

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

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Abstract

2 How should fitness be measured to determine which phenotype or “strategy” is unin-
vadable when evolution occurs in subdivided populations subject to local demographic and
4 environmental heterogeneity? Several invasion fitness measures, such as basic reproductive
number, lifetime dispersal success of a local lineage, or inclusive fitness have been proposed
6 to address this question, but the relationships between them and their generality remains
unclear. Here, we ascertain uninvasibility (all mutant strategies always go extinct) in terms
8 of the growth rate of a mutant allele arising as a single copy in a population. We show from
this growth rate that uninvasibility is equivalently characterized by at least three conceptually
10 distinct invasion fitness measures: (i) lineage fitness, giving the average personal fitness
of a randomly sampled mutant lineage member; (ii) inclusive fitness, giving a reproductive
12 value weighted average of the direct fitness cost and relatedness weighted indirect fitness
benefits accruing to a randomly sampled mutant lineage member; and (iii) three types of
14 reproductive numbers, giving lifetime success of a local lineage. Our analysis connects ap-
proaches that have been deemed different, generalizes the exact version of inclusive fitness
16 to class-structured populations, and provides a biological interpretation of selection on a
mutant allele under arbitrary strength of selection.

18 Keywords: growth rate, invasion fitness, inclusive fitness, reproductive number, invasibility

Introduction

20 It is well established (if perhaps unwelcome) that in general adaptiveness is not increased by
short-term evolution (Moran, 1964; Eshel, 1991; Ewens, 2004). In contrast, when long-term evo-
22 lution can be described by a substitution process where a population transitions from one fixed
allele to another through the recurrent invasion of mutant alleles, the population may eventually
24 evolve to an uninvadable state (i.e., a state that is resistant to invasion by any alternative strat-
egy, Eshel, 1991, 1996; Hammerstein, 1996; Weissing, 1996; Van Cleve, 2015). An uninvadable
26 strategy is “optimal” among a specified set of alternatives because it maximizes the growth rate
of the underlying coding gene when the gene is rare (Eshel, 1991, 1996; Hammerstein, 1996;
28 Weissing, 1996). Uninvadable strategies are thus adaptations (*sensu* Reeve and Sherman, 1993)
and evolutionary invasion analysis has become a very successful approach to understand theo-
30 retically long term phenotypic evolution (e.g., Maynard Smith, 1982; Eshel and Feldman, 1984;
Parker and Maynard Smith, 1990; Charlesworth, 1994; Metz et al., 1996; Ferrière and Gatto,
32 1995; McNamara et al., 2001; Lion and van Baalen, 2007; Metz, 2011; van Baalen, 2013).

When a mutant allele arises as a single copy in a population, its growth rate, ρ , determines in
34 general whether the mutant allele will eventually go extinct or survive (Tuljapurkar, 1989; Metz
et al., 1992; Rand et al., 1994; Charlesworth, 1994; Ferrière and Gatto, 1995; Caswell, 2000).
36 Intuitively, the growth rate is a gene-centered measure of evolutionary success (*sensu* Dawkins,
1978). Technically, the growth rate is the dominant eigenvalue of a matrix determining the tran-
38 sitions between the different states in which the mutant allele can reside and describes the growth
of a typical trajectory of the mutant lineage since its appearance as a single copy (Tuljapurkar,
40 1989; Tuljapurkar et al., 2003; Caswell, 2000; Ferrière and Gatto, 1995). Since evolutionary
biologists often try to understand adaptations in terms of the fitness properties exhibited by in-
42 dividuals, such as survival and fecundity, it is important to understand the exact interpretation
of the growth rate in terms of individual-centered fitness components. Interpreting the growth
44 rate this way seems clear in panmictic populations. In the absence of genetic conflict within
individuals, maximizing the growth rate amounts to maximizing the personal (lifetime) fitness
46 of an individual, which is determined by its survival and fecundity schedules in stage-structured
populations (Eshel and Feldman, 1984; Hammerstein, 1996; Weissing, 1996; Charlesworth, 1994;

48 Caswell, 2000). This result relies on the assumption that mutants are rare, which allows one to neglect the interactions between individuals carrying the mutant allele in the invasion analysis.

50 When dispersal is limited due to family or spatial population structure, interactions between mutants can no longer be neglected when evaluating the growth rate; mutant-mutant interactions
52 will occur locally at the level of the interaction group even if the mutant is globally rare. Since the mutant is no longer necessarily locally rare, one needs to track groups with different numbers
54 of mutant alleles (i.e., the local distribution of mutants). In this case, the growth rate ρ becomes the eigenvalue of a matrix describing the transitions between different group states (Motro, 1982;
56 Bulmer, 1986; van Baalen and Rand, 1998; Wild, 2011). In this case, the interpretation of the growth rate in terms of individual-centered fitness components is no longer straightforward. In
58 order to understand exactly what the growth rate represents biologically, it needs to be unpacked and expressed in terms of individual-centered properties. Until now, no general interpretation
60 of the mutant growth rate has been provided for group structured populations subject to local heterogeneities, such as demographic or environmental fluctuations.

62 In the absence of a general and clear interpretation of the growth rate of a mutant allele, several different measures of *invasion fitness*, defined as any quantity allowing to determine
64 the fate of a mutant, have been proposed. One approach computes invasion fitness as the *basic reproductive number*, R_0 , of a mutant lineage (Massol et al., 2009). This gives the total number of
66 successful emigrants produced by a mutant lineage over its lifetime when the lineage was started in a single group by some *distribution of emigrants*. It is well established in mathematical biology
68 that maximizing the basic reproductive number R_0 (the eigenvalue of the next generation matrix associated with the process) is equivalent to maximizing its growth rate (holding the resident
70 population constant), and thus predicts the direction of selection in the same way (Caswell, 2000; Ellner and Rees, 2006).

72 A closely related approach puts forward the total number of successful emigrants produced by a mutant lineage over its lifetime in a single group that was founded by a *single emigrant*,
74 called R_m , as the appropriate measure of invasion fitness (Metz and Gyllenberg, 2001; Cadet et al., 2003). By assumption, this requires that individuals disperse independently and not in
76 clusters, which excludes propagule dispersal. However, a fitness measure should in general be able to account for propagule dispersal, which is important for understanding the life cycle of

78 many species. This raises the question of the general connection between R_0 and R_m and their interpretation in terms of individual-centered fitness components.

80 Further, invasion fitness can also be computed as the personal fitness of a randomly sampled carrier of the mutant allele from the founding lineage (Day, 2001; Lehmann et al., 2015; Mullon et al., 2016), which we refer as *lineage fitness*. In contrast to R_0 and R_m , lineage fitness is expressed in terms of individual-centered fitness components, but it has not yet been generalized
82 to subdivided populations with local heterogeneities.

84 Among all alternative methods for studying evolution in structured populations, the most popular one, however, has perhaps been the direct fitness method of social evolution theory (e.g., Taylor and Frank, 1996; Frank, 1998; Rousset, 2004; Wenseleers et al., 2010). This approach
86 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*. The inclusive fitness effect is a weak selection decomposition of the change in the personal fitness of a randomly sampled carrier of the mutant allele into direct
88 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 neighbours expressing the mutant. The inclusive fitness effect has helped understand the selection pressure
90 on very diverse phenotypes including the sex-ratio, reproductive effort, genomic imprinting, dispersal, menopause, parasite virulence, interactive behavior, senescence, and niche construction
92 in groups structured populations (e.g., Taylor, 1988; Haig, 1997; Frank, 1998; Gandon, 1999; Taylor and Irwin, 2000; Pen, 2000; Lehmann, 2008; Wild et al., 2009; Lion and Gandon, 2009; Johnstone and Cant, 2010; Ronce and Promislow, 2010; Akay and Van Cleve, 2012; Lion, 2013).

