doi:10.1111/evo.12980

Invasion fitness, inclusive fitness, and reproductive numbers in heterogeneous populations

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Received January 12, 2016

Accepted May 28, 2016

How should fitness be measured to determine which phenotype or "strategy" is uninvadable when evolution occurs in a group-structured population subject to local demographic and environmental heterogeneity? Several fitness measures, such as basic reproductive number, lifetime dispersal success of a local lineage, or inclusive fitness have been proposed to address this question, but the relationships between them and their generality remains unclear. Here, we ascertain uninvadability (all mutant strategies always go extinct) in terms of the asymptotic per capita number of mutant copies produced by a mutant lineage arising as a single copy in a resident population ("invasion fitness"). We show that from invasion fitness uninvadability is equivalently characterized by at least three conceptually distinct fitness measures: (i) lineage fitness, giving the average individual fitness of a randomly sampled mutant lineage member; (ii) inclusive fitness, giving a reproductive value weighted average of the direct fitness costs and relatedness weighted indirect fitness benefits accruing to a randomly sampled mutant lineage member; and (iii) basic reproductive number (and variations thereof) giving lifetime success of a lineage in a single group, and which is an invasion fitness proxy. Our analysis connects approaches that have been deemed different, generalizes the exact version of inclusive fitness to class-structured populations, and provides a biological interpretation of natural selection on a mutant allele under arbitrary strength of selection.

KEY WORDS: **Adaptation, invasion fitness, inclusive fitness, reproductive number, uninvadability.**

It is well established that, in general, adaptiveness is not increased by short-term evolution, since recombination can interact with natural selection to decrease survival and fecundity of individuals in a population along an evolutionary trajectory (Moran 1964; Eshel 1991; Ewens 2004). In contrast, when long-term evolution can be described by a substitution process where a population transitions from one fixed allele to another through the recurrent invasion of mutant alleles, an increase in adaptiveness may occur over time as the result of natural selection being the predominant evolutionary force (with genetic drift and recombination not playing any significant role, Eshel 1991; Gillespie 1991; Hammerstein 1996; Desai and Fisher 2007).

By way of a "trait substitution sequence process" a population may then evolve in the long term toward fixation of an uninvadable strategy (i.e., a strategy that is resistant to the invasion by any alternative strategy, e.g., Eshel 1991, 1996; Hammerstein 1996; Weissing 1996; Van Cleve 2015). An uninvadable strategy characterizes an endpoint of evolution and is "the best" among a specified set of alternatives because it maximizes an evolutionary relevant fitness measure, for the resident strategy at the uninvadable state (Eshel 1991, 1996; Hammerstein 1996; Weissing 1996). Uninvadable strategies can thus be seen as adaptations (*sensu* Reeve and Sherman 1993), and they can be determined by an evolutionary invasion analysis even without knowing anything about the details and intricacies of the substitution process (or whether it will really indeed converge in the long run). As a result, evolutionary invasion analysis has become a very successful approach to understand theoretically long-term phenotypic evolution (e.g., Fisher 1930; Hamilton 1967; Maynard Smith 1982; Eshel and Feldman 1984; Parker and Maynard Smith 1990; Charlesworth 1994; Ferrière and Gatto 1995; Metz et al. 1996; McNamara et al. 2001; Lion and van Baalen 2007; Metz 2011; van Baalen 2013).

EVOLUTION
INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

When a mutant allele arises as a single copy in a population whose reproduction occurs at discrete time points, its *invasion fitness*[1] allows to determine whether the mutant allele will eventually go extinct or survive in the population (Tuljapurkar 1989; Metz et al. 1992; Charlesworth 1994; Rand et al. 1994; Ferrière and Gatto 1995; Caswell 2000). Invasion fitness is the per capita number of mutant copies produced asymptotically over a time step of the reproductive process by the mutant lineage descending from the initial mutation and when assumed overall rare in the population. Intuitively, this is a gene-centered measure of evolutionary success (*sensu* Dawkins 1976, 1978). Technically, invasion fitness is the dominant eigenvalue of a matrix determining the transitions between the different states in which the mutant allele can reside (Cohen 1979; Tuljapurkar 1989; Ferrière and Gatto 1995; Caswell 2000; Tuljapurkar et al. 2003). Since evolutionary biologists often try to understand adaptations in terms of the fitness properties exhibited by individuals, such as their survival and fecundity, it is important to understand the exact interpretation of invasion fitness in terms of individual-centered fitness components.

Interpreting invasion fitness this way seems clear in panmictic populations. In the absence of genetic conflict within individuals, maximizing invasion fitness (for the resident population at the uninvadable state) amounts to maximizing the (lifetime) fitness of a randomly sampled mutant individual, which is determined by its survival and fecundity schedules in stage-structured populations (Eshel and Feldman 1984; Charlesworth 1994; Hammerstein 1996; Weissing 1996; Caswell 2000). This result relies on the assumption that mutants are rare in the population, which allows one to neglect the interactions between individuals carrying the mutant allele in the invasion analysis. But when genetic mixing is limited, due to family or spatial population structure, interactions between mutants can no longer be neglected, as such interactions will necessarily occur locally, at the level of the interaction group even if the mutant is globally rare. In this case, three broad fitness measures have been proposed to ascertain the fate–establishment when rare or extinction–of a mutant allele.

First, one can seek to compute invasion fitness directly and exactly. Since in a group-structured population, the mutant is unlikely to be locally rare, one needs to track groups with different numbers of mutant alleles (i.e., the local distribution of mutants). Invasion fitness then becomes the eigenvalue of a matrix describing the transitions between different group states (Bulmer and Taylor 1980; Motro 1982; Bulmer 1986; van Baalen and Rand 1998; Courteau and Lessard 1999; Wild 2011). The interpretation of invasion fitness in terms of individual-centered fitness components is then no longer straightforward. In order to understand exactly what invasion fitness represents biologically, it needs to be unpacked and expressed in terms of individual-centered properties. In constant environments with stable group size, invasion fitness can be expressed as the individual fitness of a randomly sampled carrier of the mutant allele from the lineage descending from the initial mutation (Mullon et al. 2016). But so far no general interpretation of invasion fitness has been provided for group structured populations subject to local heterogeneities, such as demographic or environmental fluctuations.

Second, due to the computational difficulty to determine invasion fitness exactly, one can seek to evaluate an invasion fitness proxy that predicts the direction of selection in exactly the same way. The *basic reproductive number*–the total number of successful offspring produced by an individual over its lifetime–is the usual invasion fitness proxy for panmictic populations in evolutionary biology and epidemiology (Diekmann et al. 1990; Cochran and Ellner 1992; Mylius and Diekmann 1995; Caswell 2000; Ellner and Rees 2006). This number is computed as the eigenvalue of the next-generation matrix, whose maximization is equivalent to maximizing invasion fitness, for the resident population at the uninvadable state (Caswell 2000; Ellner and Rees 2006). In a group structured population, the usual invasion fitness proxy is the total number of successful emigrants produced by a mutant lineage over its lifetime when the lineage was started in a single group by some *distribution of immigrants* (Parvinen and Metz 2008; Massol et al. 2009). This approach to determine the fate of a mutant (introduced in Metz and Gyllenberg 2001 but see also Chesson 1984) has been used more often under the form of the total number of successful emigrants produced by a mutant lineage over its lifetime in a group that was founded by a *single* immigrant (Metz and Gyllenberg 2001; Ajar 2003; Parvinen et al. 2003; Cadet et al. 2003). These applications require that individuals disperse independently from each other and not in clusters, which excludes propagule dispersal. However, a fitness measure should in general be able to account for propagule dispersal, which is a relevant case in practice since new groups in social insect or mammals often result from fission or budding of the parental group (Clobert et al. 2001). This raises the question of the general connection between invasion fitness and the lifetime number of emigrants produced by a lineage, and more generally, the interpretation of the latter in terms of individual-centered fitness components.

Third, one can seek to compute first-order effects of selection on mutant allele frequency change, which allows to predict the fate of a mutant under weak selection and is sufficient to ascertain convergence stability (Taylor 1996; Rousset 2004). Convergence stability is required in order for a continuous or quantitative trait to be a (local) endpoint of an evolutionary trajectory characterized by a trait substitution sequence (Christiansen 1991; Geritz et al. 1998; Leimar 2009). The direct fitness method of social evolution

[1]What we here call invasion fitness is often called *geometric growth rate* in evolutionary demography and biology (Cohen 1979; Tuljapurkar 1989; Caswell 2000; Tuljapurkar et al. 2003; Ellner and Rees 2006).

theory (e.g., Taylor and Frank 1996; Frank 1998; Rousset 2004) achieves precisely that and has perhaps been the most popular approach among all alternative methods for studying evolution in (spatially) structured populations since it often leads to analytical results. This approach quantifies the effect on selection of local interactions between individuals carrying a mutant allele by using relatedness coefficients and ascertains the direction of selection on a mutant lineage by way of the *inclusive fitness effect* (Hamilton 1964). The inclusive fitness effect (*sensu* Hamilton 1964) is a weak selection decomposition of the change in the individual fitness of a randomly sampled carrier of the mutant allele into direct effects, resulting from an individual expressing the mutant (instead of the resident allele), and indirect effects weighted by relatedness among group members, resulting from group neighbors expressing the mutant. The inclusive fitness effect has helped understanding the selection pressure on very diverse phenotypes including the sex-ratio, reproductive effort, genomic imprinting, dispersal, menopause, parasite virulence, interactive behavior, senescence, and niche construction in group structured populations (e.g., Taylor 1988; Haig 1997a; Frank 1998; Gandon 1999; Pen 2000; Taylor and Irwin 2000; Lehmann 2008; Lion and Gandon 2009; Sozou 2009; Wild et al. 2009; Johnstone and Cant 2010; Ronce and Promislow 2010; Akçay and Van Cleve 2012; Lion 2013).

Despite their apparent differences, it has been emphasized that the various fitness measures are in fact tightly connected (Rousset 2004, p. 194, Akçay and Van Cleve 2016). For example, when groups are of constant size, the inclusive fitness effect amounts to evaluating the sensitivity of the number of emigrants or of invasion fitness with respect to variation in continuous trait values (Ajar 2003; Lehmann et al. 2015; Mullon et al. 2016), but the general connection between invasion fitness, inclusive fitness, and reproductive numbers (invasion fitness proxies), has not been worked out under arbitrary mutant trait types and selection strength with local demographic and/or environmental heterogeneities.

The aim of this article is to fill these gaps by providing a general interpretation of invasion fitness in terms of individual-centered fitness components and connecting formally to each other the different fitness measures. Our results highlight the conceptual unity underlying fitness measures and resolve some long standing issues about how inclusive fitness fits in under arbitrary mutant type and strength of selection.

Model

LIFE CYCLE

We consider a population of haploid individuals divided into an infinite number of groups. The population is censused at discrete time demographic periods. In each period, each group, independently from each other, can be in one of a finite number of demographic-environmental states $s \in \mathcal{S}$, where $\mathcal{S}$ is the state space. A state can specify the number of individuals in a group ("demographic" state) and/or any environmental factor affecting the survival and/or reproduction of *all* individuals within a group ("environmental" state). For simplicity of presentation, we consider a scenario without individual *heterogeneity state* (Diekmann et al. 1990; Caswell 2000) or individual *class structure* (Taylor 1996; Rousset 2004) within groups, such as age structure, sex structure, or stage structure. We will later discuss extensions to these cases, which are essentially a matter of notation.

Local state fluctuations in the population due to demographic or environmental processes will result in population level patterns of temporal and spatial heterogeneity, and this will depend on the level of dispersal between groups. Dispersal may occur between groups by individuals alone or by groups of individuals (i.e., propagule dispersal), but dispersal is always assumed to be uniform between groups in the population; in other words, we consider an island model of dispersal (Wright 1931). This setup allows us to represent classical models where the group state determines local group size, such as metapopulation processes (e.g., Chesson 1981; Metz and Gyllenberg 2001; Rousset and Ronce 2004), insect colony dynamics (e.g., Frank 1998; Avila and Fromhage 2015), compartmentalized replication like in the stochastic corrector model for prebiotic evolution (e.g., Szathmary and Demeter 1987; Grey et al. 1995), or when the state determines the local abiotic environment in a group (e.g., Greenwood-Lee and Taylor 2001; Wild et al. 2009; Rodrigues and Gardner 2012).

We assume that only two alleles can segregate in the population, a mutant allele of type τ and a resident allele of type θ where the set of all possible types is called Θ. Suppose that initially the population is monomorphic or fixed for the resident type θ and that a single individual mutates to type τ. Will the mutant "invade" the population and increase in frequency? If the resident type θ is such that any mutant type $\tau \in \Theta$ goes extinct with probability one, we will say that θ is *uninvadable*. A state that is uninvadable is an evolutionarily stable state. Our aim is to characterize uninvadability mathematically and biologically.

