol{\psi} \circ \boldsymbol{\mu}' + \boldsymbol{\delta} \circ \boldsymbol{x} + \boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}) \\ +2\boldsymbol{\psi} \circ (\boldsymbol{\varphi} \circ \boldsymbol{\mu}'^2 \circ \boldsymbol{x}) \\ +2\boldsymbol{\delta} \circ (\boldsymbol{\varphi} \circ \boldsymbol{\mu}' \circ \boldsymbol{x}^2) \\ +2(\boldsymbol{\psi} \circ \boldsymbol{\mu}' \circ \boldsymbol{\delta} \circ \boldsymbol{x}) \end{gathered}$$

The large number of terms makes analytic results for the SRN quadratic gradients more cumbersome to derive and express, particularly when SRN parameters and environmental states are not zero-centered.

Consider the quadratic gradient on SRN intercepts, again conditioning on other SRN parameters to ignore indirect selection effects

$$\mathrm{cov}(\boldsymbol{w},\boldsymbol{\mu^2})_{|\boldsymbol{\psi},\boldsymbol{\delta},\boldsymbol{\varphi}} = E(\boldsymbol{w}\circ\boldsymbol{\mu^2}) - E(\boldsymbol{w})E(\boldsymbol{\mu^2}) \qquad (\textbf{Eq. S15})$$

$$= \mathrm{E}\left(\boldsymbol{\mu^2} + \frac{1}{2}\gamma_n\boldsymbol{\mu^2}\circ\boldsymbol{\mu^2} - \mathrm{var}(\boldsymbol{\mu})\boldsymbol{\mu^2}\right) - \mathrm{E}(\boldsymbol{\mu^2})$$

$$= \mathrm{E}(\boldsymbol{\mu^2}) + \frac{1}{2}\gamma_n\left(\mathrm{E}(\boldsymbol{\mu^4}) - \mathrm{var}(\boldsymbol{\mu})\mathrm{E}(\boldsymbol{\mu^2})\right) - \mathrm{E}(\boldsymbol{\mu^2})$$

$$= \frac{1}{2}\gamma_n(\mathrm{E}(\boldsymbol{\mu^4}) - \mathrm{var}(\boldsymbol{\mu})^{\mathbf{2}})$$

$$= \frac{1}{2}\gamma_n(3\mathrm{var}(\boldsymbol{\mu})^2 - \mathrm{var}(\boldsymbol{\mu})^2)$$

$$= \frac{1}{2}\gamma_n 2\mathrm{var}(\boldsymbol{\mu})^{\mathbf{2}} = \gamma_n\mathrm{var}(\boldsymbol{\mu})^{\mathbf{2}} = \gamma_\mu\mathrm{var}(\boldsymbol{\mu})^{\mathbf{2}}$$

where $\mathrm{E}(\boldsymbol{w}) = 1$ and $\mathrm{E}(\boldsymbol{\mu^2}) = \mathrm{var}(\boldsymbol{\mu})$ is the only random individual component in $\mathrm{var}(\boldsymbol{\eta}) = \mathrm{E}(\boldsymbol{\eta^2})$ due to conditioning on the other SRN parameters. This result relies on the fact that, under multivariate normality, the fourth moment $\mathrm{E}(\boldsymbol{\mu^4})$ can be expressed in terms of the second moment $3\mathrm{var}(\boldsymbol{\mu})^2$ (Winkelbauer, 2012), which is useful for deriving quadratic gradients and predicting the adaptive response in **G** (**Eq. 8-10**; Lande & Arnold, 1983). The same approach can be taken to deriving the quadratic gradient on social plasticity ψ. Conditioning on other parameters, the phenotypic variance of character states arises from the average effects of social plasticity $V_{\mu'}V_\psi$. The expectation for relative fitness is then given by