94 Despite their apparent differences, inclusive fitness, lineage fitness, or, more generally invasion fitness measures, are in fact tightly connected (Akay and Van Cleve, 2016). For example, under
100 constant demography, the inclusive fitness effect amounts to evaluating the sensitivity of the number of emigrants R_m or the growth rate ρ with respect to variation in continuous trait values
102 and lineage fitness is equal to ρ (Ajar, 2003; Lehmann et al., 2015; Mullon et al., 2016), but the general connection between mutant growth rates, inclusive fitness, lineage fitness, and the
104 reproductive numbers, has not been worked out under arbitrary mutant trait types and selection strength with local demographic and/or environmental heterogeneities.
106

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

Model

114 Life-cycle

We consider a population of haploid individuals divided into an infinite number of groups. The
116 population is censused at discrete time demographic periods. In each period, each group, inde-
pendently from each other, can be in one of a countable number of demographic-environmental
118 states. A state can determine the number of individuals in a group (“demographic” state) and/or
any environmental factor affecting all individuals within a group (“environmental” state). Local
120 state fluctuations in the population due to demographic or environmental processes can result
in population level patterns of temporal and spatial heterogeneity.

122 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
124 population; in other words, we consider an island model of dispersal (Wright, 1931). The model
allows us to represent classical metapopulation processes with variable local group sizes (Chesson,
126 1981; Rousset and Ronce, 2004), insect colony dynamics with endogenous growth (Avila and
Fromhage, 2015), as well as compartmentalized replication as occurs in the stochastic corrector
128 model for prebiotic evolution (Szathmary and Demeter, 1987; Grey et al., 1995).

We assume that only two alleles can segregate in the population, a mutant allele with type
130 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
132 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
134 say that θ is *uninvadable*. A state that is uninvadable is an evolutionarily stable state. Our aim

is to characterize uninvasibility mathematically and biologically.

136 **The resident demographic equilibrium**

Following standard assumptions for the dynamics of mutant-resident substitutions (Eshel and
138 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
140 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
142 time Markov chain on a countable 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,
144 and other events occur).

Because groups may affect each other demographically through dispersal, the transition prob-
146 abilities for this Markov chain may depend endogenously on the resident population dynamics.
But since there is an infinite number of groups, the set of infinite interacting Markov chains (one
148 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
150 that this Markov chain is regular, irreducible and aperiodic (Karlin and Taylor, 1975; Iosifescu,
2007), and thus has a stationary distribution (see Appendix A).

152 **The mutant multitype branching process**

We now introduce a mutant into the backdrop of the resident population in its stationary demo-
154 graphic 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 $i \in I(s) = \{1, 2, \dots, n(s)\}$ mutant individuals at time $t = 0, 1, 2, \dots$
156 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
158 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
160 $t = 0$, 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,

162 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 extinction of the mutant, we assume that it
164 will always remain rare in the total population and approximate the mutant stochastic process
as a multitype branching process (Harris, 1963; Karlin and Taylor, 1975; Wild, 2011). It is then
166 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 state (s', i') that are “produced” over one demographic time
168 period by a focal group in state (s, i) when the population is otherwise monomorphic for τ . It is
useful to decompose this as

$$a(s', i' \mid s, i) = p(s', i' \mid s, i) + d(s', i' \mid s, i), \quad (1)$$

170 which consists of two terms representing two distinct biological processes. The first is the intra-
group (or intra-compartmental) change described by the transition probability $p(s', i' \mid s, i)$ that
172 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,
174 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
176 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
178 demographic time period. For compartmental replication processes (e.g., Grey et al., 1995) this
means producing a group in state (s', i') .

180 **Invasion fitness**

It follows from standard results on multitype branching processes (Harris, 1963; Karlin and
182 Taylor, 1975) that the lineage descending from a single mutant τ arising in any of the demographic
state of the resident θ population, will go extinct with probability one if the leading eigenvalue
184 $\rho(\tau, \theta)$ of $\mathbf{A}(\tau, \theta)$ is less than or equal to 1. Namely, extinction with probability one occurs if and
only if

$$\rho(\tau, \theta) \leq 1, \quad (2)$$

186 where ρ satisfies

$$\rho(\tau, \theta) \mathbf{u}(\tau, \theta) = \mathbf{A}(\tau, \theta) \mathbf{u}(\tau, \theta) \quad (3)$$

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

188 The interpretation of $\rho(\tau, \theta)$ is that it gives the asymptotic growth rate of an average trajectory of a mutant lineage; that is, the collection of individuals descending from an individual in which
190 the mutation appeared (Cohen, 1979; Tuljapurkar et al., 2003). In the long-run, the average mutant lineage grows in the direction of $\mathbf{u}(\tau, \theta)$ so that this vector can be interpreted as a quasi-
192 stationary distribution of group genetic-demographic-environmental states containing at least one individual belonging to the mutant lineage. Namely, element (s, i) of \mathbf{u} , that is $u(s, i)$, is the
194 asymptotic frequency of s -type groups with $i \geq 1$ mutants; this interpretation holds whether the mutant lineage goes extinct or invades the population (Harris, 1963).

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

$$\rho(\tau, \theta) \leq 1 \quad \forall \tau \in \Theta. \quad (4)$$

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

200 Now that we have a mathematical characterization of uninviability in terms of the growth rate $\rho(\tau, \theta)$ of the mutant lineage, we present five different measures of invasion fitness that are
202 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 Appendix from the elements
204 $a(s', i' | s, i)$, $p(s', i' | s, i)$, and/or $d(s', i' | s, i)$ (eq. (1)), and the explicit mathematical expressions are given in Table 1.

206 An ecstasy in five fits: five invasion fitness measures

Lineage fitness

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

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

where $w(s' | s, i)$ is the expected number of successful offspring, which settle in groups of type
210 s' , given that the parent is a mutant residing in a group in state (s, i) . Lineage fitness also
depends on the probability $q(i | s)$ that, conditional on being sampled in a group in state s ,
212 a randomly sampled mutant individual from the mutant lineage has $i - 1$ mutant neighbors.
This can be thought as the conditional *mutant experienced profile distribution* in the stationary
214 mutant distribution, and $q(s)$ is the probability that a randomly sampled individual from the
mutant lineage finds itself in a group in state s . When there is only one demographic state,
216 $W(\tau, \theta)$ reduces to eq. (A.1) of Day (2001) and eq. (A.7) of Mullon et al. (2016).

Lineage fitness $W(\tau, \theta)$ is the fitness of a randomly sampled carrier of the mutant allele from
218 its lineage, where $w(s' | s, i)$ is an individual-centered fitness component variously called “direct”,
“personal”, or “individual” fitness in social evolutionary theory (e.g. Frank, 1998; Rousset, 2004),
220 and will be here referred to it as personal fitness. It involves offspring reaching adulthood in the
group of the parent and in other groups through dispersal, and can thus also be written as

$$w(s' | s, i) = w_p(s' | s, i) + w_d(s' | s, i). \quad (6)$$

222 Here, $w_p(s' | s, i)$ 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 $w_d(s' | s, i)$
224 is such offspring produced by dispersal, and thus reach adulthood in other groups in state s' .
This decomposition of personal fitness matches the decomposition of the element of the transition
226 matrix of the mutant given in eq. (1) (see Table 1 and Appendix E, where we further decompose
these terms into sub-components that have appeared previously in the literature).

228 In Appendix B, we show that the growth rate of the mutant lineage is exactly equal to lineage fitness of the mutant; namely,

$$W(\tau, \theta) = \rho(\tau, \theta). \quad (7)$$

230 This equation immediately implies that τ is uninvadable if it solves the optimization problem $\max_{\tau \in \Theta} W(\tau, \theta)$. In other words, the type is uninvadable if it "maximizes" lineage fitness. Since
232 lineage fitness is the statistical average over all genetic demographic-environmental states of the personal fitness of the carrier of the mutant allele, it can be interpreted as a gene-centered
234 measure of fitness¹, since it is the maximand of the number of mutant replica copies produced by a representative individual carrying the mutant allele. The condition for uninvadability (eq. 7)
236 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
238 is over multilocus genetic states (Eshel and Feldman, 1984, eq. 10, Eshel et al., 1998, eq. 7).