THE RESIDENT DEMOGRAPHIC EQUILIBRIUM

Following standard assumptions for the dynamics of mutant-resident substitutions (Eshel and Feldman 1984; Eshel 1996; Hammerstein 1996; Weissing 1996; Metz et al. 1996), we assume that a mutant can only arise in a resident population that is at its demographic equilibrium, and we start by characterizing this equilibrium. Our main assumption is that the stochastic process describing the state dynamics of a focal group in the resident population is given by a discrete time Markov chain on a finite state space (Karlin and Taylor 1975; Iosifescu 2007), where the

time scale is that of a demographic period (i.e., the scale at which births, deaths, dispersal, and other demographic events occur).

Because groups may affect each other demographically through dispersal, the transition probabilities for this Markov chain may depend endogenously on the resident population dynamics. But since there is an infinite number of groups, the infinite set of interacting Markov chains (one for each group) can be described as a single (inhomogeneous) Markov chain, whose transition probabilities are functions of the expected value of the process (Chesson 1981, 1984). We assume that this finite Markov chain is regular, irreducible and aperiodic, and thus has a stationary distribution (Iosifescu 2007, p. 123, Supporting Information (SI) Appendix A). As any local group is assumed to be bounded in size (finite carrying capacity), the process necessarily involves density-dependent ecological feedback on the resident population (e.g., Metz and Gyllenberg 2001; Cadet et al. 2003; Lehmann et al. 2006; Alizon and Taylor 2008 for concrete applications).

THE MUTANT MULTITYPE BRANCHING PROCESS

We now introduce a mutant into the backdrop of the resident population in its stationary demographic regime. Denote by $M_t(s,i)$ the random number of groups in the population that are in state $s \in \mathcal{S}$ and have exactly $i \in I(s) = \{1, 2, \ldots, n(s)\}$ mutant individuals at time $t = 0, 1, 2, \ldots$ where $n(s)$ is the number of individuals in a group in state s and $t = 0$ is the time of appearance of the mutant. Denote by $\mathbf{m}_t = (M_t(s,i))_{s\in\mathcal{S}, i\in I(s)}$ the vector collecting the $M_t(s,i)$ random variables and $\mathbf{e}(s)$ a vector of the same dimension but whose $(s,1)$-th component is equal to one, otherwise zero. Starting with a single initial mutant of type τ in a focal group in state s at time $t = 0$, namely $\mathbf{m}_0 = \mathbf{e}(s)$, we are interested in finding a necessary and sufficient condition for the mutant type τ to go extinct in finite time with probability one for any state $s \in \mathcal{S}$ (formally, a condition for $\Pr[\mathbf{m}_t = \mathbf{0} \text{ for some } t \in \mathbb{N} \mid \mathbf{m}_0 = \mathbf{e}(s)] = 1$ for all $s \in \mathcal{S}$).

Since we are interested only in characterizing the condition under which the mutant goes extinct, we assume that it will always remain rare in the total population (conditional on extinction) and approximate the dynamics of the mutant as a multitype branching process (Harris 1963; Karlin and Taylor 1975; Kimmel and Axelrod 2015), as in previous group structured population models with selection (e.g., Grey et al. 1995; Wild 2011; Mullon et al. 2016). It is then sufficient to focus on the (regular) matrix $\mathbf{A}$ whose $(s', i'; s, i)$ element, denoted $a(s', i' \mid s, i)$, is the expected number of groups in genetic-demographic-environmental state (s', i') that are "produced" over one demographic time period by a focal group in state (s, i) when the population is otherwise monomorphic for θ. For comparison with previous formalizations, it is relevant to note that we generally interpret these elements as describing changes in group state over one demographic time period (one life cycle iteration) as going from one "adult" stage (settled individuals in a group) to the next (e.g., Rousset 2004, Fig. 3.1), and not as going from the juveniles stage after dispersal to the next such state (e.g., Metz and Gyllenberg 2001).

It is useful to decompose the $\mathbf{A}$ matrix transition elements as

$$a(s', i' \mid s, i) = p(s', i' \mid s, i) + d(s', i' \mid s, i), \tag{1}$$

which consists of two terms representing two distinct biological processes. The first is the intragroup (or intracompartmental) change described by the transition probability $p(s', i' \mid s, i)$ that a focal group in state (s, i) turns into a group in state (s', i') after one demographic time period. The second process is the success of a group in replacing other groups by reproduction or fission, which is represented by $d(s', i' \mid s, i)$ that measures the expected number of groups in state (s', i') produced by emigration from, or fission, of a focal group of state (s, i). By "producing" a group of state (s', i'), we mean that for a metapopulation process a focal group in state (s, i) in a parental generation leaves $i' \in I(s')$ mutant offspring in a group that will be in state s' after one demographic time period. For compartmental replication processes (e.g., Grey et al. 1995) this means producing (by replication) a group in state (s', i').

INVASION FITNESS

It follows from standard results on multitype branching processes (Harris 1963; Karlin and Taylor 1975; Kimmel and Axelrod 2015) that the lineage descending from a single mutant τ arising in any of the demographic states of the resident θ population, will go extinct with probability one if the leading eigenvalue $\rho(\tau, \theta)$ of $\mathbf{A}(\tau, \theta)$ is less than or equal to 1. Namely, extinction occurs with probability one if and only if

$$\rho(\tau, \theta) \leq 1, \tag{2}$$

where $\rho(\tau, \theta)$ satisfies

$$\rho(\tau, \theta)\mathbf{u}_{\mathrm{A}}(\tau, \theta) = \mathbf{A}(\tau, \theta)\mathbf{u}_{\mathrm{A}}(\tau, \theta) \tag{3}$$

and $\mathbf{u}_{\mathrm{A}}(\tau, \theta)$ is the leading right eigenvector of $\mathbf{A}(\tau, \theta)$.

The interpretation of invasion fitness $\rho(\tau, \theta)$ is that it gives the per capita number of mutant copies produced by an average trajectory of the mutant lineage; that is, the collection of individuals descending from the individual in which the mutation appeared (Cohen 1979; Tuljapurkar et al. 2003). In the long-run, the average mutant lineage grows in the direction of $\mathbf{u}_{\mathrm{A}}(\tau, \theta)$ so that this vector can be interpreted as an asymptotic distribution of group genetic-demographic-environmental states containing at least one individual belonging to the mutant lineage. Namely, element (s, i) of $\mathbf{u}_{\mathrm{A}}$, that is $u_{\mathrm{A}}(s, i)$, is the asymptotic probability of s-type groups with $i \geq 1$ mutants; this interpretation holds whether the mutant lineage goes extinct or invades the population (Harris 1963, p. 44).

It follows directly from the construction of the model that $\rho(\theta, \theta) = 1$; namely, the invasion fitness of a resident lineage in a resident population is equal to one (see SI Appendix A for a proof). This implies that a resident type $\theta \in \Theta$ is uninvadable if, and only if,

$$\rho(\tau, \theta) \leq 1 \qquad \forall \tau \in \Theta. \tag{4}$$

Thus θ is uninvadable only if θ solves the maximization problem $\max_{\tau \in \Theta} \rho(\tau, \theta)$.

Now that we have a mathematical characterization of uninvadability in terms of invasion fitness $\rho(\tau, \theta)$, we present three different fitness measures that are all related to $\rho(\tau, \theta)$ and are all expressed in term of biological quantities that have appeared previously in the literature. All these quantities are derived in the SI from the elements $a(s', i' \mid s, i)$, $p(s', i' \mid s, i)$, and/or $d(s', i' \mid s, i)$ (eq. 1), and the explicit mathematical expressions are given in Table 1.

Three ways of understanding selection

LINEAGE FITNESS

First, we let the *lineage fitness* of a mutant type τ in a resident θ population be

$$W(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' \mid s, i) q(i \mid s) q(s), \tag{5}$$

where $w(s' \mid s, i)$ is the expected number of successful "offspring" (possibly including the parent through survival), which settle in groups of type s', given that the parent is a mutant residing in a group in state (s, i). Lineage fitness also depends on the probability $q(i \mid s)$ that, conditional on being sampled in a group in state s, an individual randomly sampled from the mutant lineage has $i - 1$ mutant neighbors. This can be thought of as the conditional *mutant experienced profile distribution*, and $q(s)$ is the probability that an individuals randomly sampled from the mutant lineage finds itself in a group in demographic-environmental state s. Note that these two distributions depend on the $u_{\mathrm{A}}(s, i)$ asymptotic distribution (Table 1). When there is only one demographic state, $W(\tau, \theta)$ reduces to equation (A.1) of Day (2001) and equation (A.7) of Mullon et al. (2016).

Lineage fitness $W(\tau, \theta)$ is the statistical average over all genetic-demographic-environmental states of the number of mutant replica copies produced by a representative carrier of the mutant allele. That is, the fitness of a randomly sampled carrier of the mutant allele from its lineage, where $w(s' \mid s, i)$ is an individual-centered fitness component variously called "direct," "personal," or "individual" fitness in social evolutionary theory (e.g., Frank 1998; Rousset 2004), and will be here referred to as individual fitness. Individual fitness involves offspring reaching adulthood in the group of the parent and in other groups through dispersal, and can thus also be written as

$$w(s' \mid s, i) = w_{\mathrm{p}}(s' \mid s, i) + w_{\mathrm{d}}(s' \mid s, i). \tag{6}$$

Here, $w_{\mathrm{p}}(s' \mid s, i)$ is the expected number of philopatric offspring, which settle in a group in state s', given that the parent is a mutant that reproduced in a group in state (s, i), while $w_{\mathrm{d}}(s' \mid s, i)$ is such offspring produced by dispersal, and thus reach adulthood in other groups in state s'. This decomposition of individual fitness matches the decomposition of the element of the transition matrix of the mutant given in equation (1) (see Table 1 and SI Appendix E, where we further decompose these terms into subcomponents that have appeared previously in the literature).

In the SI Appendix B, we show that invasion fitness of the mutant is exactly equal to its lineage fitness; namely,

$$W(\tau, \theta) = \rho(\tau, \theta). \tag{7}$$

This equation immediately implies that θ is uninvadable if it solves the maximization problem $\max_{\tau \in \Theta} W(\tau, \theta)$. In other words, the type is uninvadable if it "maximizes" lineage fitness, which will prevent any mutant type from increasing when rare.

Lineage fitness can be interpreted as a gene-centered measure of fitness (Dawkins 1976, 1978), as this perspective emphasizes that it is the combined fitness effects of all replica gene copies of a mutant lineage in the population that matters for selection (e.g., Dawkins 1976; Haig 1997b; Rousset 2004; van Baalen 2013; see also Akçay and Van Cleve 2016). Accordingly, lineage fitness $W(\tau, \theta)$ can be thought of as the goal function of a focal strategic gene (Dawkins 1976; Haig 1997b, 2012); namely, a gene (lineage) attempting to maximize its own transmission for a population where individuals behave according to the strategy of another gene. Finally, we note that the condition for uninvadability, equation (7), can also be interpreted as a version for class-structured population of the seminal uninvadability condition obtained for multilocus systems in panmictic populations, where the statistical average is over multilocus equilibrium genetic states (Eshel and Feldman 1984, eq. 10; Eshel et al. 1998, eq. 7).

INCLUSIVE FITNESS

Let us now decompose individual fitness as

$$w(s' \mid s, i) = w^{\circ}(s' \mid s) - c(s' \mid s) + b(s' \mid s) \left(\frac{i - 1}{n(s) - 1} \right) + \epsilon_i(s', s), \tag{8}$$

where $w^{\circ}(s' \mid s)$ is the expected number of surviving offspring, which settle in groups of type s', given that the parent is a resident reproducing in a group in state s in a monomorphic resident population, and where the superscript $\circ$ will throughout

Table 1. Definitions of the functions and vectors used for lineage fitness, inclusive fitness, and the reproductive numbers.

