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Does evolution lead to maximizing behavior?

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Abstract

A long-standing question in biology and economics is whether individual organisms evolve to behave as if they were striving to maximize some goal function. We here formalize the "as if" question in a patch-structured population in which individuals obtain material payoffs from (perhaps very complex) multimove social interactions. These material payoffs determine personal fitness and, ultimately, invasion fitness. We ask what goal function, if any, individuals will appear to be maximizing, in uninvadable population states, when what is really being maximized is invasion fitness at the genetic level. We reach two broad conclusions. First, no simple and general individual-based goal function emerges from the analysis. This stems from the fact that invasion fitness is a complex multi-generational measure of evolutionary success. Second, when selection is weak, all multi-generational effects of selection can be summarized in a neutral type-distribution quantifying identity-by-descent within patches. Individuals then behave as if they were striving to maximize a weighted sum of material payoffs (own and others). At an uninvadable state it is as if individuals choose their actions and play a Nash equilibrium of a game with a goal function that combines selfishness (own material payoff), Kantian morality (group material payoff if everyone does the same), and local rivalry (material payoff differences).

Keywords: maximizing behavior, game theory, inclusive fitness, invadability, Nash equilibrium.

> Individuals do not consciously strive to maximize anything; they behave *as if* maximizing something. It is exactly the same “as if” logic that we apply to “intelligent genes”. Genes manipulate the world as if striving to maximize their own survival. They do not really “strive”, but in this respect they do not differ from individuals.
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> Dawkins, 1982, p. 189

Introduction

The fundamental unit of behavior in the life and social sciences is the action. In decision theory (e.g., Binmore, 2011), an individual’s behavior is determined by the individual’s choice of action or sequence of (conditional) actions from a set of feasible actions, and this choice is guided by the strife to maximize some goal function, such as, for instance, own material well-being, or some spiteful, altruistic or moral objective. The outcome of an individual’s choice in general also depends on (random) events in the individual’s environment, in which case the individual is assumed to strive to maximize the expected value of her goal function. In many, if not most cases, the environment in turn consists of other decision makers, equipped with their feasible action sets and goal functions. Then, the expectation is also taken with respect to others’ choice of action, which in turn may depend on those other individuals’ expectations about “our” decision-maker’s choice. Such interdependent decision problems are called games, and an individual’s plan for what action to take under each and every circumstance that can arise in the interaction is then called a strategy for that player. A profile of strategies, one for each player in a population, is a (Nash) equilibrium if no individual decision maker can increase her goal-function value by a unilateral change of her strategy.

A long-standing question in evolutionary biology is the extent to which natural selection leads individual organisms to behave *as if* they were maximizing some goal function. Because resources are limited, the material consequences for, and hence fitness of, one individual usually depends not only on the individual's own actions but also on the actions of others. It is thus as if the organisms were caught in a game. If the resulting behaviors can be interpreted as if each individual was choosing a strategy to maximize a goal function, this will be of importance for the understanding and prediction of behavior. This is not only of interest to biology but to the social sciences as well, and in particular to economics, which is largely built on the supposition that individual behavior can be explained as the outcome from maximization of the expected value of some goal function.

In early evolutionary biology the question of maximizing behavior was addressed by way of investigating optimality properties of mean fitness (defined as mean fertility or survival) under allele frequency change (Fisher, 1930; Wright, 1942; Kingman, 1961). The underlying scheme is that natural selection invariably increases mean fitness and thus evolves individuals to express optimal actions given current environmental conditions. This has typically been investigated in settings with no social interactions (Wright, 1942; Kingman, 1961). Even in these simplest cases of no interdependence the idea that natural selection always leads to an increase in mean fitness has been proven invalid under a multilocus genetic basis (Moran, 1964; Ewens, 2004, 2011). This suggests that individuals are unlikely to behave as if they maximize fitness.

Still for social interactions (interdependence in decision making), Hamilton (1964) proved that mean inclusive fitness increases under additive gene action in a population under allele frequency change. Organisms should thus evolve to behave in such a way that their inclusive fitness is maximized. Hamilton's (1964) concept of inclusive fitness is based, as is the work from which he took inspiration (in particular Kingman, 1961), on a measure of fitness that is ascribed to a genotype or an allele (Hamilton, 1964, p. 6). The inclusive fitness of an allele at a particular gene locus is the heritable part of the fitness of an average carrier of that allele, but where the source of variation of that fitness is decomposed into the effect of the allele in the carrier and that in other individuals from the population; hence the term "inclusive".