Inclusive fitness

240 Let us now decompose personal fitness as

$$w(s' | s, i) = w^\circ(s' | s) - \gamma(s' | s) + \beta(s' | s) \left(\frac{i-1}{n(s)-1} \right) + \epsilon_i, \quad (8)$$

where $w^\circ(s' | s)$ is the expected number of successful offspring, which settle in groups of type
242 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 denote a quantity that is
244 evaluated in the absence of natural selection, i.e., neutral process determined by the monomorphic resident population. Personal fitness also depends on $\gamma(s' | s)$, which is the additive effect on
246 the personal fitness of an individual stemming from it switching to the expression of the mutant allele, $\beta(s' | s)$, which is the additive effect on the personal fitness of a mutant stemming from a
248 neighbor 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. The *direct*

¹EA and JVC prefer the nomenclature "gene-lineage-centered" (Akay and Van Cleve, 2016).

250 effect $\gamma(s' | s)$ and the *indirect* effect $\beta(s' | s)$ are obtained by minimizing the mean squared error ϵ_i in the linear prediction of personal fitness (see Box 1 for details).

252 We let the *inclusive fitness* of a mutant type τ in a population with residents of type θ be

$$W_{\text{IF}}(\tau, \theta) = 1 + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^\circ(s') [-\gamma(s' | s) + \beta(s' | s)r(s)] q(s), \quad (9)$$

where $v^\circ(s)$ is the *neutral reproductive value* of a single individual reproducing in a group in
254 state s . This is the relative asymptotic contribution of an individual in state s to the population
(see Taylor, 1996 and Rousset, 2004 for an introduction to this concept). Inclusive fitness also
256 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 neighbour that also carries the
258 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
260 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 $W_{\text{IF}}(\tau, \theta)$ of a
262 randomly sampled mutant from the lineage distribution $q(s)$ is the reproductive-value weighted
average personal fitness cost $\gamma(s' | s)$ of carrying the mutant allele and the relatedness weighted
264 personal indirect fitness benefit $\beta(s' | s)$ of carrying the mutant.

We show in Appendix C that inclusive fitness $W_{\text{IF}}(\tau, \theta)$ predicts whether or not the mutant
266 invades in the same way as the growth rate $\rho(\tau, \theta)$; that is,

$$W_{\text{IF}}(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (10)$$

Hence, a strategy is uninvadable if and only if inclusive fitness is maximized, in the sense that
268 τ solves the problem $\max_{\tau \in \Theta} W_{\text{IF}}(\tau, \theta)$. This shows that, regardless of the force of selection,
uninvadability can be expressed in terms of the three standard measures of “value” emphasized
270 by social evolution theory (Frank, 1998): (i) the direct cost and indirect benefit within each
class of an individual expressing the mutant, (ii) the pairwise relatedness between interacting
272 individuals, and (iii) the neutral reproductive value of the descendants in each class. It is
important to note that the inclusive fitness $W_{\text{IF}}(\tau, \theta)$ is not equal to the growth rate $\rho(\tau, \theta)$, but

274 is a linear function of it (see eq. (C.5) in Appendix C).

Reproductive numbers

276 We let the *basic reproductive* number of a mutant type τ in a resident θ population be

$$R_0(\tau, \theta) = \frac{R_m(\tau, \theta)}{N_F(\tau, \theta)}, \quad (11)$$

278 which depends on the expected number $N_F(\tau, \theta)$ of mutant colonizing the same group and descending from the same natal group, and on the successful number of emigrants

$$R_m(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w_d(s' | s, i) i \bar{t}(s, i) \quad (12)$$

produced by all individuals of the mutant lineage over its lifetime in a single group. This depends on the expected number $w_d(s' | s, i)$ of emigrant offspring that settle in groups of type s' (see eq. (6)) and on the total expected amount of time $\bar{t}(s, i)$ that a mutant lineage spends in a single group in state (s, i) in the asymptotic distribution of the mutant lineage. In sum, the basic reproductive number gives the expected number of successful emigrants produced by a lineage during its whole sojourn time in a single group and until its local extinction in that group, relative to the expected number of founders of such a lineage. Although the expression on the right-hand of eq. (12) does not appear previously in the literature, it precisely corresponds to the mathematical definition of the basic reproductive number given in the literature (Caswell, 2000; Ellner and Rees, 2006, see Appendix D). Further, when there is only one demographic state, $R_m(\tau, \theta)$ reduces to eq. (3) of Ajar (2003).

290 In Appendix D, we show that the basic reproductive number $R_0(\tau, \theta)$ predicts whether or not the mutant invades in the same way as the growth rate $\rho(\tau, \theta)$; namely

$$R_0(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (13)$$

292 Hence, a strategy is uninvadable if the basic reproductive number is maximized. Suppose now that the number of founders $N_F(\tau, \theta)$ is independent of the mutant; an example would be

294 $N_F(\tau, \theta) = 1$ so there can be no propagule dispersal and individuals can only migrate inde-
pendently of each others. Then, uninvasibility can be characterized in terms of $R_m(\tau, \theta)$ alone:

296

$$R_m(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (14)$$

Hence, a strategy is uninvadable if the expected number $R_m(\tau, \theta)$ of successful emigrants is
298 maximized.

Both reproductive numbers, R_0 and R_m , count (emigrant) successful offspring as produced
300 by a whole set of individuals in the lineage, and, by contrast to $W(\tau, \theta)$ and $W_{IF}(\tau, \theta)$, are thus
not individual-centered. In order to have a reproductive number that is expressed in terms of
302 the personal fitness of a representative carrier of the mutant, we let the *lineage fitness proxy* of
a mutant type τ in a resident θ population be given by

$$R_L(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' | s, i) q_L(s, i). \quad (15)$$

304 Here, $q_L(s, i)$ 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). This expression
306 is a direct analogue to lineage fitness, with the only difference that the probability distribution
 $q_L(s, i)$ depends on the lifetime of the lineage in a single group, and not on the asymptotic lineage
308 distribution $u(s, i)$ as does lineage fitness. When there is only one demographic state, $R_L(\tau, \theta)$
reduces to eq. (3) of Lehmann et al. (2015).

310 We show in Appendix D that lineage fitness proxy $R_L(\tau, \theta)$ predicts whether or not the
mutant invades in the same way as the growth rate $\rho(\tau, \theta)$; that is,

$$R_L(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1. \quad (16)$$

312 An uninvadable strategy thus also maximizes lineage fitness proxy.

Results summary

314 Summarizing all the above results, we have shown that the growth rate is equal to lineage fitness
 $\rho(\tau, \theta) = W(\tau, \theta)$ and the following characterizations of the condition under which a mutant goes
316 extinct are equivalent:

$$W(\tau, \theta) \leq 1 \iff W_{\text{IF}}(\tau, \theta) \leq 1 \iff R_0(\tau, \theta) \leq 1 \iff R_L(\tau, \theta) \leq 1 \iff R_m(\tau, \theta) \leq 1.$$

$\underbrace{\iff}_{N_{\text{F}} \text{ does not depend on } \tau}$

Discussion

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

324 Lineage and inclusive fitness

Uninvadability can be equivalently characterized in terms of lineage fitness or inclusive fitness.
326 This duality is interesting as these two gene-centered invasion fitness measures are expressed
in terms of different individual-centered fitness components experienced by representative carri-
328 ers of the mutant allele. Lineage fitness is expressed only in terms of the personal fitness of a
randomly drawn individual carrying the mutant allele, where the carrier is drawn from the distri-
330 bution 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
332 cost and relatedness weighted indirect fitness benefit accruing to a randomly drawn carrier of
the mutant allele. Writing fitness in terms of cost and benefit requires making a comparison
334 between the number of offspring produced by an individual expressing the mutant allele relative
to expressing the resident allele. But in order for this comparison to be unbiased, how the fitness

336 value of an offspring depends on the demographic and/or environmental state in which it settles
must be taken into account. Thus, each offspring needs to be appropriately weighted.