$$E(w)_{|\boldsymbol{\mu},\boldsymbol{\delta},\boldsymbol{\varphi}} = 1 + \frac{1}{2}\Delta\gamma_{\mu'}\mathrm{E}\left(\psi^2\mu'^2 - V_{\mu'}V_\psi\right) + \frac{1}{4}\Delta\gamma_{\mu'^2}\mathrm{E}\left(\left[\mu'^2 - V_{\mu'}\right]\left[\psi^2\mu'^2 - V_{\mu'}V_\psi\right]\right) \quad (\textbf{S16.1})$$

$$= 1 + \frac{1}{2}\Delta\gamma_{\mu'}\mathrm{E}\left(\psi^2\mu'^2 - V_{\mu'}V_\psi\right) + \frac{1}{4}\Delta\gamma_{\mu'^2}\mathrm{E}\left(\mu'^4\psi^2 - \mu'^2V_{\mu'}V_\psi - V_{\mu'}\psi^2\mu'^2 + V_{\mu'}^2V_\psi\right)$$

$$= 1 + \frac{1}{2}\Delta\gamma_{\mu'}\left(V_{\mu'}V_\psi - V_{\mu'}V_\psi\right) + \frac{1}{4}\Delta\gamma_{\mu'^2}\left(3V_{\mu'}^2\mathrm{V}_\psi - V_{\mu'}^2V_\psi - V_{\mu'}^2V_\psi + V_{\mu'}^2V_\psi\right)$$

$$= 1 + \frac{1}{4}\Delta\gamma_{\mu'^2}2V_{\mu'}^2\mathrm{V}_\psi$$

$$= 1 + \frac{1}{2}\Delta\gamma_{\mu'^2} V_{\mu'}^2 \mathrm{V}_\psi$$

We see that the nonlinear $\Delta\gamma_{\mu'^2}$ rather than linear $\Delta\gamma_{\mu'}$ component of frequency-dependent quadratic selection is what determines the expectation of fitness with respect to quadratic selection on social plasticity γ_ψ. It follows that

$$\mathrm{E}(\boldsymbol{w})\mathrm{E}(\boldsymbol{\psi}^{\mathbf{2}})_{|\boldsymbol{\mu},\boldsymbol{\delta},\boldsymbol{\varphi}} = \mathrm{E}(\psi^2) + \frac{1}{2}\Delta\gamma_{\mu'^2} E(\psi^2) V_{\mu'}^2 \mathrm{V}_\psi \qquad (\mathbf{S16.2})$$

$$= V_\psi + \frac{1}{2}\Delta\gamma_{\mu'^2} V_{\mu'}^2 \mathrm{V}_\psi^2$$

and

$$\mathrm{E}(\boldsymbol{w} \circ \boldsymbol{\psi}^{\mathbf{2}})_{|\boldsymbol{\mu},\boldsymbol{\delta},\boldsymbol{\varphi}} = E(\psi^2) + \frac{1}{4}\Delta\gamma_{\mu'^2}\left(\mathrm{E}(\mu'^4)\mathrm{E}(\psi^4) - V_{\mu'}\mathrm{E}(\psi^4)\mathrm{E}(\mu'^2)\right) \qquad (\mathbf{S16.3})$$

$$= V_\psi + \frac{1}{4}\Delta\gamma_{\mu'^2}\left(9V_\psi^2 V_{\mu'}^2 - 3V_\psi^2 V_{\mu'}^2\right) = V_\psi + \frac{3}{2}\Delta\gamma_{\mu'^2} V_{\mu'}^2 V_\psi^2$$