Inclusive fitness is frequency independent under additive gene action and weak selection (although Hamilton's (1964) model captures strategic interactions arising from phenotypic interactions). But this will generally not obtain as selection can be frequency-dependent at the genetic level at a given locus. Hence, even in the one-locus case it is not a conclusion that natural selection results in individuals behaving as if they maximize their inclusive fitness (*sensu* Hamilton, 1964).

One fundamental take-home message of the population-genetic assessment of optimization under allele frequency change (Moran, 1964; Ewens, 2004, 2011) is that ideas of fitness maximization are generally not revealing much about maximizing behavior under short-term evolution. However, concepts of fitness maximization can nevertheless be illuminating under long-term evolution because they then allow to characterize evolutionarily stable states (Eshel, 1996; Eshel et al., 1998). It is indeed well-established that the maximization of the growth rate of a non-recombining heritable trait (here taken to be a gene) when rare—invasion fitness—provides a condition of uninvadability of a mutant allele in a resident population, and this is a defining property of an evolutionarily stable state (Eshel, 1983; Ferrière and Gatto, 1995; Eshel et al., 1998; Rousset, 2004; Metz, 2011).

Because different alleles have different phenotypic effects, the range of such effects can be conceived as the effective strategy space of the "strategic gene" (Haig, 1997, 2012). In a gene's perspective (Dawkins, 1978), invasion fitness can be regarded as the goal function a gene is striving to maximize. This is quite distinct from the goal function (if any such exists) that is to explain an *individual's* behavior, and where this individual can potentially interact with all others in the population. In order to answer the question of what goal function an individual is trying to maximize it is necessary to establish a link between invasion fitness and individual behavior.

We are certainly not the first to explore these links (e.g., Grafen, 2008, in biology and Alger and Weibull, 2013, in economics). However, we feel that no previous study in this area has integrated and is fully consistent with the fields of behavioral ecology, evolutionary population dynamics, and game theory. In particular, sufficient dynamic conditions under which strategically interacting individual organisms in spatially structured populations behave as if they were maximizing some goal function appear to be lacking. The aim of this paper is to fill this gap, and to provide connections between (i) explicit population-dynamic evolutionary stability, (ii) game-theoretic equilibrium in strategic interactions between individuals, and (iii) behavioral ecology formulation of behavior under different constraints. To that aim, we develop a mathematical model of strategic interactions and evolution in a spatially structured population, within which we formalize notions of personal fitness and invasion fitness, and derive from them goal functions that individual organisms will, through their behavior, appear to be maximizing (the "proximate" cause of action), while what is in fact being maximized is invasion fitness (the "ultimate" cause of action).

The rest of the paper is organized as follows. First, we present an evolutionary model of a patch-structured population and define uninvadability. Second, we present a model of behavior and social interactions, and we formulate a game-theoretic concept of strategy and goal functions for such interactions. We then we bring together these elements and postulate two goal functions that are well anchored in the evolutionary biology literature. We show that none of the two goal functions leads to general equivalence between uninvadability and equilibrium behavior. Then, we turn to the analytically less forbidding case of weak selection, and suggest a third goal function, which has not been studied before, and show that maximizing behavior under this goal function is equivalent with uninvadability under general conditions. Finally, we discuss the interpretation of our maximizing behavior under behavioral constraints and provide a general discussion of our results.

Evolutionary model

In this section we describe the evolutionary component of our model along established lines on biological evolution and population genetics (see, for instance, Frank, 1998; Rousset, 2004; and Metz, 2011 for an introduction to the concepts used here), but we sometimes make slight generalizations and reformulations to better suit our aims.