338 Importantly, we find that these weights are the neutral reproductive values of the monomor-
phic resident population regardless of the strength of selection on the mutant. The intuitive
340 reason for this result is that reproductive value weighting “converts” number of offspring in
different states into their proportionate contribution to the population. By choosing the con-
342 version factors to be the neutral reproductive values of the resident allele, the inclusive fitness
directly allows determining the increase (or decrease) in descendants into the far future that a
344 typical carrier of the mutant allele leaves relative to the typical carrier of the resident allele, in a
monomorphic resident population. This result is consistent with previous population genetic for-
346 mulations 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 inclu-
348 sive fitness (e.g., Queller, 1992; Frank, 1997; Gardner et al., 2011) to class-structured populations
with variable number of interaction partners, and shows that the standard neutral reproductive
350 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)
352 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,
354 regardless of the complexity of the biological situation at hand and the strength of selection.
These biological features, hidden in the other invasion fitness measures, also become apparent
356 if one considers only the first-order effects of selection on the growth rate when the evolving
traits have continuous values. This is the situation usually considered in the adaptive dynamics
358 and inclusive fitness literature where one looks for evolutionary attractors (Taylor, 1996; Geritz
et al., 1998; Rousset, 2004; Dercole and Rinaldi, 2008). In this situation, the sensitivity of the
360 growth rate with respect to changes in trait value boils down to the inclusive fitness effect derived
previously by the direct fitness method (Taylor and Frank, 1996; Rousset, 2004, see Box 2 and
362 Appendix E.2 for this connection). Hence, our model makes explicit that the direct fitness
method amounts to computing the sensitivity of the growth rate of the mutant with respect to
364 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).

366 Our analysis thus demonstrates connections between the various theoretical approaches for
characterizing adaptations in heterogeneous populations. But depending on the type of questions
368 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 personal fitness
370 of a representative sample of individuals of the mutant type (see Akay and Van Cleve, 2016 for
further discussions on using invasion fitness measures for empirical system).

372 **Reproductive numbers**

We also derived an explicit expression for the basic reproductive number, R_0 , for a group-
374 structured population, which was shown to depend on the ratio of the total lifetime number R_m
of successful emigrants produced by a typical group colonized by members of the mutant lineage,
376 to the expected number N_F of colonizers of such a typical group. The basic reproductive number
is the usual invasion fitness proxy in evolutionary biology and epidemiology (Caswell, 2000; Ellner
378 and Rees, 2006) and is usually used as it simplifies the characterization of the condition under
which a mutant invades. It circumvents the need to compute explicitly the growth rate ρ , (the
380 eigenvalue of the transition matrix \mathbf{A}), and only requires a matrix inversion (see Appendix D).
When individuals disperse independently and not in clusters (i.e., no propagule dispersal), the
382 basic reproductive number reduces to the number of successful emigrants R_m . Mathematically
however, our expression for R_m (eq. (12)) differs from the expression of R_m initially introduced as
384 a measure of invasion fitness by Metz and Gyllenberg (2001), insofar as the frequency distribution
of the group states of a typically colonized group may depend on the mutant type, which is
386 consistent with the formal proof of R_m derived by Massol et al. (2009).

Two further points are worth mentioning concerning the reproductive numbers, R_0 and R_m .
388 First, while no relatedness appears explicitly in them, they take inclusive fitness effects into
account in the same amount as inclusive fitness (or lineage fitness) does. Second, the reproductive
390 numbers count successful emigrant offspring produced by a whole set of individuals, and thus
do not give net successful offspring produced by a representative carrier of the mutant allele. In
392 order to have a fully individual-centered measure of invasion fitness, which keeps the attractive
computational features of the reproductive numbers, we derived an expression for lineage fitness

394 proxy R_L . This is the personal fitness of a mutant lineage member randomly sampled from the
distribution quantifying the lifetime of the mutant lineage in a local group. This allows one
396 to determine uninvasibility with the same generality and simplicity as R_0 , but with the same
biological interpretation as lineage fitness.

398 **Generalizations**

To obtain our results, we assumed a population of infinite size but allowed for limited dispersal
400 between any local group and local demographic and/or environmental state. This allows one to
describe, in at least a qualitative way, different metapopulation processes as well as group (or
402 propagule) reproduction processes subject to local demographic and environmental stochasticity.
Conceptually, our qualitative results concerning the generic form of the fitness measures should
404 carry over to isolation-by-distance models and finite total population size once the growth rate
is interpreted as the fixation probability.

406 We also only considered haploid reproduction, but diploid reproduction would not produce
qualitatively different results concerning the expressions of lineage fitness, inclusive fitness, or
408 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
410 produce these two types of offspring. The same extension is needed for class structure such as age
or stage (see Box 3 and Appendix F for an example involving stage structure). An extension to
412 continuous classes is also straightforward as it suffices to replace eigenvectors by eigenfunctions
in the characterization of the growth rate (Harris, 1963), and all other calculations should carry
414 over conceptually unchanged (but replacing sums by appropriate integrals). Our approach,
however, breaks down when there are global environmental fluctuations affecting all groups in
416 the population simultaneously, in which case the stochastic growth rate needs to be used to
ascertain uninvasibility (Svardal et al., 2015). Hence, a completely general interpretation of the
418 growth rate of a mutant in terms of individual-centered fitness components, covering all possible
biological heterogeneities, is still lacking. But for local heterogeneities, there is a generality and
420 consistency in the interpretation of the force of a selection on a mutant allele that befits the
generality of natural selection.

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Function	Definition
$a(s', i' s, i)$	Element $(s', i'; s, i)$ of the matrix $\mathbf{A} = \mathbf{P} + \mathbf{D}$.
$p(s', i' s, i)$	Element $(s', i'; s, i)$ of the matrix \mathbf{P} .
$d(s', i' s, i)$	Element $(s', i'; s, i)$ of the matrix \mathbf{D} .
$w(s' s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' a(s', i' s, i)$	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 and when there are i mutants.
$w_p(s' s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' p(s', i' s, i)$	Expected number of 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 and when there are i mutants.
$w_d(s' s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' d(s', i' s, i)$	Expected number of successful dispersing 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 and when there are i mutants.
$u(s, i)$	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} of \mathbf{A} associated to its leading positive eigenvalue ρ ; namely, $\rho \mathbf{u} = \mathbf{A} \mathbf{u}$.
$q(s) = \frac{\sum_{i \in I(s)} i u(s, i)}{\sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u(s, i)}$	Asymptotic probability that a randomly drawn mutant lineage member find itself in a group in state s .
$q(i s) = \frac{i u(s, i)}{\sum_{i \in I(s)} i u(s, i)}$	Asymptotic probability that, conditional on being sampled in a group in state s , a randomly sampled mutant individual from the mutant lineage has $i - 1$ mutant neighbors.
$r(s) = \sum_{i \in I(s)} \frac{(i-1)}{(n(s)-1)} q(i s)$	Asymptotic probability that, conditional on being sampled in a group in state s , an individual carrying the mutant experiences a randomly sampled neighbour that also carries the mutant allele. This is a measure of pairwise relatedness between individuals in a group.
$w^\circ(s' s)$	Expected number of successful offspring, which settle in groups of type s' , and are produced by a single mutant individual residing in a group in state s in a monomorphic resident population.
$v^\circ(s) = \sum_{s' \in \mathcal{S}} v^\circ(s') w^\circ(s' s)$	Reproductive value of a single individual reproducing in a group in state s in a monomorphic resident population.

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

Function	Definition
$u_0(s, i)$	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}_0 of $R_0\mathbf{u}_0 = \mathbf{R}\mathbf{u}_0$ where $\mathbf{R} = \mathbf{D}(\mathbf{I} - \mathbf{P})^{-1}$ is the next generation matrix.
$t(s', i' s, i)$	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.
$\bar{t}(s', i') = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} t(s', i' s, i) u_0(s, i)$	Average of the expected amount of time the mutant lineage spends in state (s', i') over its lifetime in a single group.
$N_F(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u_0(s, i)$	Expected number of founders in a single group of the mutant lineage.
$N_L(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i \bar{t}(s, i)$	Average total size of the mutant lineage over its lifetime in a single group.
$q_L(s, i) = \frac{i \bar{t}(s, i)}{N_L(\tau, \theta)}$	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) .