Putting this together

$$\mathrm{cov}(\boldsymbol{w}, \boldsymbol{\psi}^{\mathbf{2}})_{|\boldsymbol{\mu},\boldsymbol{\delta},\boldsymbol{\varphi}} = E(\boldsymbol{w} \circ \boldsymbol{\psi}^{\mathbf{2}}) - E(\boldsymbol{w})E(\boldsymbol{\psi}^{\mathbf{2}}) \qquad (\mathbf{Eq.\,S16.4})$$

$$= \left(V_\psi + \frac{3}{2}\Delta\gamma_{\mu'^2} V_{\mu'}^2 V_\psi^2\right) - \left(V_\psi + \frac{1}{2}\Delta\gamma_{\mu'^2} V_{\mu'}^2 \mathrm{V}_\psi^2\right)$$

$$= \Delta\gamma_{\mu'^2} V_{\mu'}^2 V_\psi^2 = \gamma_\psi V_{\mu'}^2$$

such that $\gamma_\psi = \Delta\gamma_{\mu'^2} V_{\mu'}^2$ (**Table S1**). This shows that when frequency-dependent effects on fitness change in response to extreme trait values $\Delta\gamma_{\mu'^2}$, shifting the curvature of the adaptive landscape across social environments (**Fig. 3**), fluctuating social environments $V_{\mu'}^2 > 0$ cause direct quadratic selection on ψ, acting to shrink or magnify variation among individuals attributable to social plasticity. The same considerations and general approach apply for deriving the remaining quadratic gradients in **Table S1**.

The genetic (co)variance of context dependent DGEs and IGEs

In **Fig. 2**, we consider how SRN parameters regulating plasticity affect the total additive genetic variation available to natural selection through direct genetic effects (DGEs) and indirect genetic effects (IGEs). To derive these relationships, we begin by decomposing the phenotypic trait value for a given SRN parameter *p* into the sum of additive genetic $\alpha_j{\sim}N(\bar{p},G_p)$ and random environmental effects $e_j{\sim}N(0,E_p)$, where G_p is the additive genetic variance of SRN parameter *p,* such that $p_j = p_{\alpha j} + p_{e j}$ for individual *j*. Non-additive genetic effects due to dominance and epistasis are considered as a component of the environment (with respect to a given allele's additive effect) to focus attention on the heritable component of the phenotype (Fisher, 1930). Assuming plasticity occurs in response to the same phenotype being expressed, the deterministic IGE of individual *j*'s phenotype on the phenotype of a social partner *k* in social environment *e* is then given by

$$i_{j\rightarrow k} = (\psi'_{ak} + \varphi'_{\alpha k} x_e)\mu_{\alpha j} \qquad (\textbf{Eq. S17})$$

under the SRN model (**Eq. 2**), which does not functionally decompose temporal feedback among social partners' phenotypes (see main text). This demonstrates that IGEs will be contingent on the magnitude of x_e whenever social plasticity is affected by the environment φ because of socioecological interactions. Therefore, the magnitude of IGEs may be magnified or diminished across ecological contexts.

In fluctuating social environments, the distribution of social environments experienced by individuals will contribute to the distribution of individuals' character states and IGEs in the population. We derive analytic results for these distributions assuming multivariate normality of SRN parameters and environmental effects. To do so, we need to use definitions for the variance of the sum of two Gaussian random variables *a* and *b*,

$$V_{a+b} = V_a + V_b + 2C_{a,b} \qquad (\textbf{Eq. S18})$$

the variance for the product of two Gaussian random variables *a* and *b*,

$$V_{ab} = (\bar{a}\sqrt{V_b})^2 + (\bar{b}\sqrt{V_a})^2 + (\sqrt{V_a}\sqrt{V_b})^2\left(1 + \left[\frac{C_{a,b}}{\sqrt{V_a}\sqrt{V_b}}\right]^2\right) + 2\bar{a}\bar{b}C_{a,b} \qquad (\textbf{Eq. S19})$$

as well as the covariances of the product of Gaussian random variables *ab* and *cd*

$$C_{ab,cd} = \bar{a}\bar{c}C_{b,d} + \bar{a}\bar{d}C_{b,c} + \bar{b}\bar{c}C_{a,d} + \bar{b}\bar{d}C_{a,c} + C_{a,c}C_{b,d} + C_{a,d}C_{b,c} \qquad (\textbf{Eq. S20})$$

following Bohrnstedt and Goldberger (1969). We simplified these results for the case of random social interactions and environmental exposures to derive genetic (co)variances due to DGEs and IGEs. We start with the deterministic IGE of individual *j* on partner *k*, expanding **Eq. S17**

$$i_{j\rightarrow k} = \psi'_{ak}\mu_{\alpha_j} + \varphi'_{\alpha_k}x_e\mu_{\alpha_j}$$