Life cycle and phenotypes

We consider a population of haploid individuals structured into an infinite number of patches (or islands), each subject to exactly the same environmental conditions and consisting of exactly N adult individuals (i.e., Wright's 1931 infinite island model of dispersal). The life-cycle of individuals in this population consists of the following events that occur over one *demographic time period*. (1) As an outcome of interactions with others, each adult individual produces (asexually) a very large number of offspring and then either survives into the next demographic time period or dies with a probability independent of age. (2) Each offspring either disperses or remains in its natal patch, and each migrant disperses to a (uniformly) randomly chosen non-natal patch. (3) In each patch the random number of aspiring offspring, some native and some immigrants from other patches, compete for the breeding spots vacated by the death of adults. As a result, in each patch exactly N individuals survive this density-dependent competition.

We assume that the probability for an offspring to migrate is always positive. No other assumption about fecundity, survival, migration, or competition is made at this stage of the analysis. In particular, the demography allows for exactly one, several, or all adults to die per demographic time unit (overlapping and non-overlapping generation models).

Each individual in the population is assumed to inherit faithfully from its parent a *type*, which may affect any phenotype of the individual and thus possibly any event in the individual's life cycle. Our generic notation for a type will be θ and the set of all admissible types will be denoted Θ. Because interactions, in general, may occur between individuals from the same or different patches, any phenotype of an individual may actually depend not only on its own type, but also on the types of its patch neighbors, and the types of individuals taken at large from the population. A fundamental feature of the infinite island model is that the phenotypic effects of individuals in other patches on a given individual is, by the law of large numbers, non-stochastic, however, and depends only on averages (Chesson, 1981). This implies that a given phenotype of an individual can be expressed as a function of the individual's own type, the type profile of her patch neighbors, the distribution of type-profiles across all patches in the population at large, and some random environmental effect (by following quantitative genetics, see Lynch and Walsh, 1998). In our analysis, we will not consider such random effects (such as developmental noise), and we write generically a given phenotype (such as height, number of offspring produced, resource transferred to others), of a given individual $i \in \{1, 2, ..., N\}$ on a given island as $z(\theta_i, \boldsymbol{\theta}_{-i}, \phi)$, where $\theta_i \in \Theta$ is the individual's type, $\boldsymbol{\theta}_{-i} = (\theta_1, ..\theta_{i-1}, \theta_{i+1}, ..\theta_N) \in \Theta^{N-1}$ is the *type profile* of patch neighbors, and $\phi \in \Delta\big(\Theta^N\big)$ is the population distribution of patch type-profiles, where $\Delta\big(\Theta^N\big)$ is the set of probability measures on the set Θ^N of patch type-profiles (formally $z : \Theta^N \times \Delta\big(\Theta^N\big) \to \mathcal{Z}$, where $\mathcal{Z}$ is the set of phenotypes).

We will assume, for analytical tractability, that any phenotype of an individual is expressed unconditionally on age (neither their own nor others') and does thus not vary with demographic time. Recalling that all individuals are subject to the same environmental conditions (i.e., there is no class structure, Taylor, 1990), any phenotype $z(\theta_i, \boldsymbol{\theta}_{-i}, \phi)$ of a given individual i can be considered to be invariant under permutation of the elements of the type profile $\boldsymbol{\theta}_{-i}$ of its patch neighbors, and this will be assumed throughout.

Personal fitness

One phenotype that will play a fundamental role in our analysis is the *personal fitness* of an individual, which we define as an individual's expected number of surviving descendants (possibly including the individual herself, for demographics where adults may survive) after each demographic time period. We denote by $w(\theta_i, \boldsymbol{\theta}_{-i}, \phi)$ this fitness of individual i. Due to migration and competition for breeding spots, an individual's fitness will in general depend on the vital rates (fecundity and survival) and migration rates among its patch neighbors and in the population at large (e.g., Frank, 1998; Rousset, 2004).

An example of a fitness for the island model can be obtained by assuming a Moran process (Ewens, 2004), where exactly one randomly sampled adult on each patch dies per demographic time period. Then, assuming that all offspring have the same migration probability m (for simplicity of presentation), the fitness of individual i is given by

$$\begin{aligned} w(\theta_i, \boldsymbol{\theta}_{-i}, \phi) = 1 - & \frac{h(\theta_i, \boldsymbol{\theta}_{-i}, \phi)}{\sum_{j=1}^{N} h(\theta_j, \boldsymbol{\theta}_{-j}, \phi)} \\ & + \frac{1}{N}\left[(1-m)\frac{f(\theta_i, \boldsymbol{\theta}_{-i}, \phi)}{(1-m)\frac{1}{N}\sum_{j=1}^{N} f(\theta_j, \boldsymbol{\theta}_{-j}, \phi) + m\bar{f}(\phi)} + m\frac{f(\theta_i, \boldsymbol{\theta}_{-i}, \phi)}{\bar{f}(\phi)}\right]. \quad (1) \end{aligned}$$