Continuation of Table 1.

Box I. Weighted least square regression. We here show how to obtain the cost $\gamma(s' | s)$ and benefit $\beta(s' | s)$ in eq. (8). These are found by minimizing for each state $s \in \mathcal{S}$ the sum of squared errors ϵ_i weighted by the probabilities $q(i | s)$:

$$Q(\gamma, \beta) = \sum_{i \in I(s)} \epsilon_i^2 q(i | s).$$

580 That is, from eq. (8), we minimize

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

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

Box II. Sensitivity of the growth rate. We here provide an expression for the sensitivity of the growth rate when the mutant trait value is varied; that is, the derivative of the growth rate when $\Theta = \mathbb{R}$, which is sufficient to evaluate singular strategies and convergence stable states (Taylor, 1996; Rousset, 2004). In Appendix E.2, we prove that the sensitivity of the growth rate is

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

where $w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})$ is the personal fitness of an individual with phenotype τ_j , when its group members have phenotype profile $\boldsymbol{\tau}_{-j} = (\tau_1, \dots, \tau_{j-1}, \tau_{j+1}, \dots, \tau_{n(s)-1})$, 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, see Appendix E.3.1).

Box III. Lineage and inclusive fitness for class-structure under fixed demography.

Suppose that each group is of constant size but that each individual within a group can belong to one of n_c classes where the set of classes is $\mathcal{C} = \{1, \dots, n_c\}$. An example would be age structure due to overlapping generations or different castes of social insects like workers and queens. For such a class structured population, we show in Appendix F that the lineage fitness of a mutant τ in a θ population is

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

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 $\mathbf{i} = (i_1, \dots, i_{n_c}) \in I$, which is the vector of the number of mutant alleles in class 1 to n_c . Here, $I = (I_1 \times \dots \times I_{n_c})$ is the set of possible group states with $I_x = \{0, 1, \dots, n_x\}$ 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 expression for this model is

$$W_{\text{IF}}(\tau, \theta) = 1 + \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} v^\circ(y) \left[-\gamma(y, x) + \sum_{z \in \mathcal{C}} \beta_z(y, x) r(z | x) \right] q(x),$$

where $q(x)$ is the probability that a randomly sampled individual from the mutant lineage finds itself in class x , $\gamma(y, x)$ 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, $\beta_z(y, x)$ is the additive effect on this fitness stemming from group neighbors in class z expressing the mutant instead of the resident allele, and $r(z | x)$ 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.

582

Appendix A: Properties of the monomorphic resident population

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

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

586 where $p^\circ(s)$ is the neutral stationary probability that in group is in state s and $p^\circ(s' | s)$ denotes the neutral transition probability from state s to s' (possibly depending endogenously on the
588 distribution $p^\circ(s)$).

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

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

where $v^\circ(s) > 0$ corresponds to the reproductive value of an individual in class s (see Taylor,
596 1996 and Rousset, 2004). By definition, reproductive values satisfy

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

To show that our construction of \mathbf{v}° is a left eigenvector of \mathbf{A}° , we first write the (s, i) element
598 of $\mathbf{v}^\circ \mathbf{A}^\circ$ by using eq. A.2 as

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

Then, we note that the total expected number of mutant individuals in a group of type s'

600 produced by a group of type (s, i) can be written in two ways,

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

where, owing to neutrality, fitness $w^\circ(s' | s)$ is independent of i . Using eq. (A.5) first and (A.3)

602 second, the (s, i) element of $\mathbf{v}^\circ \mathbf{A}^\circ$ can thus be written as

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

i.e., as the (s, i) element of \mathbf{v}° , which shows that our construction of \mathbf{v}° is indeed a left eigenvector

604 of \mathbf{A}° with unit eigenvalue, as required.

Appendix B: Lineage fitness

606 We here prove that $\rho(\tau, \theta) = W(\tau, \theta)$ (eq. (7) of the main text). To that aim, we first note that eq. (A.5) holds out of neutrality and that

$$\sum_{i' \in I(s')} i' a(s', i' | s, i) = w(s' | s, i) i, \quad (\text{B.1})$$

608 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) . Second, we let $\mathbf{n} = (1, 2, \dots, n(1), 1, 2, \dots, n(2), \dots, n(s))$ and premultiply $\rho \mathbf{u} = \mathbf{A} \mathbf{u}$ by \mathbf{n} gives $\mathbf{n} \cdot \rho \mathbf{u} = (\mathbf{n} \cdot \mathbf{A} \mathbf{u})$, where \cdot is the dot product. Using eq. (B.1) we have

$$\begin{aligned} \rho(\tau, \theta) &= \frac{1}{\mathbf{n} \cdot \mathbf{u}} (\mathbf{n} \cdot \mathbf{A} \mathbf{u}) \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}} \sum_{s' \in \mathcal{S}} \sum_{i' \in I(s')} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i' a(s', i' | s, i) u(s, i) \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' | s, i) i u(s, i). \end{aligned} \quad (\text{B.2})$$

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

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

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

Appendix C: Inclusive fitness

616 Here, we prove that the uninvasibility condition can be expressed in terms of inclusive fitness
 (eq. (10)). For this, we premultiply $\rho \mathbf{u} = \mathbf{A} \mathbf{u}$ by \mathbf{v}° , which gives $\mathbf{v}^\circ \cdot \rho \mathbf{u} = (\mathbf{v}^\circ \cdot \mathbf{A} \mathbf{u})$. Using eq.
 618 (A.2) then entails

$$\begin{aligned} \rho(\tau, \theta) &= \frac{1}{\mathbf{v}^\circ \cdot \mathbf{u}} \sum_{s' \in \mathcal{S}} \sum_{i' \in I(s')} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') i' a(s', i' | s, i) u(s, i) \\ &= \frac{1}{\mathbf{v}^\circ \cdot \mathbf{u}} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') w(s' | s, i) i u(s, i), \end{aligned} \quad (\text{C.1})$$

and using

$$V_T = \frac{\mathbf{v}^\circ \cdot \mathbf{u}}{\mathbf{n} \cdot \mathbf{u}} = \sum_{s \in \mathcal{S}} v^\circ(s) q(s), \quad (\text{C.2})$$

620 which is the average reproductive value, yields

$$\rho(\tau, \theta) = \frac{1}{V_T} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') w(s' | s, i) \frac{i u(s, i)}{\mathbf{n} \cdot \mathbf{u}}.$$

Using

$$\frac{i u(s, i)}{\mathbf{n} \cdot \mathbf{u}} = \left(\frac{i u(s, i)}{\sum_{i \in I(s)} i u(s, i)} \right) \left(\frac{\sum_{i \in I(s)} i u(s, i)}{\mathbf{n} \cdot \mathbf{u}} \right) = q(i | s) q(s), \quad (\text{C.3})$$

622 we have

$$\rho(\tau, \theta) = \frac{1}{V_T} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') w(s' | s, i) q(i | s) q(s). \quad (\text{C.4})$$

We now use the regression equation form for $w(s' | s, i)$ (eq. (8) of the main text), insert it into
624 eq. (C.4) and obtain

$$\rho(\tau, \theta) = \frac{1}{V_T} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') \left[w^\circ(s' | s) - \gamma(s', s) + \beta(s', s) \frac{(i-1)}{n(s)-1} + \epsilon_i \right] q(i | s) q(s),$$

which becomes

$$\rho(\tau, \theta) = \frac{1}{V_T} \left[\sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^\circ(s') w^\circ(s' | s) q(s) + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') \left(-\gamma(s', s) + \beta(s', s) \frac{(i-1)}{n(s)-1} \right) q(i | s) q(s) \right], \quad (\text{C.5})$$