Function	Definition
$a(s', i' \mid s, i)$	Expected number of groups in state (s', i') that are "produced" over one demographic time period by a focal group in state (s, i). This is element $(s', i'; s, i)$ of the matrix $\mathbf{A} = \mathbf{P} + \mathbf{D}$.
$p(s', i' \mid s, i)$	Probability that a focal group in state (s, i) turns into a group in state (s', i') after one demographic time period. This is element $(s', i'; s, i)$ of the matrix $\mathbf{P}$.
$d(s', i' \mid s, i)$	Expected number of groups in state (s', i') produced by emigration or fission by a focal group in state (s, i). This is element $(s', i'; s, i)$ of the matrix $\mathbf{D}$.
$w(s' \mid s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' a(s', i' \mid s, i)$	Expected number of successful offspring, which settle in groups of type s', and are produced by a single mutant individual given that it resides in a group in state (s, i).
$w_{\mathrm{p}}(s' \mid s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' p(s', i' \mid s, i)$	Expected number of successful philopatric offspring, which settle in groups of type s', and are produced by a single mutant individual given that it resides in a group in state (s, i).
$w_{\mathrm{d}}(s' \mid s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' d(s', i' \mid s, i)$	Expected number of successful dispersing offspring, which settle in groups of type s', and are produced by a mutant individual given that it resides in a group in state (s, i).
$w_{\mathrm{p}}(s' \mid s, i) = w_{\mathrm{p}}(s', s, i) p(s' \mid s, i)$	Here, $w_{\mathrm{p}}(s', s, i)$ is the expected number of successful philopatric offspring given that the offspring settle in a group in state s' and the parent reproduces in a group in state (s, i).
$p(s' \mid s, i) = \sum_{i' \in I(s')} p(s', i' \mid s, i)$	Probability that a group will be in state s' in the offspring generation given that it was in state (s, i) in the parental generation.
$w_{\mathrm{d}}(s' \mid s, i) = \sum_{x \in \mathcal{S}} w_{\mathrm{d}}(s', x, s, i) \tilde{p}(s' \mid x, s, i) p^{\circ}(x)$	Here, $w_{\mathrm{d}}(s', x, s, i)$ is the expected number of dispersing offspring that a single mutant produces given that it resides in a group in state (s, i) and given that the group where the offspring settle is in state s in the offspring generation and was in state x in the parental generation (with 0 mutants).
$\tilde{p}(s' \mid x, s, i)$	Probability that a group that was in state $(x, 0)$ in the parental generation, and has been colonized by a mutant descending from a group in state (s, i), will become a group in state s' in the offspring generation.
$u_{\mathrm{A}}(s, i)$	Asymptotic probability that a mutant lineage finds itself in a group in state (s, i). This is element (s, i) of the right eigenvector $\mathbf{u}_{\mathrm{A}}$ of $\mathbf{A}$ associated to its leading positive eigenvalue ρ, namely, $\rho \mathbf{u}_{\mathrm{A}} = \mathbf{A}\mathbf{u}_{\mathrm{A}}$.
$q(s) = \frac{\sum_{i \in I(s)} i u_{\mathrm{A}}(s,i)}{\sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u_{\mathrm{A}}(s,i)}$	Asymptotic probability that a randomly drawn mutant lineage member find itself in a group in state s. Note that the denominator $\sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u_{\mathrm{A}}(s, i)$ is the average size of the mutant lineage in a group.
$q(i \mid s) = \frac{i u_{\mathrm{A}}(s,i)}{\sum_{i \in I(s)} i u_{\mathrm{A}}(s,i)}$	Asymptotic probability that, conditional on being sampled in a group in state s, a randomly sampled mutant individual from the mutant lineage finds itself in a group with i mutants.
$w^{\circ}(s' \mid s)$	Expected number of successful offspring, which settle in groups of type s', and are produced by a single mutant individual given that it resides in a group in state s in a monomorphic resident population.
$v^{\circ}(s) = \sum_{s' \in \mathcal{S}} v^{\circ}(s') w^{\circ}(s' \mid s)$	Reproductive value of a single individual reproducing in a group in state s in a monomorphic resident population.
$-c(s' \mid s)$	Additive effect on the individual fitness of an individual stemming from it switching to the expression of the mutant allele and holding everything else constant.
$b(s' \mid s)$	Additive effect on the individual fitness of a mutant stemming from the whole set of neighbors switching to the expression of the mutant allele and holding everything else constant.
$r(s) = \sum_{i \in I(s)} \frac{(i-1)}{(n(s)-1)} q(i \mid s)$	Asymptotic probability that, conditional on being sampled in a group in state s, an individual carrying the mutant experiences a randomly sampled neighbor that also carries the mutant allele. This is a measure of pairwise relatedness between individuals in a group.

(*Continued*)

Table 1. Continued.

Function	Definition
$w(s' \mid s, \tau_j, \tau_{-\mathbf{j}})$	Expected number of successful offspring, which settle in groups of type s', and are produced by a single individual j with phenotype τ_j given that it resides in a group in state s and that its group neighbors have phenotype profile $\tau_{-\mathbf{j}} = (\tau_{\mathbf{1}}, \ldots, \tau_{\mathbf{j-1}}, \tau_{\mathbf{j+1}}, \ldots \tau_n(s) - \mathbf{1})$.
$q^\circ(s') = \sum_{s \in \mathcal{S}} w^\circ(s' \mid s) q^\circ(s)$	Stationary probability of randomly sampling an individual from its lineage in a group in state s when the population is monomorphic for the resident allele.
$q^\circ(s) = p^\circ(s) n(s) / \bar{n}^\circ$	Here, $\bar{n}^\circ = \sum_{s \in \mathcal{S}s} n(s) p^\circ(s)$ is the average group size in a monomorphic resident population.
$p^\circ(s') = \sum_{s \in \mathcal{S}} p^\circ(s' \mid s) p^\circ(s)$	Stationary probability that a group is in state s in a resident monomorphic population, where $p^\circ(s' \mid s)$ denotes the neutral transition probability from state s to s' (possibly depending endogenously on the distribution $p^\circ(s)$).
$u_{\mathrm{R}}(s, i)$	Asymptotic probability that a group initiated by a local lineage starts in state (s, i). This is element (s, i) of the right eigenvector $\mathbf{u}_{\mathrm{R}}$ satisfying $R_{\mathrm{m}} \mathbf{u}_{\mathrm{R}} = \mathbf{R} \mathbf{u}_{\mathrm{R}}$, where $\mathbf{R} = \mathbf{D}(\mathbf{I} - \mathbf{P})^{-1}$ is the next-generation matrix and R_{m} the metapopulation reproductive number.
$q_0(s, i) = \frac{i \bar{t}(s,i)}{N_{\mathrm{L}}(\tau, \theta)}$	Probability that an individual randomly sampled from the mutant lineage over its lifetime in a single group finds itself in a group in state (s, i).
$\bar{t}(s', i') = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} t(s', i' \mid s, i) u_{\mathrm{R}}(s, i)$	Average of the expected amount of time the mutant lineage spends in state (s', i') over its lifetime in a single group.
$t(s', i' \mid s, i)$	Expected number of demographic times steps the mutant lineage spends in state (s', i') over its lifetime in a single group given that the group started in state (s, i). This is element $(s', i'; s, i)$ of the matrix $(\mathbf{I} - \mathbf{P})^{-1}$ of sojourn times.
$N_{\mathrm{L}}(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i \bar{t}(s, i)$	Average total size of the mutant lineage over its lifetime in a single group.
$N_{\mathrm{F}}(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u_{\mathrm{R}}(s, i)$	Expected number of founders in a single group of the mutant lineage.

Notes **See the SI for a proof of these quantities**

denote a quantity that is evaluated in the absence of natural selection, that is a process determined by the monomorphic resident population. Individual fitness also depends on $-c(s' \mid s)$, which is the additive effect on its individual fitness stemming from an individual switching to the expression of the mutant allele, $b(s' \mid s)$, which is the additive effect on the individual fitness of a mutant stemming from the whole set of neighbors switching to the expression of the mutant, and $(i-1)/(n(s)-1)$, which is the frequency of mutants in a the neighborhood of a mutant individual in a group with i mutants in state s. The *direct* effect $c(s' \mid s)$ and the *indirect* effect $b(s' \mid s)$ are obtained by minimizing the mean squared error $\epsilon_i(s', s)$ in the linear prediction of individual fitness (see Box 1 for details).

BOX 1. Weighted least square regression

We here show how to obtain the cost $c(s' \mid s)$ and benefit $b(s' \mid s)$ in equation (8). These are found by minimizing for each pairs of states (s', s) the sum of squared errors $\epsilon_i(s', s)$ weighted by the probabilities $q(i \mid s)$:

$$Q(c, b) = \sum_{i \in I(s)} \epsilon_i(s', s)^2 q(i \mid s).$$

That is, from equation (8), we minimize

$$Q(c, b) = \sum_{i \in I(s)} \left[w(s' \mid s, i) - \left(w^\circ(s' \mid s) - c(s' \mid s) + b(s' \mid s) \frac{(i-1)}{n(s)-1} \right) \right]^2 q(i \mid s),$$

with respect to c and b. From the prediction theorem for minimum square error prediction (Karlin and Taylor 1975, p. 465), we then have $\sum_{i \in I(s)} \epsilon_i(s', s) q(i \mid s) = 0$ for all $s' \in \mathcal{S}$ and $s \in \mathcal{S}$, which is one of the main features we use to obtain the expression for inclusive fitness (SI Appendix C).

We let the *inclusive fitness* of a mutant type τ in a resident θ population be

$$W_{\mathrm{IF}}(\tau, \theta) = 1 + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^\circ(s') \left[-c(s' \mid s) + b(s' \mid s) r(s) \right] q(s), \quad (9)$$

where $v^\circ(s)$ is the *reproductive value* of a single individual reproducing in a group in state s in a monomorphic population of the resident type. This is the relative expected asymptotic contribution of a single resident individual in state s to the population when it is monomorphic for the resident (Table 1 and see Taylor 1990; Taylor and Frank 1996; Rousset 2004; Grafen 2006; Lehmann and Rousset 2014 for discussions of this concept).

Inclusive fitness also depends on the probability $r(s)$ that, conditional on being sampled in a group in state s, an individual carrying the mutant experiences a randomly sampled neighbor that also carries the mutant allele. This is a measure of pairwise relatedness between two individuals in a group (see Table 1). In a monomorphic resident population, relatedness [then given by $r^{\circ}(s)$] reduces to the standard concept of probability of identity by descent between two randomly sampled group members (e.g., Frank 1998; Rousset 2004). In sum, the inclusive fitness $W_{\mathrm{IF}}(\tau, \theta)$ of a randomly sampled mutant from the lineage distribution $q(s)$ is the reproductive-value weighted average individual fitness cost $c(s' \mid s)$ of carrying the mutant allele and the relatedness weighted individual indirect fitness benefit $b(s' \mid s)$ of carrying the mutant.

We show in the SI Appendix C that inclusive fitness is exactly equal to invasion fitness of the mutant; that is,

$$W_{\mathrm{IF}}(\tau, \theta) = \rho(\tau, \theta). \tag{10}$$

Hence, a strategy θ is uninvadable if and only if inclusive fitness is maximized at θ in the sense that θ solves the problem $\max_{\tau \in \Theta} W_{\mathrm{IF}}(\tau, \theta)$. This shows that, regardless of the force of selection, uninvadability can be expressed in terms of the three standard measures of "value" emphasized by social evolution theory (Frank 1998; Rousset 2004): (i) the direct cost and indirect benefit within each class of an individual expressing the mutant, (ii) the pairwise relatedness between interacting individuals, and (iii) the neutral reproductive value of the descendants in each class.

Three points about inclusive fitness $W_{\mathrm{IF}}(\tau, \theta)$ are worth emphasizing. First, the regression approach displayed in equation (8) (and Box 1) is standard in population genetics, it underlies quantitive genetics and has been used before in social evolution (e.g, Fisher 1930; Queller 1992; Frank 1997; Lynch and Walsh 1998; Ewens 2004; Gardner et al. 2011). Second, while the regression coefficients in equation (8) may be very difficult to evaluate in practice and do not solve any computation problem, they can be useful for interpretation, for instance for defining altruism in an operational way (Rousset 2015). Third, for inclusive fitness to be equal to invasion fitness, the normalization of the reproductive values (the $v^{\circ}(s)$'s) cannot be arbitrary chosen and must satisfy the constraint

$$\sum_{s \in \mathcal{S}} v^{\circ}(s) q(s) = 1, \tag{11}$$

(see SI Appendix C; otherwise, we only obtain the weaker result that $W_{\mathrm{IF}}(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1$). This normalization means that the reproductive value weighted average fitness $w^{\circ}(s' \mid s)$ of a resident individual living in a resident monomorphic population and sampled from the mutant lineage asymptotic demographic-environmental state distribution is equal to one [since $\sum_{s \in \mathcal{S}} \sum_{s' \in \mathcal{S}} v^{\circ}(s') w^{\circ}(s' \mid s) q(s) = \sum_{s \in \mathcal{S}} v^{\circ}(s) q(s)$]. This expectation of the fitness of resident individuals weighted according to how mutants are distributed among states has an intuitive meaning: it corresponds to the expected per capita number of gene copies produced in the long term by the collection of residents that are "replaced" by members of the mutant lineage. This idea can be seen as the generalization to class-structured populations of the "basic reproductive unit which, if possessed by all the individuals alike, would render the population both stationary and nonevolutionary" (Hamilton 1964, p. 2). This basic unit is part of the foundational construction of inclusive fitness at the level of the allele or type (Hamilton 1964, p. 6). As such, we suggest that the normalization, equation (11), is an integral part of the definition of the exact version of inclusive fitness.

REPRODUCTIVE NUMBERS

We now turn to invasion fitness proxies. Let the *metapopulation reproductive number* of a mutant type τ in a resident θ population be

$$R_{\mathrm{m}}(\tau, \theta) = \frac{1}{N_{\mathrm{F}}(\tau, \theta)} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w_{\mathrm{d}}(s' \mid s, i) i \bar{t}(s, i), \tag{12}$$

where $N_{\mathrm{F}}(\tau, \theta)$ is the expected number of mutants settling in the same group and that descend from the same natal group initially settled by some distribution of mutant immigrants (see Table 1). The triple sum represents the expected number of successful emigrants produced by all individuals descending from these settlers over the lifetime of their lineage in a single group. This depends on the expected number $w_{\mathrm{d}}(s' \mid s, i)$ of emigrant offspring that settle in groups of type s' (see eq. 6) and on the expected amount of time $\bar{t}(s, i)$ that a mutant lineage spends in a single group in state (s, i) in the stationary distribution of initial group states of the mutant lineage. In summary, the metapopulation reproductive number gives the expected number of successful emigrants produced by a lineage during its whole sojourn time in a single group and per capita of the number of founders belonging to that lineage. When there is only one demographic-environmental state and one founding mutant, equation (12) reduces to equation (3) of Ajar (2003).