The right-hand side of the first line is the part of fitness stemming from own survival; it is the probability of survival, where survival is a random variable that takes the value one if the individual survives and zero if it dies. We assume the death probability to be of the form $h(\theta_i, \boldsymbol{\theta}_{-i}, \phi)/\left[\sum_{j=1}^{N} h(\theta_j, \boldsymbol{\theta}_{-j}, \phi)\right]$, where $h(\theta_i, \boldsymbol{\theta}_{-i}, \phi)$ is the *risk-factor* for death of individual i.

The second line in eq. 1 is the fitness through settlement of offspring in vacated breeding spots. This depends on the *fecundity* $f(\theta_i, \boldsymbol{\theta}_{-i}, \phi)$ of individual i, which is defined as its expected number of offspring produced in a demographic time unit, and also on the average fecundity in the population as a whole,

$$\bar{f}(\phi) = \int \left[\frac{1}{N}\sum_{i=1}^{N} f(\theta_i, \boldsymbol{\theta}_{-i}, \phi)\right] \mathrm{d}\phi(\boldsymbol{\theta}), \quad (2)$$

where, for any patch-profile $\boldsymbol{\theta} = (\theta_1, .., \theta_N)$, the expression in square brackets is the average fecundity of the N individuals in the patch. The first term inside the square brackets in eq. 1 is the individual's fitness through her philopatric offspring, each of whom competes for the local vacated breeding spot with all philopatric offspring from the same patch and with all migrating offspring from other patches who also aspire for this breeding spot. The second term inside the square brackets is the component of the focal individual's fitness that stems from its dispersing progeny to other patches. We note that since the total population is constant in size, average fitness in the population at large is always one. In particular, in a monomorphic population—irrespective of what is the resident type—all individuals' personal fitness is unity.

Uninvadability

Suppose that initially the population is monomorphic for some resident type θ and that a single individual mutates to some new type τ. Will this mutant type "invade" the population? 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*. We denote by Θ_{U} the set of types that are uninvadable. Uninvadability could also informally be thought of as evolutionary stability. But this terminology will not be used here, since it is slightly weaker than the strict definition of evolutionary stability (Maynard Smith and Price, 1973), which subsumes that an evolutionarily stable state should be an attractor of the evolutionary dynamics (in particular, our notion of uninvadability is weaker than evolutionary stability in that we consider demographic processes in which migrating mutants never meet each other).

In order to get a hold on uninvadability, consider a single individual i_0, of type $\theta' \in \{\tau, \theta\}$ in one patch, to be called the focal patch, in a population that is otherwise monomorphic for type θ. Through reproduction, this individual may found a lineage with local descendants as well as descendants reaching adulthood in other patches. Owing to our assumption that the number of patches is infinite, the probability that a descendant of the individual founding the lineage will migrate back to the focal patch is zero, as long as the lineage is small in the population so that the population can be considered as being (almost) monomorphic for θ. This implies that the time-varying size of the subpopulation of descendants (including the founder i_0) in the focal patch can be represented as a (time-) homogeneous Markov chain on the finite state space $K = \{0, 1, .., N\}$. The state of this process in any demographic time period $\ell = 0, 1, 2, ..$ thus specifies the size $k \in K$ of the local lineage in the demographic time period ℓ.