626 since the minimum mean square error used to obtain $\gamma(s', s)$ and $\beta(s', s)$ ensures that $\sum_{i \in I(s)} \epsilon_i q(i | s) = 0$ for all $s \in \mathcal{S}$ (see Box 1). Using eq. (A.3), the double sum in the first line of eq. (C.5) is
628 seen to be V_T , and using the definition of relatedness $r(s) = \sum_{i \in I(s)} [(i-1)/(n(s)-1)] q(i | s)$ (see Table 1), we can simplify the sum on the second line of eq. (C.5) using the expression for
630 inclusive fitness (eq. (9) of the main text) to obtain

$$\rho(\tau, \theta) = \frac{1}{V_T(\tau, \theta)} [V_T(\tau, \theta) - 1 + W_{\text{IF}}(\tau, \theta)], \quad (\text{C.6})$$

whence

$$\rho(\tau, \theta) = 1 + \frac{1}{V_T(\tau, \theta)} [W_{\text{IF}}(\tau, \theta) - 1].$$

632 Since, $V_T(\tau, \theta) > 0$, we finally have

$$\rho(\tau, \theta) \leq 1 \iff W_{\text{IF}}(\tau, \theta) \leq 1. \quad (\text{C.7})$$

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

634 Appendix D: Reproductive numbers

D.1 Basic reproductive number and expected number of emigrants

636 Here, we prove the uninvadability condition expressed in terms of the basic reproductive number (eq. (13) of the main text and Table). According to our notations, the mean matrix of the
638 branching process can be decomposed as

$$\mathbf{A} = \mathbf{P} + \mathbf{D}, \quad (\text{D.1})$$

where \mathbf{P} is the matrix collecting the $p(s', i' | s, i)$ elements and \mathbf{D} is the matrix collecting the
640 $d(s', i' | s, i)$ elements (see eq. (1) or Table 1). Then an application of the next generation theorem (Caswell, 2000; Thieme, 2009) shows that

$$R_0 \leq 1 \iff \rho \leq 1, \quad (\text{D.2})$$

642 where R_0 is the leading eigenvalue of the next generation matrix

$$\mathbf{R} = \mathbf{D}(\mathbf{I} - \mathbf{P})^{-1}. \quad (\text{D.3})$$

This matrix has leading right eigenvector \mathbf{u}_0 whose element $u_0(s, i)$ is the asymptotic probability
644 that a group initiated by a local lineage starts in state (s, i) ($R_0 \mathbf{u}_0 = \mathbf{R} \mathbf{u}_0$). The elements of \mathbf{R} are

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

646 where $t(\varsigma, j | s, i)$ 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
648 sojourn times are elements of the “fundamental matrix” $(\mathbf{I} - \mathbf{P})^{-1}$ (Grinstead and Snell, 1997). The interpretation of $r(s', i' | s, i)$ is that it gives the total expected number of groups in state

650 (s', i') produced through dispersal over the lifetime of the mutant lineage in a single group that started in state (s, i) .

652 Using the above, we now rewrite R_0 using the same line of argument as for lineage fitness. Hence, we first let

$$\sum_{i' \in I(s')} i' d(s', i' | s, i) = w_d(s' | s, i) i, \quad (\text{D.5})$$

654 where $w_d(s' | s, i)$ is the total expected successful number of immigrants in groups in state s' produced by a single mutant in a group in state (s, i) . Premultiplying $R_0 \mathbf{u}_0 = \mathbf{R} \mathbf{u}_0$ by \mathbf{n} and using eq. (D.5) entails that

$$\begin{aligned} R_0(\tau, \theta) &= \frac{1}{\mathbf{n} \cdot \mathbf{u}_0} \sum_{s' \in \mathcal{S}} \sum_{i' \in I(s')} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i' r(s', i' | s, i) u_0(s, i) \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}_0} \sum_{s' \in \mathcal{S}} \sum_{i' \in I(s')} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} \sum_{\varsigma \in \mathcal{S}} \sum_{j \in I(\varsigma)} i' d(s', i' | \varsigma, j) t(\varsigma, j | s, i) u_0(s, i) \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}_0} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} \sum_{\varsigma \in \mathcal{S}} \sum_{j \in I(\varsigma)} w_d(s' | \varsigma, j) j t(\varsigma, j | s, i) u_0(s, i). \end{aligned} \quad (\text{D.6})$$

In order to further simplify R_0 we set

$$\bar{t}(\varsigma, j) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} t(\varsigma, j | s, i) u_0(s, i), \quad (\text{D.7})$$

658 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

$$N_{\mathbb{F}}(\tau, \theta) = \mathbf{n} \cdot \mathbf{u}_0 = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i u_0(s, i), \quad (\text{D.8})$$

660 which is the expected number of founders of the mutant lineage. By further denoting

$$R_{\text{m}}(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{\varsigma \in \mathcal{S}} \sum_{j \in I(\varsigma)} w_d(s' | \varsigma, j) j \bar{t}(\varsigma, j), \quad (\text{D.9})$$

and inserting into eq. (D.6), we have

$$R_0(\tau, \theta) = \frac{R_m(\tau, \theta)}{N_F(\tau, \theta)}. \quad (\text{D.10})$$

662 D.2 Lineage fitness proxy

We will now rewrite eq. (D.10) in terms of lineage fitness proxy (eq. (15) of the main text). For
664 this, we set

$$N_L(\tau, \theta) = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i \bar{t}(s, i), \quad (\text{D.11})$$

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

$$N_L(\tau, \theta) = N_F(\tau, \theta) + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w_p(s' | s, i) i \bar{t}(s, i), \quad (\text{D.12})$$

since $N_F(\tau, \theta)$ is the expected number of mutant individuals founding a single group and the sum
668 is the expected number of mutant offspring settling locally and produced over the lifetime of the
lineage in that group. Subtracting eq. (D.11) from eq. (D.12), inserting into eq. (D.9) and using
670 eq. (6), we can write

$$\begin{aligned} R_m(\tau, \theta) &= N_F(\tau, \theta) + \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s' | s, i) i \bar{t}(s, i) - N_L(\tau, \tau) \\ &= N_F(\tau, \theta) + N_L(\tau, \theta) R_L(\tau, \theta) - N_L(\tau, \theta), \end{aligned} \quad (\text{D.13})$$

where the second line follows from using eq. (15). Inserting eq. (15) of the main text and
672 eq. (D.13) into eq. (D.10) gives

$$R_0(\tau, \theta) = 1 + \frac{N_L(\tau, \theta)}{N_F(\tau, \theta)} (R_L(\tau, \theta) - 1), \quad (\text{D.14})$$

which shows that $R_0(\tau, \theta) \leq 1 \iff R_L(\tau, \theta) \leq 1$, whereby

$$R_L(\tau, \theta) \leq 1 \iff \rho(\tau, \theta) \leq 1, \quad (\text{D.15})$$

674 **Appendix E: Connections to previous work**

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

676 **E.1 Fitness decomposition: philopatric and dispersed**

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

$$w_p(s' | s, i) = w_p(s', s, i)p(s' | s, i), \quad (\text{E.1})$$

678 where $p(s' | s, i)$ 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 $w_p(s', s, i)$ is the expected number
680 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) . We can also write

$$w_d(s' | s, i) = \sum_{x \in \mathcal{S}} w_d(s', x, s, i)k(s' | x, s, i)p^\circ(x), \quad (\text{E.2})$$

682 where $p^\circ(x)$ is the (neutral) probability that a group randomly sampled in the monomorphic
resident population is in state x . Here, $k(s' | x, s, i)$ is the probability that a group that was in
684 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 $w_d(s', x, s, i)$
686 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'
688 in the offspring generation and was in state x in the parental generation (with 0 mutants).
The conditional fitness functions $w_p(s', s, i)$ and $w_d(s', x, s, i)$ are the elementary individual-
690 based fitness components of models in demographically structured populations (e.g., eqs. 31-32
of Rousset and Ronce, 2004).

692 We now prove the expressions for the two above conditional expectations (eqs. (E.1)–(E.2)).

From Table 1, the first conditional expectation can be written as

$$w_p(s' | s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' p(s', i' | s, i) = \frac{p(s' | s, i)}{i} \sum_{i' \in I(s')} i' \underbrace{\frac{p(s', i' | s, i)}{p(s' | s, i)}}_{p(i' | s', s, i)} = p(s' | s, i) w_p(s', s, i), \quad (\text{E.3})$$

694 where $p(i' | s', s, i)$ 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.