Although the explicit expression of $R_{\mathrm{m}}(\tau, \theta)$ (the right-hand of eq. 12) does not appear previously in the literature, this expression corresponds precisely to the leading eigenvalue of the next-generation matrix often considered in the evolutionary demography literature (Caswell 2000; Ellner and Rees 2006, see Table 1 and SI Appendix D). Further, if the number of founders is always equal to one ($N_{\mathrm{F}}(\tau, \theta) = 1$), then R_{m} (eq. 12) is consistent with the expression for the metapopulation reproductive number given in Massol et al. (2009, eqs. 12–13), who considered the next-generation matrix under a continuous time reproductive process. It then follows from these considerations and standard results

(see SI Appendix D) that the reproductive number $R_m(\tau, \theta)$ predicts whether or not the mutant invades in the same way as invasion fitness $\rho(\tau, \theta)$; namely

$$R_m(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (13)$$

Hence, a strategy is uninvadable if, and only if, the basic metapopulation reproductive number is maximized.

The reproductive number R_m counts (emigrant) successful offspring as produced by a whole set of individuals in the lineage, and, by contrast to $W(\tau, \theta)$ and $W_{IF}(\tau, \theta)$, is not individual centered. In order to have a reproductive number that is expressed in terms of the individual fitness of a representative carrier of the mutant allele, we let *lineage fitness proxy* of a mutant type τ in a resident θ population be given by

$$R_0(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' \mid s, i) q_0(i \mid s) q_0(s). \quad (14)$$

Here, $q_0(i \mid s)q_0(s) = q_0(s, i)$ is the probability that an individual randomly sampled from the mutant lineage over its lifetime in a single group finds itself in a group in state (s, i) (see Table 1), with $q_0(s)$ being the probability of being in state s and $q_0(i \mid s)$ the conditional probability that there are i mutants in that state. The expression in (14) is a direct analogue of lineage fitness, equation (5), the only difference is in the mutant profile distributions; for $R_0(\tau, \theta)$ the profile distribution depends on the average time the lineage spends in a single group in state (s, i) (which depends on the stationary distribution of initial groups states, see Table 1), whereas for lineage fitness the profile distribution depends on the asymptotic distribution $u_A(s, i)$ that the lineage is in a group in state (s, i). Because the right hand side of equation (14) corresponds to the general verbal individual-centered interpretation of the basic reproductive number given in previous work (e.g., Diekmann et al. 1990; Caswell 2000), we used the notation R_0 to denote it. When there is only one demographic state, $R_0(\tau, \theta)$ reduces to equation (3) of Lehmann et al. (2015).

We show in the SI Appendix D that the reproductive number $R_0(\tau, \theta)$ predicts whether or not the mutant invades in the same way as invasion fitness $\rho(\tau, \theta)$; that is,

$$R_0(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (15)$$

RESULTS SUMMARY

Summarizing all the above results, we have shown that for an uninvadable type θ:

$$\rho(\tau, \theta) = W(\tau, \theta) = W_{IF}(\tau, \theta) \leq 1$$
$$\iff R_m(\tau, \theta) \leq 1 \iff R_0(\tau, \theta) \leq 1 \quad \forall \tau \in \Theta. \quad (16)$$

Discussion

Our results demonstrate that the different fitness measures that have been proposed so far all equivalently determine which strategy is uninvadable, and that they can all be connected through their relationship to invasion fitness. The mathematical theory we present thus provides a formal framework for understanding the broad notion that fitness measures must align (e.g., Metz et al. 1992; Rousset 2004; Roff 2008; Akçay and Van Cleve 2016). Our results also reveal interesting features of the different fitness measures, which we now discuss.

LINEAGE AND INCLUSIVE FITNESS

Uninvadability can be equivalently characterized in terms of lineage fitness or inclusive fitness. This duality is interesting as these two gene-centered fitness measures are expressed in terms of different individual-centered fitness components experienced by representative carriers of the mutant allele. Lineage fitness is expressed only in terms of the individual fitness of a randomly drawn individual carrying the mutant, where the carrier is drawn from the asymptotic distribution of group states experienced by members of the mutant lineage (all genetic-demographic-environmental states). In contrast, inclusive fitness is expressed in terms of the direct fitness cost and relatedness weighted indirect fitness benefit accruing to a randomly drawn carrier of the mutant allele from its lineage. Writing fitness in terms of costs and benefits requires making a comparison between the number of offspring produced by an individual expressing the mutant allele relative to expressing the resident allele from its lineage. But in order for this comparison to depend only on selective effects and not on environmental features (like being lucky to be born in a resource full environment), how the fitness value of an offspring depends on the demographic and/or environmental state in which it settles needs to be taken into account. Thus, each offspring needs to be appropriately weighted according to the demographic and/or environmental state in which it will reproduce to guarantee that in the absence of selection the mutant will not increase (or decrease) in frequency in the population (Taylor 1990; Rousset 2004; Grafen 2006).

We find that these weights are the reproductive values of the monomorphic resident population regardless of the strength of selection on the mutant. The intuitive interpretation for this result is that reproductive value weighting allows one to average the number of offspring produced by an individual in different demographic-environmental states by taking into account their proportionate long-term contribution to the population, such that in the absence of selection invasion fitness is equal to one (SI Appendix A). By averaging over the reproductive values in a monomorphic resident population, inclusive fitness then allows determining whether the increase (or decrease) of the number

of descendants that a typical carrier of the mutant allele leaves in a resident population and relative to the typical carrier of the resident allele, is due solely to effects of selection. This result is consistent with previous population genetic formulations of allele frequency change in class-structured populations under arbitrary strength of selection (Lehmann and Rousset 2014). Our analysis thus generalizes the exact version of inclusive fitness (e.g., Queller 1992; Frank 1997; Gardner et al. 2011; Rousset 2015) to class-structured populations and variable number of interaction partners, and shows that the standard neutral reproductive value weighting (e.g., Taylor and Frank 1996; Rousset 2004) is maintained in this generalization.

Inclusive fitness makes explicit that the force of selection on a mutant allele depends on (i) how individuals in different demographic and environmental states contribute differently to the gene pool and on (ii) the genetic association between individuals due to local common ancestry, regardless of the complexity of the biological situation at hand and the strength of selection. These biological features, hidden in the other fitness measures, also become apparent if one considers only the first-order effects of selection on invasion fitness when the evolving traits have continuous values. This is the situation usually considered in the adaptive dynamics and inclusive fitness literature where one looks for local evolutionary attractors, the so-called convergence stable strategies (Taylor 1996; Geritz et al. 1998; Rousset 2004; Dercole and Rinaldi 2008). In this situation, the selection gradient on the mutant allele we derive (i.e., the sensitivity of invasion with respect to changes in trait value, Box 2) boils down to and generalizes the inclusive fitness effect derived previously by the direct fitness method (Taylor and Frank 1996; Rousset 2004, see Box 2 and the SI Appendix E for this connection). Hence, our model makes explicit that the direct fitness method amounts to computing the sensitivity of the invasion fitness of the mutant with respect to changes in mutant strategy under a general class structure and with environmental heterogeneity (see also Rousset 2004, pp. 194–196 for a conjecture on that point).

BOX 2. Sensitivity of invasion fitness and invasion implies substitution

We here provide an expression for the derivative of invasion fitness (i.e., the sensitivity of invasion fitness) for a one-dimensional quantitative trait; that is, when $\Theta = \mathbb{R}$. This derivative is sufficient to evaluate singular strategies and convergence stable states (Taylor 1996; Rousset 2004; Lehmann and Rousset 2014). In the SI Appendix E, we prove that the sensitivity of invasion fitness is

$$\frac{\partial \rho(\tau,\theta)}{\partial \tau} = \sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}} v^{\circ}(s')\left[\frac{\partial w(s' \mid s,\tau_j,\tau_{-j})}{\partial \tau_j} + (n(s)-1)\frac{\partial w(s' \mid s,\tau_j,\tau_{-j})}{\partial \tau_k} r^{\circ}(s)\right] q^{\circ}(s)$$

where $w(s' \mid s,\tau_j,\tau_{-j})$ is the individual fitness of an individual with phenotype τ_j, when its group members have phenotype profile $\tau_{-j} = (\tau_1,\ldots,\tau_{j-1},\tau_{j+1},\ldots\tau_{n(s)-1})$, which is the vector collecting the phenotypes of the $n(s)-1$ neighbors of an individual j and $k \neq j$, and all derivatives are evaluated at the resident values θ. Note that here, both the probability $q^{\circ}(s)$ that a mutant experiences a group in state s and relatedness $r^{\circ}(s)$ are evaluated in a monomorphic resident population (neutral process). Given further specific biological assumptions on the underlying demographic process, we then recover from the above derivative the expression for the inclusive fitness effect derived by the direct fitness method for the island model (Taylor and Frank 1996; Rousset and Ronce 2004 and SI Appendix E).

The arguments developed in Rousset (2004, p. 149, p. 196) and Rousset and Ronce (2004) show that, when the phenotypic deviation $\delta = \tau - \theta$ between mutant and resident is small ($|\delta| \ll 1$), the change $\Delta\bar{p}$ in reproductive value weighted average mutant frequency $\bar{p}$ in the total population is

$$\Delta\bar{p} = \bar{p}(1-\bar{p})\delta S(\theta) + O(\delta^2), \tag{X.1}$$

where $S(\theta) = \partial\rho(\tau,\theta)/\partial\tau|_{\tau=\theta}$ is the selection gradient on the mutant allele. Hence, under weak selection and when $\delta S(\theta) > 0$ invasion of the mutant implies substitution, a result that holds generally under spatial structure (Rousset 2004, p. 206, Lehmann and Rousset 2014). It follows immediately that under a trait substitution sequence dynamics, the selection gradient $S(\theta)$ is sufficient to ascertain convergence stability (Leimar 2009); a convergence stable strategy θ^* satisfying

$$\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*} < 0. \tag{X.2}$$

Importantly, under weak selection, the selection gradient on the mutant allele derived from invasion fitness allows not only to determine wether the mutant invades the population when at low frequency, but also whether it will fixate in the whole population (Box 2). Hence, invasion implies substitution can be predicted from the selection gradient alone in which case evolution can be described as a trait substitution sequence process. The selection gradient is thus sufficient to compute local convergence stability,

and to establish which strategies will be local attractors of the evolutionary dynamic (Box 2).

Overall, our analysis demonstrates connections between the various theoretical approaches for characterizing adaptations in heterogeneous populations. But depending on the type of questions and insight desired, either inclusive or lineage fitness formulations might be better suited. For instance, lineage fitness may be easier to measure, as it only relies on measuring the individual fitness of a representative sample of individuals of the mutant type (see Akçay and Van Cleve 2016 for further discussions on using invasion fitness measures for empirical system).

REPRODUCTIVE NUMBERS

We also derived an explicit expression for the metapopulation reproductive number, R_m, which was shown to depend on the ratio of the total lifetime number of successful emigrants produced by a typical group colonized by members of the mutant lineage, to the expected number of colonizers of such a typical group. Reproductive numbers are the usual invasion fitness proxies in evolutionary biology and epidemiology (Diekmann et al. 1990; Cochran and Ellner 1992; Mylius and Diekmann 1995; Caswell 2000; Ellner and Rees 2006) and are usually used as they simplify the characterization of the condition under which a mutant invades. They circumvent the need to compute explicitly invasion fitness ρ, (the eigenvalue of the transition matrix $\mathbf{A}$), and only require a matrix inversion (SI Appendix D). When individuals disperse independently and not in clusters (i.e., no propagule dispersal), the metapopulation reproductive number reduces to the number of successful emigrants produced over the lifetime of a lineage initiated by a single mutant, which has been often used as a fitness proxy in concrete applications as it even further simplifies the computation (Metz and Gyllenberg 2001; Ajar 2003; Parvinen et al. 2003; Cadet et al. 2003). Our results are consistent with the formal proof of the use of this number derived by Massol et al. (2009) for a continuous time demographic-environmental process.

Three points are worth mentioning concerning the reproductive number R_m. First, while no relatedness appears explicitly in it, its take inclusive fitness effects into account in qualitatively the same way as inclusive fitness (or lineage fitness) does. Second, the metapopulation reproductive number counts successful emigrant offspring produced by a whole set of individuals, and thus does not give net successful offspring produced by a representative carrier of the mutant allele. In order to have the latter invasion fitness proxy, which keeps the attractive computational features of the metapopulation reproductive number, we derived an expression for lineage fitness proxy R_0. This is the individual fitness of a mutant lineage member randomly sampled from the distribution quantifying the lifetime of the mutant lineage in a single group. This allows one to determine uninvadability with the same generality and computational cost as R_m, but with the same biological interpretation as lineage fitness.