The variance of these IGEs across the population will be a function of individuals' genetic variation in intrinsic trait values μ_a, the genetic variation of SRN slopes $\psi_\alpha{}'$, φ'_α in the social environment, as well as variation in the ecological component x_e of the social environment. From **Eq. S18**, the total variance of IGEs $G_{\boldsymbol{i}}$ will be due to the sum of the variance of the products $\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}$ and $\boldsymbol{\varphi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}$ and their covariance

$$G_i = \mathrm{var}\left(\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}} + \boldsymbol{\varphi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}\right) \qquad (\textbf{Eq. S21})$$

$$= \mathrm{var}\left(\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}\right) + \mathrm{var}\left(\boldsymbol{\varphi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}\right) + 2\mathrm{cov}\left(\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}, \boldsymbol{\varphi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}\right)$$

$$= G_{\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}} + G_{\boldsymbol{\varphi'_\alpha} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}} + 2G_{\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}, \boldsymbol{\varphi'_\alpha} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}}$$

where $'$ indicates the SRN slopes for individuals in the social environment of a focal individual. Using **Eq. S19** for the first term, we find

$$\mathrm{G}_{\boldsymbol{\psi'}_{\boldsymbol{\alpha}} \circ \boldsymbol{\mu}_{\boldsymbol{\alpha}}} = \left(\bar{\psi}'\sqrt{G_\mu}\right)^2 + \left(\bar{\mu}\sqrt{G_{\psi'}}\right)^2 + \left(\sqrt{G_{\psi'}}\sqrt{G_\mu}\right)^2 + \qquad (\textbf{Eq. S22})$$

$$\left(\sqrt{G_{\psi'}}\sqrt{G_\mu}\right)^2\left[\frac{G_{\psi',\mu}}{\sqrt{G_{\psi'}}\sqrt{G_\mu}}\right]^2 + 2\overline{\psi'}\overline{\mu'}G_{\psi',\mu}$$

where it is assumed that the mean additive genetic value determines the expected phenotypic mean of each SRN parameter, such that $\bar{\mu} = \bar{\mu}_a$, $\bar{\psi} = \bar{\psi}_a$, and $\bar{\varphi} = \bar{\varphi}_a$ (i.e. random environmental effects are zero-centered).

We simplify **Eq S.22** by assuming that interactions are random with respect to genetic values, so that the intercepts and slopes of focal individuals are independent of the intercepts and slopes of individuals in their social environment, $G_{\psi',\mu} = 0$, which removes the second line of the result. We also assume that individuals and their social partners engage in symmetric interactions and are not drawn from distinct subpopulations with different genetic means and (co)variances, so that e.g. $\bar{\psi} = \bar{\psi}'$ and $G_{\psi} = G_{\psi'}$. The variance then becomes

$$G_{\boldsymbol{\psi}'_{\alpha}\circ\boldsymbol{\mu}_{\alpha}} = \left(\bar{\psi}\sqrt{G_{\mu}}\right)^2 + \left(\bar{\mu}\sqrt{G_{\psi}}\right)^2 + \left(\sqrt{G_{\psi}}\sqrt{G_{\mu}}\right)^2 \qquad (\textbf{Eq. S23})$$

$$= \bar{\mu}^2 G_{\psi} + G_{\mu}\left(\bar{\psi}^2 + G_{\psi}\right)$$

Equivalent considerations apply to $\boldsymbol{\varphi}'_{\alpha} \circ \boldsymbol{x} \circ \boldsymbol{\mu}_{\alpha}$, with additional variance V_x due to stochastic ecological fluctuations, such that

$$G_{\boldsymbol{\varphi}'_{\alpha}\circ\boldsymbol{x}\circ\boldsymbol{\mu}_{\alpha}} = \bar{\mu}^2 G_{\varphi} V_x + G_{\mu} V_x\left(\bar{\varphi}^2 + G_{\varphi}\right) \qquad (\textbf{Eq. S24})$$