696 Here, we used

$$w_p(s', s, i) i = \sum_{i' \in I(s')} i' p(i' | s', s, i), \quad (\text{E.4})$$

where $w_p(s', s, i)$ the expected number of successful philopatric offspring that a single mutant
698 produces given that it resides in a group in state (s, i) and that the group state in the offspring generation is s' .

700 From Table 1, the second conditional expectation is

$$w_d(s' | s, i) = \frac{1}{i} \sum_{i' \in I(x)} i' d(s', i' | s, i), \quad (\text{E.5})$$

where, conditioning on the state of the group in the parental generation where the offspring
702 disperse to, we can write

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

Here, we used in the conditioning the neutral probability $p^\circ(x)$ that a group randomly sampled
704 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 $d(s', i' | x, s, i)$ is the expected number of groups in (s', i') produced by a
706 group in state (s', i') and given that they were in state $(0, x)$ in the parental generation (with 0

708 mutants). We now let

$$d(i' | s', x, s, i) = \frac{d(s', i' | x, s, i)}{k(s' | x, s, i)}, \quad (\text{E.7})$$

where $k(s' | x, s, i)$ 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

$$w_d(s', x, s, i) = \frac{1}{i} \sum_{i' \in I(s')} i' d(i' | s', x, s, i), \quad (\text{E.8})$$

712 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 into eq. (E.6), we then obtain eq. (E.2).

716 E.2 Connection to the direct fitness method

We now connect our results to the direct fitness approach (Taylor and Frank, 1996; Rousset, 718 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 should match $\partial\rho(\tau, \theta)/\partial\tau$ when 720 the type space is real valued and one dimensional ($\Theta = \mathbb{R}$), which we henceforth assume. 722

E.3 Sensitivity of the growth rate

724 To prove the connection to the direct fitness approach we first derive a generic expression for the growth rate sensitivity $\partial\rho(\tau, \theta)/\partial\tau$ under our model assumptions. To that aim, we rewrite the growth rate by using eq. (C.4) as

$$\rho(\tau, \theta) = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') w(s' | s, i) q(i | s) q_v(s), \quad (\text{E.9})$$

where

$$q_v(s) = \frac{q(s)}{V_T}. \quad (\text{E.10})$$

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

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

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

$$\sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s') w^\circ(s' | s) \frac{\partial [q(i | s) q_v(s)]}{\partial \tau} = \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s) \frac{\partial [q(i | s) q_v(s)]}{\partial \tau}. \quad (\text{E.12})$$

Further, we have

$$\begin{aligned} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s) \frac{\partial [q(i | s) q_v(s)]}{\partial \tau} &= \frac{\partial}{\partial \tau} \left[\sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s) q(i | s) q_v(s) \right] \\ &= \frac{\partial}{\partial \tau} \left[\sum_{s \in \mathcal{S}} \sum_{i \in I(s)} v^\circ(s) \frac{i u(i, s)}{\mathbf{v}^\circ \cdot \mathbf{u}} \right] \\ &= \frac{\partial}{\partial \tau} (1) \\ &= 0. \end{aligned} \quad (\text{E.13})$$

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

$$\frac{\partial \rho(\tau, \theta)}{\partial \tau} = \frac{1}{V_T^\circ} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^\circ(s') \left[\sum_{i \in I(s)} \frac{\partial w(s' | s, i)}{\partial \tau} q^\circ(i | s) \right] q^\circ(s), \quad (\text{E.14})$$

where without loss of generality we can normalize the elements $v^\circ(s')$ such that $V_T^\circ = 1$.

734 Note that $w(s' | s, i)$ is the personal 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

736 θ . Thus, we can write

$$\frac{\partial w(s' | s, i)}{\partial \tau} = \frac{\partial w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + (n(s) - 1) \frac{\partial w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} \frac{i - 1}{n(s) - 1}, \quad (\text{E.15})$$

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

$$\frac{\partial \rho(\tau, \theta)}{\partial \tau} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^\circ(s') \left[\frac{\partial w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + (n(s) - 1) \frac{\partial w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} r^\circ(s) \right] q^\circ(s). \quad (\text{E.16})$$

740 E.3.1 Connection to direct fitness method results

Here, we prove that eq. (E.16) returns exactly eqs. 26–27 of Rousset and Ronce (2004) when
742 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
744 of Rousset and Ronce (2004) generalize those of Taylor and Frank (1996) to demographically
structured populations.

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

$$q^\circ(s) = \frac{p^\circ(s)n(s)}{\bar{n}^\circ}, \quad (\text{E.17})$$

748 where $\bar{n}^\circ = \sum_{s \in \mathcal{S}_s} n(s)p^\circ(s)$ 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

$$\begin{aligned} q^\circ(s') &= \sum_{i' \in I(s')} q^\circ(s', i') \\ &= \sum_{i' \in I(s')} \frac{i' u^\circ(s', i')}{\mathbf{n} \cdot \mathbf{u}^\circ} \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}^\circ} \sum_{i' \in I(s')} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} i' a(s', i' | s, i) u^\circ(s, i) \\ &= \frac{1}{\mathbf{n} \cdot \mathbf{u}^\circ} \sum_{s \in \mathcal{S}} \sum_{i \in I(s)} w(s', s) i u^\circ(s, i), \end{aligned} \quad (\text{E.18})$$

which yields

$$q^\circ(s') = \sum_{s \in \mathcal{S}} w^\circ(s' | s) q^\circ(s) \quad (\text{E.19})$$

750 and shows that the vector collecting the $q^\circ(s)$ is a right unit eigenvector of the matrix with
 elements $w^\circ(s' | s)$. Let us now substitute the trial solution $q^\circ(s) = n(s)p^\circ(s)/\bar{n}^\circ$ into eq. (E.19),
 752 whereby

$$n(s')p^\circ(s') = \sum_{s \in \mathcal{S}} w^\circ(s' | s) n(s)p^\circ(s). \quad (\text{E.20})$$

The right hand side is the total expected number of successful offspring in groups in state s'
 754 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
 756 the number of successful offspring in that group. Hence, $q^\circ(s) = n(s)p^\circ(s)/\bar{n}^\circ$ satisfies eq. (E.19)
 and eq. (E.17) holds.

758 We now expand eq. (E.16) by using the decomposition of personal fitness $w(s' | s, i) = w_p(s' | s, i) + w_d(s' | s, i)$ (eq. (6) of the main text), which allows us to write

$$\frac{\partial w(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \frac{\partial w_p(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_d(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j}. \quad (\text{E.21})$$

760 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

$$\frac{\partial w_p(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \frac{\partial w_p(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} p^\circ(s' | s) + w_p^\circ(s', s) \frac{\partial p(s' | s, \boldsymbol{\tau})}{\partial \tau_j}, \quad (\text{E.22})$$

762 where $\boldsymbol{\tau} = (\tau_1, \dots, \tau_{n(s)-1})$. For a neighbour $k \neq j$ of a focal mutant j we have

$$\frac{\partial w_p(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} = \frac{\partial w_p(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} p^\circ(s' | s) + w_p^\circ(s', s) \frac{\partial p(s' | s, \boldsymbol{\tau})}{\partial \tau_k}. \quad (\text{E.23})$$

In order to expand the dispersal component in eq. (E.21), we follow the assumption of Rousset
 764 and Ronce, 2004 that the composition of a natal group of mutants does not affect the transition

probability of other groups (owing to the fact that individuals migrate independently from each
 766 other) and set $k(s' | \varsigma, s, i) = p^\circ(s' | \varsigma)$ in eq. (E.2). Then, we can write

$$\frac{\partial w_d(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} = \sum_{\varsigma \in \mathcal{S}} \frac{\partial w_d(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} p^\circ(s' | \varsigma) p^\circ(\varsigma) \quad (\text{E.24})$$

and for $k \neq j$

$$\frac{\partial w_d(s' | s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} = \sum_{\varsigma \in \mathcal{S}} \frac{\partial w_d(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_k} p^\circ(s' | \varsigma) p^\circ(\varsigma). \quad (\text{E.25})$$