Finally, if one is interested only in ascertaining local convergence stability, then computing the selection gradient in the form of the inclusive fitness effect (Box 2) is even simpler than evaluating the basic reproductive number. This is because the full mutant distribution need not be known in order to ascertain convergence stability, and all relevant information about mutant–mutant interactions is captured by neutral relatedness coefficients, whose computations requires matrices of much lower dimensions than those for evaluating the reproductive numbers (Rousset and Ronce 2004, p. 134 provide a procedure of how to evaluate numerically the selection gradient for complex models). In summary, if only convergence stability is of interest, then compute the inclusive fitness effect. If higher order terms are needed (for instance to determine disruptive selection), then evaluate a reproductive number (see Mullon et al. 2016 for situations where convergence stability and disruptive selection can be ascertained analytically). If the exact extinction probability is needed, then there is no way out and one must compute the exact expression for invasion fitness (i.e., invasion fitness $\rho(\tau, \theta)$).

LIMITATIONS AND GENERALIZATIONS

To obtain our results, we assumed a population of infinite size but allowed for limited dispersal between any group and local demographic and/or environmental state fluctuations. This allows to describe, in at least a qualitative way, different metapopulation processes as well as group (or propagule) reproduction processes subject to local demographic and environmental stochasticity. Conceptually, our qualitative results concerning the generic form of the fitness concepts considered here should carry over to isolation-by-distance models and to finite total population size where evolutionary success is ascertained by the fixation probability of the mutant allele.

We also only considered discrete time halploid reproduction, but diploid reproduction would not produce qualitatively different results concerning the expressions of lineage fitness, inclusive fitness, or the reproductive numbers. In the case of diploidy, one needs to add an additional class structure within each demographic state so that individuals are either homozygous or heterozygous and produce these two types of offspring. The same extension is needed for individual heterogeneity or class structure within groups such as age or stage structure (see Box 3 and SI Appendix F for an example involving stage structure). Further, provided one places some biological reasonable restrictions on the growth of group sizes, standard results about multitype branching processes suggest that extensions to (i) a countable number of demographic-environmental states, (ii) an uncountable number of such states, and (iii) continuous time processes (respectively, Kimmel and

Axelrod 2015, p. 160, Harris 1963, p. 70, and Athreya 1968, p. 351) should be relatively straightforward and all calculations should carry over conceptually unchanged [where sums over state $\mathcal{S}$ are replaced by appropriate integrals for case (ii)]. To paraphrase Metz et al. (1992, p. 198), such extensions require some care with definitions, replacing the word matrix by linear operator, some mathematical headaches, but are unlikely to yield to any new fundamental biological insight.

BOX 3. Lineage and inclusive fitness for within group heterogeneity

Suppose that each group is of constant size and that there is no demographic-environmental heterogeneity, but that each individual within a group can belong to one of n_c classes (like age-structure) where the set of classes is $\mathcal{C} = \{1, \ldots, n_c\}$. For such a class structured population, we show in the SI Appendix F that the lineage fitness of a mutant τ in a θ population is

$$W(\tau, \theta) = \sum_{\mathbf{i} \in I} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} w(y, x, \mathbf{i}) q(x, \mathbf{i}), \qquad \text{(X.3)}$$

where $w(y, x, \mathbf{i})$ is the expected number of class y offspring produced by a class x mutant when in a group in state $\mathbf{i} = (i_1, \ldots, i_{n_c}) \in I$, which is the vector of the number of mutant alleles in class 1 to n_c. Here, $I = (I_1 \times \cdots \times I_{n_c}) \backslash \mathbf{0}$ is the set of possible group states with $I_x = \{0, 1, \ldots, n_x\}$ being the set of the number of mutant alleles in class x and n_x is the number of individuals in that class. In complete analogy with the demographically structured population case, $q(x, \mathbf{i})$ is the probability that a randomly sampled lineage member finds itself in class x and its group state is $\mathbf{i}$. The inclusive fitness for this model is

$$W_{\mathrm{IF}}(\tau, \theta) = 1 + \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} v^{\circ}(y) \Bigg[-c(y, x) + \sum_{z \in \mathcal{C}} b_z(y, x)\, r(z \mid x) \Bigg] q(x),$$

where $q(x)$ is the probability that a randomly sampled individual from the mutant lineage finds itself in class x, $c(y, x)$ is the additive effect on the number of class y offspring produced by a class x individual when expressing the mutant instead of the resident allele, $b_z(y, x)$ is the additive effect on this fitness stemming from group neighbors in class z expressing the mutant instead of the resident allele, and $r(z \mid x)$ is the probability that, conditional on being sampled in class x, an individual carrying the mutant experiences a randomly sampled neighbor in class z that also carries the mutant allele.

For this class-structured population the sensitivity of invasion fitness, $\partial \rho(\tau, \theta)/\partial \tau$, is again equivalent to the selection gradient computed by the direct fitness method and is available in the literature (Leturque and Rousset 2002, eq. 2). Allowing for both within group heterogeneity and demographic-environmental fluctuations is only a matter of extending the notations. In that case, each demographic state will determine a distribution over the number of individuals in each class within groups.

Our approach, however, breaks down conceptually when there are global environmental fluctuations affecting all groups in the population simultaneously, in which case a stochastic version of invasion fitness (the stochastic growth rate) needs to be used to ascertain uninvadability (Svardal et al. 2015), and where the basic reproductive number does not necessarily alleviate any computation (Bacaër and Khaladi 2013). Hence, a completely general interpretation of invasion fitness in terms of individual-centered fitness components, covering all possible biological heterogeneities, is still lacking. But for local heterogeneities, there is a generality and consistency in the interpretation of the force of a selection on a mutant allele that befits the generality of natural selection.

ACKNOWLEDGMENTS

It is a pleasure to thank an anomalous reviewer for his very careful reading of the model and many suggestions that allowed us to improve on several points.

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Associate Editor: C. Rueffler
Handling Editor: P. Tiffin

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

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Online Supplementary material for "Invasion fitness, inclusive fitness, and reproductive numbers in heterogeneous populations"

Appendix A: Properties of the monomorphic resident population

The demographic equilibrium for a monomorphic resident θ population described in the main text can be expressed as

$$p^\circ(s') = \sum_{s\in\mathcal{S}} p^\circ(s' \mid s)p^\circ(s), \tag{A.1}$$

where $p^\circ(s)$ is the neutral stationary probability that a group is in state s and $p^\circ(s' \mid s)$ denotes the (neutral) transition probability from state s to s' (possibly depending endogenously on the distribution $p^\circ(s)$, e.g., Metz and Gyllenberg, 2001; Cadet et al., 2003; Lehmann et al., 2006; Alizon and Taylor, 2008).

We now prove that in a monomorphic θ population the neutral transition matrix $\mathbf{A}^\circ$ has dominant eigenvalue $\rho(\theta,\theta) = 1$. We do so by constructing a positive left eigenvector $\mathbf{v}^\circ > \mathbf{0}$ of $\mathbf{A}^\circ$ with unit eigenvalue (i.e., such that $\mathbf{v}^\circ\mathbf{A}^\circ = \mathbf{v}^\circ$). Then, since $\mathbf{A}^\circ$ is irreducible and non-negative (and $\mathbf{v}^\circ > \mathbf{0}$), the Perron-Frobenius theorem tells us that the dominant eigenvalue of $\mathbf{A}^\circ$ is one (e.g., Karlin and Taylor, 1975). We construct $\mathbf{v}^\circ = (v^\circ(1,1),\ldots,v^\circ(1,n(1)),v^\circ(1,2),\ldots)$ with (s,i) element

$$v^\circ(s,i) = v^\circ(s)i, \tag{A.2}$$

where $v^\circ(s) > 0$ corresponds to the reproductive value of an individual in class s (see Taylor, 1996 and Rousset, 2004). By definition, the reproductive value satisfies the recursion

$$v^\circ(s) = \sum_{s'\in\mathcal{S}} v^\circ(s')w^\circ(s' \mid s). \tag{A.3}$$

To show that our construction of $\mathbf{v}^\circ$ is a left eigenvector of $\mathbf{A}^\circ$, we first write the (s,i) element

of $\mathbf{v}^\circ\mathbf{A}^\circ$ by using eq. A.2 as

$$\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')} v^\circ(s',i')a^\circ(s',i' \mid s,i) = \sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')} v^\circ(s')i'a^\circ(s',i' \mid s,i). \tag{A.4}$$

Then, we note that the total expected number of mutant individuals in a group of type s' produced by a group of type (s,i) can be written as

$$\sum_{i'\in I(s')} i'a^\circ(s',i' \mid s,i) = w^\circ(s' \mid s)i, \tag{A.5}$$

since the right hand side is the total expected number of mutant individuals in a group of type s' produced by a group of type (s,i), and where, owing to neutrality, fitness $w^\circ(s' \mid s)$ is independent of i. Using eq. (A.5) first and (A.3) second, the (s,i) element of $\mathbf{v}^\circ\mathbf{A}^\circ$ can thus be written as

$$\begin{aligned}\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')} v^\circ(s')i'a^\circ(s',i' \mid s,i) &= \sum_{s'\in\mathcal{S}} v^\circ(s')w^\circ(s' \mid s)i \\ &= v^\circ(s)i \\ &= v^\circ(s,i),\end{aligned} \tag{A.6}$$

i.e., as the (s,i) element of $\mathbf{v}^\circ$, which shows that our construction of $\mathbf{v}^\circ$ (as given by eq. (A.2)) is indeed a left eigenvector of $\mathbf{A}^\circ$ with unit eigenvalue, as required.

Appendix B: Lineage fitness

We here prove that $\rho(\tau,\theta) = W(\tau,\theta)$. To that aim, we first note that eq. (A.5) holds out of neutrality so that

$$\sum_{i'\in I(s')} i'a(s',i' \mid s,i) = w(s' \mid s,i)i. \tag{B.1}$$

Second, we let $\mathbf{n} = (1,2,\ldots,n(1),1,2\ldots,n(2),1,2,\ldots,n(s),...)$, which lists the number of mutants in each state. Premultiplying $\rho\mathbf{u}_\mathrm{A} = \mathbf{A}\mathbf{u}_\mathrm{A}$ by $\mathbf{n}$ gives $\mathbf{n}\cdot\rho\mathbf{u}_\mathrm{A} = (\mathbf{n}\cdot\mathbf{A}\mathbf{u}_\mathrm{A})$, where $\cdot$ is the

dot product. Using eq. (B.1) we have

$$\begin{aligned}\rho(\tau,\theta) &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}(\mathbf{n}\cdot\mathbf{A}\mathbf{u}_{\mathrm{A}}) \\ &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} i'a(s',i'\mid s,i)u_{\mathrm{A}}(s,i) \\ &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} w(s'\mid s,i)iu_{\mathrm{A}}(s,i). \end{aligned} \tag{B.2}$$

Using the definitions of $q(i\mid s)$ and $q(s)$ given in the Table 1 of the main text (where $\sum_{s\in\mathcal{S}} q(s) = 1$ and $\sum_{i\in I(s)} q(i\mid s) = 1$), we can then write

$$\rho(\tau,\theta) = \sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} w(s'\mid s,i)q(i\mid s)q(s). \tag{B.3}$$

The right hand side is exactly $W(\tau,\theta)$, whereby $\rho(\tau,\theta) = W(\tau,\theta)$.

Appendix C: Inclusive fitness

Here, we prove that the uninvadability condition can be expressed in terms of inclusive fitness. For this, we premultiply $\rho\mathbf{u}_{\mathrm{A}} = \mathbf{A}\mathbf{u}_{\mathrm{A}}$ by $\mathbf{v}^{\circ}$, which gives $\mathbf{v}^{\circ}\cdot\rho\mathbf{u}_{\mathrm{A}} = (\mathbf{v}^{\circ}\cdot\mathbf{A}\mathbf{u}_{\mathrm{A}})$. Using eq. (A.2) then entails

$$\begin{aligned}\rho(\tau,\theta) &= \frac{1}{\mathbf{v}^{\circ}\cdot\mathbf{u}_{\mathrm{A}}}\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} v^{\circ}(s')i'a(s',i'\mid s,i)u_{\mathrm{A}}(s,i) \\ &= \frac{1}{\mathbf{v}^{\circ}\cdot\mathbf{u}_{\mathrm{A}}}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} v^{\circ}(s')w(s'\mid s,i)iu_{\mathrm{A}}(s,i). \end{aligned} \tag{C.1}$$

We now let

$$V_{\mathrm{T}}(\tau,\theta) = \frac{\mathbf{v}^{\circ}\cdot\mathbf{u}_{\mathrm{A}}}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}} = \sum_{s\in\mathcal{S}} v^{\circ}(s)q(s), \tag{C.2}$$

which is the average reproductive value in a monomorphic resident population of an individual that is randomly sampled from the asymptotic mutant lineage distribution (instead of being

sampled from the resident lineage distribution). With this, we have

$$\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')w(s'\mid s,i)\frac{iu_{\mathrm{A}}(s,i)}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}. \tag{C.3}$$

Using

$$\frac{iu_{\mathrm{A}}(s,i)}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}=\left(\frac{iu_{\mathrm{A}}(s,i)}{\sum_{i\in I(s)}iu_{\mathrm{A}}(s,i)}\right)\left(\frac{\sum_{i\in I(s)}iu_{\mathrm{A}}(s,i)}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}}\right)=q(i\mid s)q(s), \tag{C.4}$$

we have

$$\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')w(s'\mid s,i)q(i\mid s)q(s). \tag{C.5}$$