This Markov chain has exactly one absorbing state, namely, the extinction of the local lineage ($k = 0$). Moreover, since the migration probability is positive, and patch populations are finite and constant, this extinction will with probability one occur in finite time. Let $t_k(\theta', \theta)$ denote the expected finite *sojourn time* (number of demographic time periods) spent in state $k \in \{1, .., N\}$ of the Markov chain. Since the local lineage goes extinct within finite time, the expected total size of the local lineage, $\bar{t}(\theta', \theta) = \sum_{k=1}^{N} k t_k(\theta', \theta)$, is finite, and this fact allows us to define

$$p_k(\theta', \theta) = \frac{k t_k(\theta', \theta)}{\bar{t}(\theta', \theta)} \text{ for } k = 1, .., N. \tag{3}$$

This is the probability, for a randomly drawn local lineage member, to co-exist with $k-1$ other local lineage members. Overall, then, $(p_1(\theta', \theta), .., p_N(\theta', \theta))$ is the *experienced lineage-size distribution*; the probability distribution of lineage size—the number of individuals who are identical-by-descent—as experienced by a randomly drawn lineage member. A standard statistic describing the magnitude of identity-by-descent is the relatedness between patch members (Wright, 1931; Frank, 1998; Rousset, 2004). Let the coefficient of *pairwise relatedness* be defined as

$$r(\theta', \theta) = \sum_{k=1}^{N} \frac{k-1}{N-1} p_k(\theta', \theta). \tag{4}$$

This coefficient is the probability that a randomly drawn neighbor of a local lineage member will also be a local lineage member, that is, that they both descend from i_0, the founder of the local lineage.

For $\theta' = \theta$, the expression on the right-hand side of (4) boils down to the standard coefficient of relatedness evaluated in the *neutral process*—that is, when every individual has exactly the same fitness (e.g., Crow and Kimura, 1970). For instance, for the Moran island model one obtains

$$r(\theta, \theta) = \frac{1-m}{1-m+Nm}, \tag{5}$$

which displays the canonical feature that relatedness is decreasing in the migration probability and in patch size (calculations for the Moran process are given in the Appendix).

We now turn to defining the *lineage fitness* of a type $\theta' \in \{\tau, \theta\}$, i.e., the expected personal fitness of members of the local lineage founded by some individual i_0 of this type, during the lifespan of this local lineage, and assuming the population is otherwise monomorphic for type θ. For this purpose we first note that the personal fitness of a member i of the local lineage, and whose type is therefore θ', is $w(\theta', \boldsymbol{\theta}_{-i}, 1_\theta)$, where $\boldsymbol{\theta}_{-i} \in \{\tau, \theta\}^{N-1}$, and 1_θ is the type-profile distribution that places unit probability on the homogeneous type profile $(\theta, .., \theta) \in \Theta^N$. Letting $S_{k-1}(\theta', \theta)$ denote the set of neighbor type-profiles $\boldsymbol{\theta}_{-i} \in \{\tau, \theta\}^{N-1}$ such that exactly $k-1$ neighbors are also members of the local lineage, the *lineage fitness* of type $\theta' \in \{\tau, \theta\}$ in a resident θ-population writes

$$W(\theta', \theta) = \sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\theta', \theta)} q_k(\theta', \theta) w(\theta', \boldsymbol{\theta}_{-i}, 1_\theta), \tag{6}$$

where, for each $k = 1, ..., N$,

$$q_k(\theta', \theta) = \binom{N-1}{k-1}^{-1} p_k(\theta', \theta) \tag{7}$$

is the probability that a particular neighbor type-profile $\boldsymbol{\theta}_{-i}$ with exactly $k-1$ local lineage members realizes. The factorial in eq. 7 accounts for all the ways that a profile of length $N-1$ can contain $k-1$ such members. In particular, then, for $\theta' = \theta$, we have $W(\theta, \theta) = w\left(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta\right) = 1$, where $\boldsymbol{\theta}^{(N-1)}$ is the $(N-1)$-dimensional type vector whose components all equal θ.

A necessary and sufficient condition for a type to be , $\theta \in \Theta_{\mathrm{U}}$, is that no other type has a mutant lineage-fitness above that of the resident lineage:

Result 1 *A type $\theta \in \Theta$ is uninvadable if and only if*

$$W(\tau, \theta) \leq W(\theta, \theta) \qquad \forall \tau \in \Theta. \tag{8}$$

(Proofs of all results are given in the Appendix). This shows that lineage fitness is a measure of invasion fitness, and that $W(\tau, \theta) - W(\theta, \theta)$ has the same sign as the growth rate of a mutant when rare in the population (Appendix Result 1), which is the usual and general measure of invasion fitness (Ferrière and Gatto, 1995; Caswell, 2000; Metz, 2011).