We can now use **Eq. S20** to calculate the third term in **Eq. S21**.

$$G_{\boldsymbol{\psi}'_{\alpha}\circ\boldsymbol{\mu}_{\alpha},\boldsymbol{\varphi}'_{\alpha}\circ\boldsymbol{x}\circ\boldsymbol{\mu}_{\alpha}} = V_x\left[\bar{\psi}\,\bar{\varphi}\,G_{\mu,\mu} + \bar{\psi}\,\bar{\mu}\,G_{\mu,\varphi'} + \bar{\mu}\,\bar{\varphi}\,G_{\mu,\psi'}\right] \qquad (\textbf{Eq. S25.1})$$

$$+V_x\left[\bar{\mu}\,\bar{\mu}\,G_{\psi',\varphi'} + G_{\psi',\varphi'}G_{\mu,\mu} + G_{\mu,\psi'}G_{\mu,\varphi'}\right]$$

Here $G_{\mu,\mu} = G_{\mu}$ and terms $G_{\mu,\psi'}$ and $G_{\mu,\varphi'}$ are eliminated in random interactions, leaving

$$G_{\boldsymbol{\psi}'_{\alpha}\circ\boldsymbol{\mu}_{\alpha},\boldsymbol{\varphi}'_{\alpha}\circ\boldsymbol{x}\circ\boldsymbol{\mu}_{\alpha}} = V_x\left[\bar{\psi}\,\bar{\varphi}\,G_{\mu} + \bar{\mu}\,\bar{\mu}\,G_{\psi',\varphi'} + G_{\psi',\varphi'}G_{\mu}\right] \qquad (\textbf{Eq. S25.2})$$

$$= V_x\left[G_{\mu}\left(\bar{\psi}\,\bar{\varphi} + G_{\psi,\varphi}\right) + \bar{\mu}^2 G_{\psi,\varphi}\right]$$

Where $G_{\psi',\varphi'} = G_{\psi,\varphi}$ when the SRN parameters of focal individuals and their social partners are drawn from the same joint distribution. Adding **Eq. S23-25** together following **Eq. S18** gives the full result for genetic variance due to IGEs

$$G_i = \bar{\mu}^2\left(G_{\psi} + V_x G_{\varphi}\right) + G_{\mu}\left[\bar{\psi}^2 + G_{\psi} + V_x\left(\bar{\varphi}^2 + G_{\varphi}\right)\right] \qquad (\textbf{Eq. S26})$$
$$+2V_x\left[\bar{\mu}^2 G_{\psi,\varphi} + G_{\mu}\left(\bar{\psi}\,\bar{\varphi} + G_{\psi,\varphi}\right)\right]$$

The same approach can be taken to calculate the variance of DGEs and the genetic covariance between DGEs and IGEs. Based on the SRN model (**Eq. 2**, **S2**) we expect that DGEs will be influenced by ecological plasticity

$$d_j = \mu_{\alpha j} + \left(\delta_{\alpha j} + \varphi_{\alpha j}\mu'_{\alpha_k}\right)x_e = \mu_{\alpha j} + \delta_{\alpha j}x_e + \varphi_{\alpha j}\mu'_{\alpha_k}x_e \qquad (\textbf{Eq. S27})$$

resulting from the moderation φ_j of individual *j*'s plasticity δ_j toward x_e by the trait value μ'_{α_k} of partner *k* in the social environment. In a stochastically fluctuating environment, the variance of DGEs is given by

$$G_d = G_\mu + V_x\left[\bar{\delta}^2 + G_\delta + \bar{\mu}^2 G_\varphi + G_\mu\left(\bar{\varphi}^2 + G_\varphi\right)\right] \qquad (\mathbf{Eq.\,S28})$$

This result uses **Eq. S19** to reduce the variance for the products $\boldsymbol{\varphi_\alpha} \circ \boldsymbol{\mu'_a}$ and $\boldsymbol{\varphi_\alpha} \circ \boldsymbol{\mu'_a}$, under the assumptions of $\bar{x} = 0$ and equivalent genetic variances $G_\mu = G_{\mu'}$ among focal individuals and their social partners.