We now use the regression equation form for $w(s'\mid s,i)$ (eq. (8) of the main text), insert it into eq. (C.5) and obtain

$$\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')\left[w^{\circ}(s'\mid s)-c(s',s)+b(s',s)\frac{(i-1)}{n(s)-1}+\epsilon_i(s',s)\right]q(i\mid s)q(s)\,,$$

which becomes

$$\begin{aligned}\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\Bigg[&\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}v^{\circ}(s')w^{\circ}(s'\mid s)q(s)\\&+\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')\left(-c(s',s)+b(s',s)\frac{(i-1)}{n(s)-1}\right)q(i\mid s)q(s)\Bigg],\end{aligned} \tag{C.6}$$

since the minimum mean square error used to obtain $c(s',s)$ and $b(s',s)$ ensures that $\sum_{i\in I(s)}\epsilon_i(s',s)q(i\mid s)=0$ for all $s'\in\mathcal{S}$ and $s\in\mathcal{S}$ (see Box 1). Using eq. (A.3), the double sum in the first line of eq. (C.6) is seen to be $V_{\mathrm{T}}(\tau,\theta)$, and using the definition of relatedness $r(s)=\sum_{i\in I(s)}\left[(i-1)/(n(s)-1)\right]q(i\mid s)$ (Table 1), we can simplify the sum on the second line of eq. (C.6) using the expression for inclusive fitness (eq. (9) of the main text) to obtain

$$\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\left[V_{\mathrm{T}}(\tau,\theta)-1+W_{\mathrm{IF}}(\tau,\theta)\right], \tag{C.7}$$

whence

$$\rho(\tau,\theta) = 1 + \frac{1}{V_{\mathrm{T}}(\tau,\theta)}\left[W_{\mathrm{IF}}(\tau,\theta) - 1\right]. \tag{C.8}$$

Since, $V_{\mathrm{T}}(\tau,\theta) > 0$, we have

$$\rho(\tau,\theta) \leq 1 \iff W_{\mathrm{IF}}(\tau,\theta) \leq 1. \tag{C.9}$$

Hence, a type τ is uninvadable if it solves $\max_{\tau\in\Theta} W_{\mathrm{IF}}(\tau,\theta)$.

This results (eq. (C.9)) holds regardless of the normalization of the neutral reproductive values $v^{\circ}(s)$, which, so far, we made no assumptions about. Hence, we can choose a constant of proportionality in the reproductive values (normalize) such that

$$v^{\circ}(s) = \sum_{s'\in\mathcal{S}} v^{\circ}(s')w^{\circ}(s' \mid s) \qquad \text{and} \qquad V_{\mathrm{T}}(\tau,\theta) = \sum_{s\in\mathcal{S}} v^{\circ}(s)q(s) = 1. \tag{C.10}$$

When this holds, eq. (C.7) gives

$$\rho(\tau,\theta) = W_{\mathrm{IF}}(\tau,\theta), \tag{C.11}$$

namely, invasion fitness is exactly equal to inclusive fitness. However, when eq. (C.10) holds, the constant of proportionality in the neutral reproductive values is a function of the mutant type τ as well as the resident type θ (since $q(s)$ depends on the mutant), which should be taken into mind when explicit calculations are done under this assumption.

Appendix D: Reproductive numbers

D.1 Metapopulation reproductive number R_{m}

Here, we prove the uninvadability condition expressed in terms of the metapopulation reproductive number. According to our notations, the mean matrix of the branching process can be

decomposed as

$$\mathbf{A} = \mathbf{P} + \mathbf{D}, \tag{D.1}$$

where $\mathbf{P}$ is the matrix collecting the $p(s', i' \mid s, i)$ elements and $\mathbf{D}$ is the matrix collecting the $d(s', i' \mid s, i)$ elements (see eq. (6) or Table 1). Note that matrix $\mathbf{P}$ is formally the transient matrix of the absorbing Markov chain (Grinstead and Snell, 1997, p. 417) describing the dynamics of the mutant in a single group and whose only absorbing state is the extinction of the mutant in that group.

An application of the next generation theorem (Caswell, 2000; Thieme, 2009) shows that

$$R_{\mathrm{m}}(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1, \tag{D.2}$$

where R_{m} is the leading eigenvalue of the next generation matrix

$$\mathbf{R} = \mathbf{D} \left(\mathbf{I} - \mathbf{P}\right)^{-1}. \tag{D.3}$$

The elements of this matrix are

$$r(s', i' \mid s, i) = \sum_{\varsigma \in \mathcal{S}} \sum_{j \in I(\varsigma)} d(s', i' \mid \varsigma, j) t(\varsigma, j \mid s, i), \tag{D.4}$$

where $t(\varsigma, j \mid s, i)$ is the expected number of demographic time steps the mutant lineage spends in state (ς, j) over its lifetime in a single group given that the group started in state (s, i). These sojourn times are elements of the so-called fundamental matrix $(\mathbf{I} - \mathbf{P})^{-1}$ (Grinstead and Snell, 1997, p. 419). The interpretation of $r(s', i' \mid s, i)$ is that it gives the total expected number of groups in state (s', i') produced through dispersal over the lifetime of the mutant lineage in a single group that started in state (s, i). Accordingly, matrix $\mathbf{R}$ has a leading right eigenvector $\mathbf{u}_{\mathrm{R}}$, which satisfies

$$R_{\mathrm{m}} \mathbf{u}_{\mathrm{R}} = \mathbf{R} \mathbf{u}_{\mathrm{R}}, \tag{D.5}$$

and whose element $u_{\mathrm{R}}(s,i)$ is the asymptotic probability that a group initiated by a local mutant lineage starts in state (s,i) and where $\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}u_{\mathrm{R}}(s,i)=1$.

Using the above, we now rewrite R_{m} using the same line of argument as for lineage fitness. Hence, we first let

$$\sum_{i'\in I(s')} i'd(s',i'\mid s,i)=w_{\mathrm{d}}(s'\mid s,i)i, \tag{D.6}$$

where $w_{\mathrm{d}}(s'\mid s,i)$ is the total expected successful number of immigrants in groups in state s' produced by a single mutant given that it was reproducing in a group in state (s,i). Premultiplying $R_{\mathrm{m}}\mathbf{u}_{\mathrm{R}}=\mathbf{R}\mathbf{u}_{\mathrm{R}}$ by $\mathbf{n}$ and using eq. (D.6) entails that

$$\begin{aligned}
R_{\mathrm{m}}(\tau,\theta) &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{R}}}\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} i'r(s',i'\mid s,i)u_{\mathrm{R}}(s,i)\\
&= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{R}}}\sum_{s'\in\mathcal{S}}\sum_{i'\in I(s')}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}\sum_{\varsigma\in\mathcal{S}}\sum_{j\in I(\varsigma)} i'd(s',i'\mid\varsigma,j)t(\varsigma,j\mid s,i)u_{\mathrm{R}}(s,i)\\
&= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{R}}}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}\sum_{\varsigma\in\mathcal{S}}\sum_{j\in I(\varsigma)} w_{\mathrm{d}}(s'\mid\varsigma,j)jt(\varsigma,j\mid s,i)u_{\mathrm{R}}(s,i).
\end{aligned} \tag{D.7}$$

In order to further simplify R_{m} we set

$$\bar{t}(\varsigma,j)=\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} t(\varsigma,j\mid s,i)u_{\mathrm{R}}(s,i), \tag{D.8}$$

which is the average of the expected amount of time the mutant lineage spends in state (ς,j) over its lifetime in a single group. We also let

$$N_{\mathrm{F}}(\tau,\theta)=\mathbf{n}\cdot\mathbf{u}_{\mathrm{R}}=\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} iu_{\mathrm{R}}(s,i), \tag{D.9}$$

which is the expected number of founders of the mutant lineage in a group. Inserting these expressions into eq. (D.7), we have

$$R_{\mathrm{m}}(\tau,\theta)=\frac{1}{N_{\mathrm{F}}(\tau,\theta)}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} w_{\mathrm{d}}(s'\mid s,i)i\bar{t}(s,i). \tag{D.10}$$

D.2 Reproductive number R_0

We will now rewrite eq. (D.10) in terms of the individual-centered lineage fitness proxy $R_0(\tau, \theta)$. For this, we set

$$N_{\mathrm{L}}(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i\bar{t}(s, i), \tag{D.11}$$

which is the expected total size of the mutant lineage over its lifetime in a single group. Extending the argument of Mullon and Lehmann (2014, Appendix A), this is also

$$N_{\mathrm{L}}(\tau, \theta) = N_{\mathrm{F}}(\tau, \theta) + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w_{\mathrm{p}}(s' \mid s, i) i\bar{t}(s, i), \tag{D.12}$$

since $N_{\mathrm{F}}(\tau, \theta)$ is the expected number of mutant individuals founding a single group and the sum is the expected number of mutant offspring settling locally and produced over the lifetime of the mutant lineage in that group. Subtracting eq. (D.11) from eq. (D.12), inserting into eq. (D.10) and using eq. (6)of of the main text, we can write

$$\begin{aligned} R_{\mathrm{m}}(\tau, \theta) &= \frac{1}{N_{\mathrm{F}}(\tau, \theta)} \left(N_{\mathrm{F}}(\tau, \theta) + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' \mid s, i) i\bar{t}(s, i) - N_{\mathrm{L}}(\tau, \theta) \right) \\ &= \frac{1}{N_{\mathrm{F}}(\tau, \theta)} \big(N_{\mathrm{F}}(\tau, \theta) + N_{\mathrm{L}}(\tau, \theta) R_0(\tau, \theta) - N_{\mathrm{L}}(\tau, \theta) \big), \end{aligned} \tag{D.13}$$

where the second line follows from using eq. (14). Inserting eq. (14) of the main text and eq. (D.13) into eq. (D.10) gives

$$R_{\mathrm{m}}(\tau, \theta) = 1 + \frac{N_{\mathrm{L}}(\tau, \theta)}{N_{\mathrm{F}}(\tau, \theta)} \left(R_0(\tau, \theta) - 1 \right), \tag{D.14}$$

which shows that $R_{\mathrm{m}}(\tau, \theta) \leq 1 \iff R_0(\tau, \theta) \leq 1$, whereby

$$R_0(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \tag{D.15}$$

We note that in order to compute $R_0(\tau, \theta)$ (or $R_{\mathrm{m}}(\tau, \theta)$) one needs to compute the matrix

R and its leading right eigenvector (eq. (D.5)), which allows to evaluate $\bar{t}(s,i)$ and $q_0(s,i)$ (see Table 1). Matrix **R** will often be of much smaller dimensions that **A** (see Massol et al., 2009) and is obtained from the transient matrix **P** of the absorbing Markov chain describing the dynamics of the mutant in a single group (the discrete time analogue of matrix $\tilde{G}$ in Massol et al., 2009, eq. 11 and of matrix $\tilde{B}$ in Metz and Gyllenberg, 2001, eq. 5.a, who both considered a continuous time process) and matrix **D** (the analogue of the second term in eq. 11 of Massol et al., 2009).

Appendix E: Connections to previous inclusive fitness theory results

We here provide different connections to fitness components that appear in the literature.

E.1 Fitness decomposition: philopatric and dispersed

We start by further decomposing the two fitness components in eq. (6) of the main text. First, we can write

$$w_{\mathrm{p}}(s' \mid s,i) = w_{\mathrm{p}}(s',s,i)p(s' \mid s,i), \tag{E.1}$$

where $p(s' \mid s,i)$ is the probability that a group will be in state s' in the offspring generation given that it was in state (s,i) in the parental generation and $w_{\mathrm{p}}(s',s,i)$ is the expected number of successful philopatric offspring given that the offspring settle in a group in state s' and the parent reproduced in a group in state (s,i). We can also write

$$w_{\mathrm{d}}(s' \mid s,i) = \sum_{x\in\mathcal{S}} w_{\mathrm{d}}(s',x,s,i)\tilde{p}(s' \mid x,s,i)p^{\circ}(x), \tag{E.2}$$

where $p^{\circ}(x)$ is the (neutral) probability that a group randomly sampled in the monomorphic resident population is in state x (see eq. (A.1)). Here, $\tilde{p}(s' \mid x,s,i)$ is the probability that a group that was in state $(x,0)$ in the parental generation and has been colonized by a mutant descending from a group in state (s,i) will become a group in state s' in the offspring generation, and $w_{\mathrm{d}}(s',x,s,i)$ is the expected number of dispersing offspring that a single mutant produces given that it resides in a group in state (s,i) and given that the group where the offspring settle is in state s' in the offspring generation and was in state $(x,0)$ in the parental generation.

The conditional fitness functions $w_{\mathrm{p}}(s',s,i)$ and $w_{\mathrm{d}}(s',x,s,i)$ are the elementary individual-based fitness components of models in demographically structured populations (e.g., eqs. 31-32 of Rousset and Ronce, 2004, or eqs. A-7–A-9 of Lehmann et al., 2006). Most demographic explicit models in the literature further usually assume that $\tilde{p}(s' \mid \varsigma, s, i) = p^{\circ}(s' \mid \varsigma)$; namely, that the composition of a natal group of mutants does not affect the transition probability of other groups (usually owing to the fact that individuals migrate independently from each other, e.g., Metz and Gyllenberg, 2001; Parvinen et al., 2003; Cadet et al., 2003; Rousset and Ronce, 2004; Lehmann et al., 2006; Alizon and Taylor, 2008; Rodrigues and Gardner, 2012).