768 Substituting eqs. (E.21)–(E.25) into eq. (E.16) yields

$$\frac{\partial \rho(\tau, \theta)}{\partial \tau} = \sum_{s \in \mathcal{S}} [S_f(s) + S_{Pr}(s)] \frac{n(s) p^\circ(s)}{\bar{n}^\circ}, \quad (\text{E.26})$$

where

$$\begin{aligned} S_f(s) = & \sum_{s' \in \mathcal{S}} v^\circ(s') \left[\left(\frac{\partial w_p(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_p(s', s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} (n(s) - 1) r^\circ(s) \right) p^\circ(s' | s) \right. \\ & \left. + \sum_{\varsigma \in \mathcal{S}} \left(\frac{\partial w_d(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} + \frac{\partial w_d(s', \varsigma, s, \tau_j, \boldsymbol{\tau}_{-j})}{\partial \tau_j} (n(s) - 1) r^\circ(s) \right) p^\circ(s' | \varsigma) p^\circ(\varsigma) \right], \end{aligned} \quad (\text{E.27})$$

770 and

$$S_{Pr}(s) = \sum_{s' \in \mathcal{S}} v^\circ(s') \left[w_p^\circ(s', s) \frac{\partial p(s' | s, \boldsymbol{\tau})}{\partial \tau_j} [1 + (n(s) - 1) r^\circ(s)] \right] \quad (\text{E.28})$$

If we let s be group size and set $n(s) = s$, then eqs. (E.27)–(E.28) are proportional to eqs. (A.33)–
 772 (A.36) of Lehmann and Rousset (2010). If we multiply eq. (E.26) 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
 774 Ronce (2004, eqs. 33–34), then eqs. (E.27)–(E.28) are proportional to eqs. (26)–(27) of Rousset
 and Ronce (2004).

776 Appendix F: Fixed number of age or stage classes

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

Let $\mathbf{i} = (i_1, \dots, i_{n_c}) \in \mathcal{I}$ be the vector of the number of mutant alleles of type τ in class 1 to
 782 n_c in a group where \mathcal{I} is the set of possible configurations. Let $I = (I_1 \times \dots \times I_{n_c}) \setminus \mathbf{0}$ where
 $I_x = \{0, 1, \dots, n_x\}$ is set of the number of mutant alleles in class x and n_x is the number of
 784 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 $a(\mathbf{i}' | \mathbf{i})$ giving the
 786 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
 788 \mathbf{n} is given by $x(\mathbf{i}) = \sum_{y \in \mathcal{C}} i_y$.

We now prove the expression for lineage fitness (e.g., eq. 5) for this model and proceed in
 790 the same way as in Appendices A–C. Hence, we first note that

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

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

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

where

$$q(x, \mathbf{i}) = \frac{i_x u(\mathbf{i})}{\mathbf{n} \cdot \mathbf{u}}, \quad (\text{F.3})$$

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

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

eq. (F.2) shows that $\rho(\tau, \theta) = W(\tau, \theta)$, which is the same result as eq. (7).

796 Second, we derive an expression for the inclusive fitness $W_{\text{IF}}(\tau, \theta)$. Inclusive fitness requires that we calculate reproductive values, so we gather into the vector \mathbf{v}° the elements

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

798 where $v^\circ(x)$ is the reproductive value of an individual in class x . Now, from $\mathbf{v}^\circ \cdot \rho \mathbf{u} = (\mathbf{v}^\circ \cdot \mathbf{A} \mathbf{u})$ and eq. (F.5), we have

$$\begin{aligned} \rho(\tau, \theta) &= \frac{1}{\mathbf{v}^\circ \cdot \mathbf{u}} \sum_{\mathbf{i}' \in I} \sum_{\mathbf{i} \in I} v^\circ(\mathbf{i}') a(\mathbf{i}' | \mathbf{i}) u(\mathbf{i}) \\ &= \frac{1}{\mathbf{v}^\circ \cdot \mathbf{u}} \sum_{y \in \mathcal{C}} \sum_{\mathbf{i}' \in I} \sum_{\mathbf{i} \in I} i'_y v^\circ(y) a(\mathbf{i}' | \mathbf{i}) u(\mathbf{i}) \\ &= \frac{1}{\mathbf{v}^\circ \cdot \mathbf{u}} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} \sum_{\mathbf{i} \in I} v^\circ(y) w(y, x, \mathbf{i}) i_x u(\mathbf{i}) \\ &= \frac{1}{V_{\text{T}}} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} \sum_{\mathbf{i} \in I} v^\circ(y) w(y, x, \mathbf{i}) q(x, \mathbf{i}), \end{aligned} \quad (\text{F.6})$$

800 where

$$V_{\text{T}} = \frac{\mathbf{v}^\circ \cdot \mathbf{u}}{\mathbf{n} \cdot \mathbf{u}} = \sum_{x \in \mathcal{C}} v^\circ(x) q(x) \quad (\text{F.7})$$

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

802 now form a weighted multiple regression

$$w(y, x, \mathbf{i}) = w^\circ(y, x) - \gamma(y, x) + \beta_x(y, x) \frac{i_x - 1}{n_x - 1} + \sum_{z \in \mathcal{C} \setminus x} \beta_z(y, x) \frac{i_z}{n_z} + e_x(\mathbf{i}) \quad (\text{F.8})$$

and least square fit γ and the β 's by minimizing

$$\sum_{\mathbf{i} \in I} e_x(\mathbf{i})^2 q(x, \mathbf{i}) / q(x) \quad (\text{F.9})$$

804 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 $\sum_{\mathbf{i} \in I} e_x(\mathbf{i})(q_x(\mathbf{i})/q_x) = 0$. Let us further define

$$q(i_y | x) = \sum_{\mathbf{i} \in I(i_y)} q(x, \mathbf{i}) / q(x), \quad (\text{F.10})$$

806 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 $q(i_y | x)$ as the probability that there are i_y mutants in class y given that

808 a mutant has a sampled a mutant in class x . Substituting all this into eq. (F.6), we have

$$\begin{aligned} \rho(\tau, \theta) = \frac{1}{V_{\text{T}}(\tau, \theta)} \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} v^\circ(y) \left[w^\circ(y, x) - \gamma(y, x) \right. \\ \left. + \sum_{i_x \in I_x^+} \beta_x(y, x) \frac{i_x - 1}{n_x - 1} q(i_x | x) + \sum_{z \in \mathcal{C} \setminus x} \sum_{i_z \in I_z^+} \beta_z(y, x) \frac{i_z}{n_z} q(i_z | x) \right] q(x) \quad (\text{F.11}) \end{aligned}$$

where we only sum over the elements $I_x^+ = \{1, \dots, n_x\}$ in the first sum of the second line since

810 $w(y, x, \mathbf{i}) = 0$ 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

$$W_{\text{IF}}(\tau, \theta) = 1 + \sum_{y \in \mathcal{C}} \sum_{x \in \mathcal{C}} v^\circ(y) \left[-\gamma(y, x) + \sum_{z \in \mathcal{C}} \beta_z(y, x) r(z | x) \right] q(x), \quad (\text{F.12})$$

812 where

$$r(z | x) = \sum_{i_z \in I_z^+} \left[\delta_{zx} \frac{i_x - 1}{n_x - 1} + (1 - \delta_{zx}) \frac{i_z}{n_z} \right] q(i_z | x) \quad (\text{F.13})$$

is the probability that, conditional on being sampled in class x , an individual carrying the mutant
814 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.12)–(F.13)
816 into eq. (F.11) and using the definition of reproductive value we obtain

$$\rho(\tau, \theta) = \frac{1}{V_T(\tau, \theta)} [V_T(\tau, \theta) + W_{IF}(\tau, \theta)], \quad (\text{F.14})$$

whereby

$$\rho(\tau, \theta) \leq 1 \iff W_{IF}(\tau, \theta) \leq 1. \quad (\text{F.15})$$