Genetic covariance of DGEs and IGEs, combining **Eq. S17** and **Eq. S27**, is then

$$G_{d,i} = \mathrm{cov}\left(\mu_{\alpha j} + \delta_{\alpha_j} x_e + \varphi_{\alpha_j} {\mu'}_{\alpha_k} x_e,\ \psi'_{\alpha_k}\mu_{\alpha_j} + \varphi'_{\alpha_k} x_e \mu_{\alpha_j}\right) \qquad (\mathbf{Eq.\,S29.1})$$

which by the additive property of covariance can be given as

$$\begin{aligned} G_{\boldsymbol{d,i}} = {} & \mathrm{cov}\left(\mu_{\alpha_j}, \psi'_{\alpha_k}\mu_{\alpha_j}\right) + V_x \mathrm{cov}\left(\mu_{\alpha_j}, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) + \qquad (\mathbf{Eq.\,S29.2}) \\ & V_x \mathrm{cov}\left(\delta, \psi'_{\alpha_k}\mu_{\alpha_j}\right) + V_x \mathrm{cov}\left(\varphi_{\alpha_j}{\mu'}_{\alpha_k}, \psi'_{\alpha_k}\mu_{\alpha_j}\right) + \\ & V_x^2 \mathrm{cov}\left(\delta_{\alpha_j}, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) + V_x^2 \mathrm{cov}\left(\varphi_{\alpha_j}{\mu'}_{\alpha_k}, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) \end{aligned}$$

Where V_x^2 results from the presence of x_e in both the focal and partner traits and the bilinearity property of covariance. Substituting into **Eq. S18-19** provides solutions for these results. Considering the first two terms of covariance with μ_{α_j}, the covariance for the product of random variables can be used by treating μ_{α_j} as a random variable multiplied by 1. Any terms including covariances with this constant are eliminated, so that the result simplifies to

$$\mathrm{cov}\left(\mu_{\alpha_j}, \psi'_{\alpha_k}\mu_{\alpha_j}\right) = 1\bar{\psi}G_{\mu,\mu} + 1\bar{\mu}G_{\mu,\psi'} = \bar{\psi}G_\mu$$

for random interactions where $G_{\mu,\psi'} = 0$. Similarly, for socioecological plasticity

$$V_x \mathrm{cov}\left(\mu_{\alpha_j}, \varphi'_{\alpha_k} x_e \mu_{\alpha_j}\right) = V_x\left[1\bar{\varphi}G_{\mu,\mu} + 1\bar{\mu}G_{\mu,\varphi'}\right] = V_x\bar{\varphi}G_\mu$$

such that

$$\mathrm{cov}\left(\mu_{\alpha_j}, \psi'_{\alpha_k}\mu_{\alpha_j}\right) + V_x \mathrm{cov}\left(\mu_{\alpha_j}, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) = \bar{\psi}G_\mu + V_x\bar{\varphi}G_\mu = \mathrm{G}_{\boldsymbol{\mu}}(\bar{\psi} + V_x\bar{\varphi})$$