We now prove the expressions for the two above conditional expectations (eqs. (E.1)–(E.2)). From Table 1, the first conditional expectation (eq. (E.1)) can be written as

$$w_{\mathrm{p}}(s' \mid s,i) = \frac{1}{i}\sum_{i' \in I(s')} i' p(s', i' \mid s, i) = \frac{p(s' \mid s,i)}{i} \sum_{i' \in I(s')} i' \underbrace{\frac{p(s', i' \mid s, i)}{p(s' \mid s, i)}}_{p(i' \mid s', s, i)} = w_{\mathrm{p}}(s', s, i) p(s' \mid s, i), \tag{E.3}$$

where $p(i' \mid s', s, i)$ is the probability that a group will have i' mutants in the offspring generation given that it is in state (s, i) in the parental generation and in state s' in the offspring generation. For the last equality we used

$$w_{\mathrm{p}}(s', s, i) i = \sum_{i' \in I(s')} i' p(i' \mid s', s, i), \tag{E.4}$$

where $w_{\mathrm{p}}(s', s, i)$ the expected number of successful philopatric offspring that a single mutant produces given that it resides in a group in state (s, i) and that the group state in the offspring generation is s'.

From Table 1, the second conditional expectation (eq. (E.2)) is

$$w_{\mathrm{d}}(s' \mid s,i) = \frac{1}{i}\sum_{i' \in I(x)} i' d(s', i' \mid s, i), \tag{E.5}$$

where, conditioning on the state of the group in the parental generation where the offspring

disperse to, we can write

$$d(s',i' \mid s,i) = \sum_{x\in\mathcal{S}} d(s',i' \mid x,s,i)p^{\circ}(x) = \sum_{x\in\mathcal{S}} \underbrace{\frac{d(s',i' \mid x,s,i)}{\tilde{p}(s' \mid x,s,i)}}_{d(i'|s',x,s,i)} \tilde{p}(s' \mid x,s,i)p^{\circ}(x). \tag{E.6}$$

Here, we used in the conditioning the neutral probability $p^{\circ}(x)$ that a group randomly sampled in the monomorphic resident population is in demographic state x, since dispersing offspring can only land in a group whose state in the parental generation is determined by the resident dynamics. The term $d(s',i' \mid x,s,i)$ is the expected number of groups in (s',i') produced by a group in state (s',i') and given that they were in state $(0,x)$ in the parental generation (with 0 mutants). We now let

$$d(i' \mid s',x,s,i) = \frac{d(s',i' \mid x,s,i)}{\tilde{p}(s' \mid x,s,i)}, \tag{E.7}$$

where $\tilde{p}(s' \mid x,s,i)$ is the probability that a group will be in state s' in the offspring generation, given that it was in state $(x,0)$ in the parental generation and has been colonized by a mutant descending from a group in state (s,i). Further we have

$$w_{\mathrm{d}}(s',x,s,i) = \frac{1}{i} \sum_{i'\in I(s')} i' d(i' \mid s',x,s,i), \tag{E.8}$$

which is the expected number of dispersing offspring that a single mutant produces given that it resides in a group in state (s,i) and given that the group where the offspring settle is in demographic state s' in the offspring generation and was in state $(x,0)$ in the parental generation. Substituting eq. (E.6), we then obtain eq. (E.2).

E.2 Connection to the direct fitness method

We now connect our results to the direct fitness method (Taylor and Frank, 1996; Rousset, 2004), which, formally, consists of computing the selection gradient on a mutant type when mutant phenotypic deviations are small relative to the resident and is sufficient to evaluate the condition of convergence stability under essentially all conditions (Rousset, 2004; Lehmann and Rousset, 2014). Hence, results from the direct fitness method for one-dimensional quantitative

traits should match $\partial\rho(\tau,\theta)/\partial\tau$ when the type space is real valued ($\Theta=\mathbb{R}$), which we henceforth assume.

E.3 Sensitivity of invasion fitness

To prove the connection to the direct fitness approach we first derive a generic expression for invasion fitness sensitivity $\partial\rho(\tau,\theta)/\partial\tau$ under our model assumptions. To that aim, we rewrite invasion fitness by using eq. (C.5) as

$$\rho(\tau,\theta)=\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')w(s'\mid s,i)q(i\mid s)q_{\mathrm{v}}(s), \tag{E.9}$$

where

$$q_{\mathrm{v}}(s)=\frac{q(s)}{V_{\mathrm{T}}(\tau,\theta)}. \tag{E.10}$$

Since, $v^{\circ}(s')$ depends only on the resident, we have

$$\frac{\partial\rho(\tau,\theta)}{\partial\tau}=\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')\left[\frac{\partial w(s'\mid s)}{\partial\tau}q^{\circ}(i\mid s)q_{\mathrm{v}}^{\circ}(s)+w^{\circ}(s'\mid s,i)\frac{\partial\left[q(i\mid s)q_{\mathrm{v}}(s)\right]}{\partial\tau}\right], \tag{E.11}$$

where all derivatives, here and throughout, are evaluated at $\tau=\theta$. Using the neutral reproductive values (eq. (A.3)), we have

$$\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s')w^{\circ}(s'\mid s)\frac{\partial\left[q(i\mid s)q_{\mathrm{v}}(s)\right]}{\partial\tau}=\sum_{s\in\mathcal{S}}\sum_{i\in I(s)}v^{\circ}(s)\frac{\partial\left[q(i\mid s)q_{\mathrm{v}}(s)\right]}{\partial\tau}. \tag{E.12}$$

Further, we have

$$\begin{aligned}\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} v^{\circ}(s)\frac{\partial\left[q(i\mid s)q_{\mathrm{v}}(s)\right]}{\partial\tau} &= \frac{\partial}{\partial\tau}\left[\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} v^{\circ}(s)q(i\mid s)q_{\mathrm{v}}(s)\right]\\ &= \frac{\partial}{\partial\tau}\left[\sum_{s\in\mathcal{S}}\sum_{i\in I(s)} v^{\circ}(s)\frac{iu_{\mathrm{A}}(i,s)}{\mathbf{v}^{\circ}\cdot\mathbf{u}_{\mathrm{A}}}\right]\\ &= \frac{\partial}{\partial\tau}(1)\\ &= 0. \end{aligned} \tag{E.13}$$

Hence, substituting eq. (E.13) into eq. (E.11) using eq. (E.10) gives

$$\frac{\partial\rho(\tau,\theta)}{\partial\tau} = \frac{1}{V_{\mathrm{T}}^{\circ}}\sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}} v^{\circ}(s')\left[\sum_{i\in I(s)}\frac{\partial w(s'\mid s,i)}{\partial\tau}q^{\circ}(i\mid s)\right]q^{\circ}(s), \tag{E.14}$$

where $V_{\mathrm{T}}^{\circ} = V_{\mathrm{T}}(\theta,\theta)$ and without loss of generality we can normalize the elements $v^{\circ}(s')$ such that

$$V_{\mathrm{T}}^{\circ} = \sum_{s\in\mathcal{S}} v^{\circ}(s)q^{\circ}(s) = 1, \tag{E.15}$$

which is usually assumed in sensitivity analysis.

Note that $w(s'\mid s,i)$ is the individual fitness of a mutant with phenotype τ when its group members consist of $i-1$ individuals with phenotype τ and $n(s)-i$ individuals with phenotype θ. Thus, we can write

$$\frac{\partial w(s'\mid s,i)}{\partial\tau} = \frac{\partial w(s'\mid s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial\tau_j} + (n(s)-1)\frac{\partial w(s'\mid s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial\tau_k}\frac{i-1}{n(s)-1}, \tag{E.16}$$

where $\boldsymbol{\tau}_{-j} = (\tau_1,...,\tau_{j-1},\tau_{j+1},...\tau_{n(s)-1})$ is the vector collecting the phenotypes of the neighbors of an individual j and $k\neq j$. Substituting into eq.(E.14), setting $V_{\mathrm{T}}^{\circ}=1$, and using the definition of relatedness given in the Table 1 gives

$$\frac{\partial\rho(\tau,\theta)}{\partial\tau} = \sum_{s'\in\mathcal{S}}\sum_{s\in\mathcal{S}} v^{\circ}(s')\left[\frac{\partial w(s'\mid s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial\tau_j} + (n(s)-1)\frac{\partial w(s'\mid s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial\tau_k}r^{\circ}(s)\right]q^{\circ}(s). \tag{E.17}$$

E.3.1 Connection to direct fitness method results

Here, we prove that eq. (E.17) returns exactly eqs. 26–27 of Rousset and Ronce (2004) when states are population sizes and each individuals migrates independently from each other. This proves that we recover in general the results obtained by the direct fitness method since the results of Rousset and Ronce (2004) generalize those of Taylor and Frank (1996) to demographically structured populations.

In order to show the connection, we need to prove that

$$q^{\circ}(s) = \frac{p^{\circ}(s)n(s)}{\bar{n}^{\circ}}, \tag{E.18}$$

where $\bar{n}^{\circ} = \sum_{s\in\mathcal{S}} n(s)p^{\circ}(s)$ is the average group size in a monomorphic θ population. For this, we first note that from the definition of $q(s)$ (Table 1), we have

$$\begin{aligned} q^{\circ}(s') &= \sum_{i'\in I(s')} q^{\circ}(s', i') \\ &= \sum_{i'\in I(s')} \frac{i'u^{\circ}(s', i')}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}^{\circ}} \\ &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}^{\circ}} \sum_{i'\in I(s')} \sum_{s\in\mathcal{S}} \sum_{i\in I(s)} i'a(s', i' \mid s, i)u^{\circ}(s, i) \\ &= \frac{1}{\mathbf{n}\cdot\mathbf{u}_{\mathrm{A}}^{\circ}} \sum_{s\in\mathcal{S}} \sum_{i\in I(s)} w(s', s)iu^{\circ}(s, i), \end{aligned} \tag{E.19}$$

which yields

$$q^{\circ}(s') = \sum_{s\in\mathcal{S}} w^{\circ}(s' \mid s)q^{\circ}(s) \tag{E.20}$$

and shows that the vector collecting the $q^{\circ}(s)$ is a right unit eigenvector of the matrix with elements $w^{\circ}(s' \mid s)$. Let us now substitute the trial solution $q^{\circ}(s) = n(s)p^{\circ}(s)/\bar{n}^{\circ}$ into eq. (E.20), whereby

$$n(s')p^{\circ}(s') = \sum_{s\in\mathcal{S}} w^{\circ}(s' \mid s)n(s)p^{\circ}(s). \tag{E.21}$$

The right hand side is the total expected number of successful offspring in groups in state s' that descend from a randomly sampled group in the population. At stationarity this must be equal to $n(s')p^\circ(s')$, since $p^\circ(s')$ is the probability of sampling a group in state s' and $n(s')$ is the number of successful offspring in that group. Hence, $q^\circ(s) = n(s)p^\circ(s)/\bar{n}^\circ$ satisfies eq. (E.20) and eq. (E.18) holds.