Behavioral model

In this section we describe the behavioral component of our model. We begin with a discussion of the notion of "behavior" along established lines in behavioral ecology and the neurosciences (see for instance McFarland and Houston, 1981; Leimar, 1997; Enquist and Ghirlanda, 2005; and Haykin, 1999), and then show how this can be translated into the notion of "behavior" in game theory (see for instance Fudenberg and Tirole, 1991 and Osborne and Rubinstein, 1994), which will finally allow us to formulate an unambiguous concept of maximizing behavior.

Due to the notational complexity involved in describing behavior throughout the whole lifespan of an individual, we will focus on behavior affecting interactions between individuals leading to reproduction and survival, and eventually migration (stage (1) in the life cycle until (2) starts). We envision these interactions as being extended over T social time periods, although they take place within a single unit of the demographic time period. We thus deal with two time scales, one (slow) for the demographic period and one (fast) for social interactions taking place over a possibly infinite number of time periods (T is either finite or infinite). For instance, one-shot interactions will be covered as the special case when the social time scale has only one time period, $T = 1$, and repeated interactions are obtained when $T > 1$. (These can be thought of as the stages of a multi-stage game form, which is a special but broad class of extensive-form games that includes all one-shot game forms, finitely and infinitely repeated game forms, see Fudenberg and Tirole, 1991, chapter 4 or Osborne and Rubinstein, 1994).

Behavior rules and strategies

We take the *action* (e.g., a motor pattern, a signal, or a transfer of resources to a neighbor) as the fundamental behavioral unit by which an individual interacts in each social period with others. We assume, for simplicity, that the set of feasible actions, $\mathcal{A}$, is the same for all individuals at all times (and thus do not depend on type) and that this includes the possibility of taking no action so that actions can be taken asynchronously in the social interaction setting. The action taken by individual i at social time $t \in T$,

$$a_i(t) = d_i(s_i(t)), \tag{9}$$

is assumed to be determined by the individual's *internal state* $s_i(t) \in \mathcal{S}$ at t, where $\mathcal{S}$ is the set of internal states that an individual can be in and d_i is the *decision rule* of individual i, and which can result in the randomization of action [formally $d_i : \mathcal{S} \to \Delta(\mathcal{A})$]. An individual's (internal) state changes (possibly randomly) over time and the state of individual i at any time $t > 1$,

$$s_i(t) = g_i(s_i(t-1), e_i(t-1)), \tag{10}$$

is assumed to be determined by the individual's state $s_i(t-1)$ in the previous social time period and the information $e_i(t-1)$ obtained during that time period, where $\mathcal{E}$ the set of information [formally $g_i : \mathcal{S} \times \mathcal{E} \to \Delta(\mathcal{S})$]. This information could consist of any more or less noisy private or public signals about the individual's own action and/or that of others. A simple example is the (public) profile of actions $e_i(t) = (a_1(t-1), .., a_N(t-1))$ taken by all individuals in individual i's patch, which entails the perfect monitoring of patch members actions.

We call the triplet $b_i = (d_i, g_i, s_i(1))$ the *behavior rule* of individual i. This rule defines how the individual will act and react to others during the whole social interaction period. When the set of states S is finite (infinite), a behavior rule is a finite (infinite) state machine (Minsky, 1967), and as such neural networks can be implemented by a behavior rule (Haykin, 1999). We assume that the behavior rule of an individual is fixed at birth and is thus determined only by its own type (i.e., $b_i = b_i(\theta_i)$, which does not depend on $\boldsymbol{\theta}_{-i}$ nor ϕ).

Our definition of a behavior rule entails that it can implement a *behavior strategy* as defined in non-cooperative game theory. To see this connection, suppose that g_i concatenates the most recent information to all previous information (by setting $s_i(1) = \varnothing$ and $s_i(t) = (s_i(t-1), e_i(t-1))$ for all $t > 1$). Then an individual's internal state $s_i(t)$ in social time period $t > 1$ depends on the whole history of information up to time $t-1$, that is, $s_i(t) = (e_i(1), ..., e_i(t-1))$ for $t > 1$ [the whole history of actions if $e_i(t) = (a_1(t-1), .., a_N(t-1))$]. In this case, the set of internal states is given by the set $\mathcal{H}$ of all possible histories of information [all possible histories of actions if $e_i(t) = (a_1(t-1), .., a_N(t-1))$]. We denote by x_i the decision rule of individual i in this specific case where the internal state records the whole history of information until the time point where a decision has to be taken [formally $x_i : \mathcal{H} \to \Delta(\mathcal{A})$]. In game-theoretic terminology x_i is a *behavior strategy* (see, e.g., Fudenberg and Tirole, 1991 or Osborne and Rubinstein, 1994).