The same approach applies to the other terms

$$V_x \mathrm{cov}\left(\delta, \psi'_{\alpha_k}\mu_{\alpha_j}\right) + V_x^2 \mathrm{cov}\left(\delta, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) = V_x\left[\bar{\psi}G_{\mu,\delta} + \bar{\varphi}V_x G_{\mu,\delta}\right]$$

$$V_x \mathrm{cov}\left(\varphi_j {\mu'}_{\alpha_k}, \psi'_{\alpha_k}\mu_{\alpha_j}\right) = V_x\left[\bar{\varphi}\bar{\mu}G_{\mu',\psi'} + \bar{\mu}\bar{\psi}G_{\mu,\varphi} + C_{\mu,\varphi}G_{\mu',\psi'}\right]$$

$$= V_x\left[\bar{\varphi}\bar{\mu}G_{\mu\,,\psi} + \bar{\mu}\bar{\psi}G_{\mu,\varphi} + G_{\mu,\varphi}G_{\mu\,,\psi}\right]$$

$$V_x^2 \mathrm{cov}\left(\varphi_{\alpha_j}{\mu'}_{\alpha_k}, \varphi'_{\alpha_k}\mu_{\alpha_j}\right) = \bar{\varphi}\bar{\mu}G_{\mu',\varphi'} + \bar{\mu}\bar{\varphi}G_{\mu,\varphi} + G_{\mu,\varphi}G_{\mu',\varphi'}$$
$$= V_x^2\left[2\left(\bar{\mu}\bar{\varphi}G_{\mu,\varphi}\right) + G^2_{\mu\,,\varphi}\right]$$

under the assumption that focal individuals and their social partners are characterized by common genetic means and (co)variances, such that e.g. $G_{\mu\varphi} = G_{\mu'\varphi'}$. Putting these results together in **Eq. S29** and simplifying, the total genetic covariance is

$$G_{d,i} = \left(G_{\boldsymbol{\mu}} + G_{\mu,\delta}\right)(\bar{\psi} + V_x\bar{\varphi}) + \qquad (\mathbf{Eq. S30})$$

$$V_x\left[\bar{\varphi}\bar{\mu}G_{\mu\,,\psi} + \bar{\mu}\bar{\psi}G_{\mu,\varphi} + G_{\mu,\varphi}G_{\mu\,,\psi} + V_x\left[2\left(\bar{\mu}\bar{\varphi}G_{\mu,\varphi}\right) + G^2_{\mu\,,\varphi}\right]\right]$$

The total additive genetic variance G_A available for response to selection on the phenotype in the presence of IGEs is simply (Bijma et al., 2007; McGlothlin & Brodie, 2009)

$$G_A = G_d + G_i\bar{n}^2 + 2\bar{n}G_{d,i} \qquad (\mathbf{Eq. S31})$$

where $\bar{n}$ is the average number of social partners involved in interactions with the focal individual in a social environment. Results visualized in **Fig. 2** were determined using **Eq. S31**. Given **Eq. S26-31**, it is clear that the evolvability of a trait, i.e. the heritable variation facilitating adaptive microevolution in the phenotype (Hansen & Pélabon, 2021), can be highly contingent on the way in which genetic and ecological variation are currently interacting to shape the expression of social plasticity in a population, as a consequence of context dependent IGEs (**Fig. 1-2,6**). These results also show that rapid evolutionary acceleration or constraint may not only result from the effects of environmental change on selection of socially plastic traits, but also because of how environmental change shapes genetic variation in their expression.

Adaptive response in IGEs and character states

By including response terms from **Eq. 5** and **Eq. 8**, we can use these results for context dependent IGEs to predict how directional and quadratic selection in a fluctuating environment will shape the magnitude of IGEs across generations.

$$\Delta G_d = \Delta G_\mu + V_x\left[\left(\bar{\delta} + \Delta\bar{\delta}\right)^2 + \Delta G_\delta + (\bar{\mu} + \Delta\bar{\mu})^2(G_\varphi + \Delta G_\varphi)\right] \qquad (\mathbf{Eq.\,S32.1})$$

$$+V_x\left[\left(G_\mu + \Delta G_\mu\right)\left((\bar{\varphi} + \Delta\bar{\varphi})^2 + G_\varphi + \Delta G_\varphi\right)\right]$$

$$\Delta G_i = (\bar{\mu} + \Delta\bar{\mu})^2\left(\Delta G_\psi + V_x\Delta G_\varphi\right) + \qquad (\mathbf{Eq.\,S32.2})$$