We now expand eq. (E.17) by using the decomposition of individual fitness $w(s' \mid s, i) = w_{\mathrm{p}}(s' \mid s, i) + w_{\mathrm{d}}(s' \mid s, i)$ (eq. (6) of the main text), which allows us to write

$$\frac{\partial w(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \frac{\partial w_{\mathrm{p}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_{\mathrm{d}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j}. \tag{E.22}$$

Each of these component will be further expanded by using eqs. (E.1)–(E.2). For the philopatric component, from eq. (E.1) we can write

$$\frac{\partial w_{\mathrm{p}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \frac{\partial w_{\mathrm{p}}(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} p^\circ(s' \mid s) + w_{\mathrm{p}}^\circ(s', s) \frac{\partial p(s' \mid s, \boldsymbol{\tau})}{\partial \tau_j}, \tag{E.23}$$

where $\boldsymbol{\tau} = (\tau_1, ..., \tau_{n(s)})$ is the vector collecting the phenotype of all individuals in a focal patch. For a neighbour $k \neq j$ of a focal mutant j we have

$$\frac{\partial w_{\mathrm{p}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} = \frac{\partial w_{\mathrm{p}}(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} p^\circ(s' \mid s) + w_{\mathrm{p}}^\circ(s', s) \frac{\partial p(s' \mid s, \boldsymbol{\tau})}{\partial \tau_k}. \tag{E.24}$$

In order to expand the dispersal component in eq. (E.22), we follow the assumption of Rousset and Ronce, 2004 that the composition of a natal group of mutants does not affect the transition probability of other groups and thus set $\tilde{p}(s' \mid \varsigma, s, i) = p^\circ(s' \mid \varsigma)$ in eq. (E.2). Then, we can write

$$\frac{\partial w_{\mathrm{d}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \sum_{\varsigma \in \mathcal{S}} \frac{\partial w_{\mathrm{d}}(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} p^\circ(s' \mid \varsigma) p^\circ(\varsigma) \tag{E.25}$$

and for $k \neq j$

$$\frac{\partial w_{\mathrm{d}}(s' \mid s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} = \sum_{\varsigma \in \mathcal{S}} \frac{\partial w_{\mathrm{d}}(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} p^\circ(s' \mid \varsigma) p^\circ(\varsigma). \tag{E.26}$$

Substituting eqs. (E.22)–(E.26) into eq. (E.17) yields

$$\frac{\partial \rho(\tau,\theta)}{\partial \tau} = \sum_{s\in\mathcal{S}} \left[S_{\mathrm{f}}(s) + S_{\mathrm{Pr}}(s)\right] \frac{n(s)p^{\circ}(s)}{\bar{n}^{\circ}}, \tag{E.27}$$

where

$$S_{\mathrm{f}}(s) = \sum_{s'\in\mathcal{S}} v^{\circ}(s') \left[\left(\frac{\partial w_{\mathrm{p}}(s',s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_{\mathrm{p}}(s',s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial \tau_j}(n(s)-1)r^{\circ}(s) \right) p^{\circ}(s' \mid s) \right.$$
$$\left. + \sum_{\varsigma\in\mathcal{S}} \left(\frac{\partial w_{\mathrm{d}}(s',\varsigma,s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_{\mathrm{d}}(s',\varsigma,s,\tau_j,\boldsymbol{\tau}_{-j})}{\partial \tau_j}(n(s)-1)r^{\circ}(s) \right) p^{\circ}(s' \mid \varsigma) p^{\circ}(\varsigma) \right], \tag{E.28}$$

and

$$S_{\mathrm{Pr}}(s) = \sum_{s'\in\mathcal{S}} v^{\circ}(s') \left[w_{\mathrm{p}}^{\circ}(s',s) \frac{\partial p(s' \mid s,\boldsymbol{\tau})}{\partial \tau_j} \left[1 + (n(s)-1)r^{\circ}(s)\right] \right] \tag{E.29}$$

If we let s be group size and set $n(s) = s$, then eqs. (E.28)–(E.29) are equivalent to eqs. (A.34)–(A.36) of Lehmann and Rousset (2010). If we multiply eq. (E.27) by $n(s')/n(s')$ and use class reproductive values $\alpha^{\circ}(s') = v^{\circ}(s')n(s')$ and the definition of frequency functions of Rousset and Ronce (2004, eqs. 33–34), then eqs. (E.28)–(E.29) are proportional to eqs. (26)–(27) of Rousset and Ronce (2004).

Appendix F: Fixed number of age or stage classes

We here consider a situation where there is a uniform demography, i.e., each group is of constant and same size but now each individual belongs to one of a set of fixed classes where the set of class is given by $\mathcal{C} = \{1,\dots,n_{\mathrm{c}}\}$. An example would be age structure due to overlapping generations or different castes of social insects like workers and queens.

Let $\mathbf{i} = (i_1,...,i_{n_{\mathrm{c}}}) \in i$ be the vector of the number of mutant alleles of type τ in class 1 to n_{c} in a group where i is the set of possible configurations. Let $I = (I_1 \times \cdots \times I_{n_{\mathrm{c}}}) \setminus \mathbf{0}$ where $I_x = \{0,1,...,n_x\}$ is set of the number of mutant alleles in class x and n_x is the number of individuals in that class. We remove the all zero state $\mathbf{0}$ from I so that we only track states

with at least one mutant in some class. Let $\mathbf{A}$ be the matrix with elements $a(\mathbf{i}' \mid \mathbf{i})$ giving the expected number of groups in state $\mathbf{i}'$ produced by a focal group in state $\mathbf{i}'$. Further, let $\mathbf{n}$ be the vector collecting the total number of mutant individuals for each state; i.e., the $\mathbf{i}$-th state of $\mathbf{n}$ is given by $x(\mathbf{i}) = \sum_{y \in \mathcal{C}} i_y$.

We now prove the expression for lineage fitness for a class-structured population (see Box 3) for this model and proceed in the same way as in Appendices A–C. Hence, we first note that

$$\sum_{\mathbf{i}' \in i} i'_y a(\mathbf{i}' \mid \mathbf{i}) = \sum_{x \in \mathcal{C}} w(y, x, \mathbf{i}) i_x, \tag{F.1}$$

where $w(y, x, \mathbf{i})$ is the expected number of class y offspring produced by a class x mutant when in a group in state $\mathbf{i}$. Now, from $\mathbf{n} \cdot \rho \mathbf{u}_{\mathrm{A}} = (\mathbf{n} \cdot \mathbf{A}\mathbf{u}_{\mathrm{A}})$ and eq. (F.1), we have

$$\begin{aligned}
\rho(\tau, \theta) &= \frac{1}{\mathbf{n} \cdot \mathbf{u}_{\mathrm{A}}} \sum_{\mathbf{i}' \in I} \sum_{\mathbf{i} \in I} x(\mathbf{i}') a(\mathbf{i}' \mid \mathbf{i}) u_{\mathrm{A}}(\mathbf{i}) \\
&= \frac{1}{\mathbf{n} \cdot \mathbf{u}_{\mathrm{A}}} \sum_{\mathbf{i}' \in I} \sum_{\mathbf{i} \in I} \sum_{y \in \mathcal{C}} i'_y a(\mathbf{i}' \mid \mathbf{i}) u_{\mathrm{A}}(\mathbf{i}) \\
&= \frac{1}{\mathbf{n} \cdot \mathbf{u}_{\mathrm{A}}} \sum_{\mathbf{i} \in I} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} w(y, x, \mathbf{i}) i_x u_{\mathrm{A}}(\mathbf{i}) \\
&= \sum_{\mathbf{i} \in I} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} w(y, x, \mathbf{i}) q(x, \mathbf{i})
\end{aligned} \tag{F.2}$$

where

$$q(x, \mathbf{i}) = \frac{i_x u_{\mathrm{A}}(\mathbf{i})}{\mathbf{n} \cdot \mathbf{u}_{\mathrm{A}}}, \tag{F.3}$$

which satisfies $\sum_{x \in \mathcal{C}} \sum_{\mathbf{i} \in I} q_x(\mathbf{i}) = 1$. Defining lineage fitness as

$$W(\tau, \theta) = \sum_{\mathbf{i} \in I} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} w(y, x, \mathbf{i}) q(x, \mathbf{i}) \ , \tag{F.4}$$

eq. (F.2) shows that $\rho(\tau, \theta) = W(\tau, \theta)$.

Second, we derive an expression for the inclusive fitness $W_{\mathrm{IF}}(\tau, \theta)$. Inclusive fitness requires

that we calculate reproductive values, so we gather into the vector $\mathbf{v}^\circ$ the elements

$$v^\circ(\mathbf{i}) = \sum_{x\in\mathcal{C}} i_x v^\circ(x), \tag{F.5}$$

where $v^\circ(x)$ is the reproductive value of an individual in class x, which satisfies the recursion

$$v^\circ(x) = \sum_{y\in\mathcal{C}}\sum_{x\in\mathcal{C}} v^\circ(y) w^\circ(y,x), \tag{F.6}$$

where $w^\circ(y,x)$ is the neutral fitness (fitness in a monomorphic resident population). Now, from $\mathbf{v}^\circ\cdot\rho\mathbf{u}_\mathrm{A} = (\mathbf{v}^\circ\cdot\mathbf{A}\mathbf{u}_\mathrm{A})$ and eq. (F.6), we have

$$\begin{aligned}
\rho(\tau,\theta) &= \frac{1}{\mathbf{v}^\circ\cdot\mathbf{u}_\mathrm{A}}\sum_{\mathbf{i}'\in I}\sum_{\mathbf{i}\in I} v^\circ(\mathbf{i}')a(\mathbf{i}'\mid\mathbf{i})u_\mathrm{A}(\mathbf{i}) \\
&= \frac{1}{\mathbf{v}^\circ\cdot\mathbf{u}_\mathrm{A}}\sum_{y\in\mathcal{C}}\sum_{\mathbf{i}'\in I}\sum_{\mathbf{i}\in I} i'_y v^\circ(y)a(\mathbf{i}'\mid\mathbf{i})u_\mathrm{A}(\mathbf{i}) \\
&= \frac{1}{\mathbf{v}^\circ\cdot\mathbf{u}_\mathrm{A}}\sum_{y\in\mathcal{C}}\sum_{x\in\mathcal{C}}\sum_{\mathbf{i}\in I} v^\circ(y)w(y,x,\mathbf{i})i_x u_\mathrm{A}(\mathbf{i}) \\
&= \frac{1}{V_\mathrm{T}(\tau,\theta)}\sum_{y\in\mathcal{C}}\sum_{x\in\mathcal{C}}\sum_{\mathbf{i}\in I} v^\circ(y)w(y,x,\mathbf{i})q(x,\mathbf{i}),
\end{aligned} \tag{F.7}$$

where

$$V_\mathrm{T}(\tau,\theta) = \frac{\mathbf{v}^\circ\cdot\mathbf{u}_\mathrm{A}}{\mathbf{n}\cdot\mathbf{u}_\mathrm{A}} = \sum_{x\in\mathcal{C}} v^\circ(x)q(x) \tag{F.8}$$

and $q(x) = \sum_{\mathbf{i}\in I} q(x,\mathbf{i})$ is the probability of sampling a lineage member in class x. Suppose we now form a weighted multiple regression

$$w(y,x,\mathbf{i}) = w^\circ(y,x) - c(y,x) + b_x(y,x)\frac{i_x-1}{n_x-1} + \sum_{z\in\mathcal{C}\setminus x} b_z(y,x)\frac{i_z}{n_z} + \epsilon_\mathbf{i}(y,x) \tag{F.9}$$

and least square fit the c's and the b's by minimizing

$$\sum_{\mathbf{i}\in I}\epsilon_\mathbf{i}(y,x)^2 q(x,\mathbf{i})/q(x), \tag{F.10}$$

where the weights are given by $q(x,\mathbf{i})/q(x)$. This procedure guarantees that the weighted sum of errors is zero, or that $\sum_{\mathbf{i}\in I}\epsilon_{\mathbf{i}}(y,x)(q(x,\mathbf{i})/q(x))=0$. Let us further define

$$q(i_y \mid x)=\sum_{\mathbf{i}\in I(i_y)} q(x,\mathbf{i})/q(x), \tag{F.11}$$

where $I(i_y)$ denotes the elements of the set I whose number of class y mutants is equal to i_y. Then, we can interpret $q(i_y \mid x)$ as the probability that there are i_y mutants in class y given that a mutant has a sampled a mutant in class x. Substituting all this into eq. (F.7), we have

$$\begin{aligned}\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\sum_{y\in\mathcal{C}}\sum_{x\in\mathcal{C}}v^{\circ}(y)\Bigg[&w^{\circ}(y,x)-c(y,x)\\&+\sum_{i_x\in I_x^+}b_x(y,x)\frac{i_x-1}{n_x-1}q(i_x\mid x)+\sum_{z\in\mathcal{C}\setminus x}\sum_{i_z\in I_z^+}b_z(y,x)\frac{i_z}{n_z}q(i_z\mid x)\Bigg]q(x)\end{aligned} \tag{F.12}$$

where we only sum over the elements $I_x^+=\{1,\ldots,n_x\}$ in the first sum of the second line since $w(y,x,\mathbf{i})=0$ for all $i_x=0$ (the second sum in the second line uses i_z^+ for ease of notation).

Let us now define inclusive fitness as

$$W_{\mathrm{IF}}(\tau,\theta)=1+\sum_{y\in\mathcal{C}}\sum_{x\in\mathcal{C}}v^{\circ}(y)\left[-c(y,x)+\sum_{z\in\mathcal{C}}b_z(y,x)\,r(z\mid x)\right]q(x), \tag{F.13}$$

where

$$r(z\mid x)=\sum_{i_z\in I_z^+}\left[\delta_{zx}\frac{i_x-1}{n_x-1}+(1-\delta_{zx})\frac{i_z}{n_z}\right]q(i_z\mid x) \tag{F.14}$$

is the probability that, conditional on being sampled in class x, an individual carrying the mutant experiences a randomly sampled neighbour in class z that also carries the mutant allele, and where δ_{zx} is the Kronecker Delta ($\delta_{zx}=1$ if $z=x$, zero otherwise). Substituting eqs. (F.13)–(F.14) into eq. (F.12) and using the definition of reproductive value (eq. (F.5)), we obtain

$$\rho(\tau,\theta)=\frac{1}{V_{\mathrm{T}}(\tau,\theta)}\left[V_{\mathrm{T}}(\tau,\theta)-1+W_{\mathrm{IF}}(\tau,\theta)\right], \tag{F.15}$$

whereby

$$\rho(\tau,\theta) \leq 1 \iff W_{\mathrm{IF}}(\tau,\theta) \leq 1. \tag{F.16}$$

If we now choose the normalization of the reproductive values $v^{\circ}(x)$ (as in the section C) such that

$$V_{\mathrm{T}}(\tau,\theta) = \sum_{x\in\mathcal{C}} v^{\circ}(x)q(x) = 1, \tag{F.17}$$

then eq. (F.15) implies

$$\rho(\tau,\theta) = W_{\mathrm{IF}}(\tau,\theta).$$

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