$$\Delta G_\mu\left[(\bar{\varphi} + \Delta\bar{\varphi})^2 + \Delta G_\psi + V_x\left((\bar{\varphi} + \Delta\bar{\varphi})^2 + \Delta G_\varphi\right)\right] +$$

$$2V_x\left[(\bar{\mu} + \Delta\bar{\mu})^2\Delta G_{\psi,\varphi} + \Delta G_\mu\left(\Delta\bar{\psi}\,\bar{\varphi} + \bar{\psi}\,\Delta\bar{\varphi} + \Delta\bar{\psi}\,\Delta\bar{\varphi} + \Delta G_{\psi,\varphi}\right)\right]$$

$$\Delta G_{d,i} = \left(\mathrm{G}_{\boldsymbol{\mu}} + \Delta\mathrm{G}_\mu + G_{\mu,\delta} + \Delta G_{\mu,\delta}\right)(\Delta\bar{\psi} + V_x\Delta\bar{\varphi}) + \left(\Delta G_\mu + \Delta G_{\mu,\delta}\right)(\bar{\psi} + V_x\bar{\varphi}) + \qquad (\mathbf{Eq.\,S32.3})$$

$$V_x\left[(\bar{\varphi}\Delta\bar{\mu} + \Delta\bar{\varphi}\bar{\mu} + \Delta\bar{\varphi}\Delta\bar{\mu})\left(G_{\mu,\varphi} + \Delta G_{\mu,\varphi}\right) + (\bar{\psi}\Delta\bar{\mu} + \Delta\bar{\psi}\bar{\mu} + \Delta\bar{\psi}\Delta\bar{\mu})\left(G_{\mu,\psi} + \Delta G_{\mu,\psi}\right)\right] +$$

$$V_x\left[\Delta G_{\mu,\varphi}\Delta G_{\mu,\psi} + V_x\left[2\left(G_{\boldsymbol{\mu}} + \Delta G_\mu + G_{\mu,\delta} + \Delta G_{\mu,\delta}\right)(\Delta\bar{\psi} + V_x\Delta\bar{\varphi}) + \left(G_{\mu,\varphi} + \Delta G_{\mu,\varphi}\right)^2\right]\right]$$

These responses are complex but make clear that both directional and quadratic selection play an important role in shaping the context dependent expression of IGEs across generations, through their effects on adaptive microevolutionary change in SRN parameter means and genetic (co)variances. The same approach is taken for calculating the response to selection expressed at the level of character states (**Eq. 6, Eq. 10**). Variances for the products $V_{\psi\mu'}$ and $V_{\varphi\mu'}$ are calculated with **Eq. S19** so that

$$V_{\psi\mu'} = \left(\bar{\mu}'\sqrt{V_\psi}\right)^2 + \left(\bar{\psi}\sqrt{V_{\mu'}}\right)^2 + \left(\sqrt{V_\psi}\sqrt{V_{\mu'}}\right)^2\left(1 + \left[\frac{C_{\psi\mu'}}{\sqrt{V_\psi}\sqrt{V_{\mu'}}}\right]^2\right) + 2\,\bar{\mu}'\bar{\psi}C_{\psi\mu'} (\mathbf{Eq.\,S33.1})$$

$$V_{\varphi\mu'} = \left(\bar{\mu}'\sqrt{V_\varphi}\right)^2 + \left(\bar{\varphi}\sqrt{V_{\mu'}}\right)^2 + \left(\sqrt{V_\varphi}\sqrt{V_{\mu'}}\right)^2\left(1 + \left[\frac{C_{\varphi\mu'}}{\sqrt{V_\varphi}\sqrt{V_{\mu'}}}\right]^2\right) + 2\,\bar{\mu}'\bar{\varphi}C_{\varphi\mu'}\ (\mathbf{Eq.\,S33.2})$$

Simplifying by assuming random interactions gives the result presented in **Eq. 9.2**.

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