Goal functions and games

With this precise concept of a strategy (x_i) in hand, we can formally represent interactions in the population at large as a game with infinitely many players, where all players on each patch use strategies from the same strategy set, denoted X. A strategy profile is the vector consisting of the strategies played by all the players. To complete the definition of such a game, it is necessary to define each player's utility or goal function, i.e., the function that describes the value that the player attaches to every possible strategy profile. In the present setting, let $u(x_i, \boldsymbol{x}_{-i}, \phi)$ represent how individual i values that particular *strategy constellation* $(x_i, \boldsymbol{x}_{-i}, \phi)$, where $x_i \in X$ is her own strategy, $\boldsymbol{x}_{-i} \in X^{N-1}$ is the strategy profile for her patch neighbors, and $\phi \in \Delta\big(X^N\big)$ is the patch-profile distribution in the population at large. The interpretation is simple. Consider two alternative strategy constellations, $(x_i, \boldsymbol{x}_{-i}, \phi)$ and $\big(x'_i, \boldsymbol{x}'_{-i}, \phi'\big)$; $u(x_i, \boldsymbol{x}_{-i}, \phi) > u(x'_i, \boldsymbol{x}'_{-i}, \phi')$ holds if individual i strictly prefers $(x_i, \boldsymbol{x}_{-i}, \phi)$ to $\big(x'_i, \boldsymbol{x}'_{-i}, \phi'\big)$, while $u(x_i, \boldsymbol{x}_{-i}, \phi) = u(x'_i, \boldsymbol{x}'_{-i}, \phi')$ holds if she is indifferent between the two constellations. Thus, u is a goal function for individual i (formally, $u : X^N \times \Delta\big(X^N\big) \to \mathbb{R}$). We here assume that the function u is symmetric in the same way as the fitness and fecundity functions are, i.e., u is invariant under permutation of the elements of the strategy profile $\boldsymbol{x}_{-i}$ of *the individual's* patch neighbors.

Since individual i can only choose her strategy $x_i \in X$, but not the others', her choice problem, in the social interaction, is to choose the strategy $x_i \in X$ that she prefers, given the strategies of her patch neighbors and the patch-profile distribution in the population at large. Mathematically, this boils down to solving the maximization program

$$\max_{x_i \in X} u(x_i, \boldsymbol{x}_{-i}, \phi). \tag{11}$$

This set-up then defines a *symmetric normal-form game* with infinitely many players, a game we will denote $G = (\mathbb{N}, X, u)$, where the first item is the set of players, the second item the strategy set for each player, and the third item is each player's payoff function, the goal (or utility) function u. A concept that is a canonical prediction for behavior in such a game is that of a Nash equilibrium, a strategy profile in which no individual can get a higher utility by a unilateral deviation. For our purposes it is sufficient to consider *symmetric* Nash equilibria, i.e., equilibria in which all players use the same strategy. Such a strategy $x \in X$ satisfies

$$u(x, \mathbf{x}^{(N-1)}, 1_x) \geq u(x_i, \mathbf{x}^{(N-1)}, 1_x) \quad \forall x_i \in X, \tag{12}$$

where $\mathbf{x}^{(N-1)}$ denotes the $(N-1)$-dimensional vector whose components all equal x. Letting $X_{\mathrm{E}}(u) \subseteq X$ denote the (potentially empty) set of symmetric Nash equilibrium strategies, we thus have $x \in X_{\mathrm{E}}(u)$ if and only if

$$x \in \arg\max_{x' \in X} u\big(x', \mathbf{x}^{(N-1)}, 1_x\big) . \tag{13}$$

In other words: if all other individuals in the population use strategy $x \in X_{\mathrm{E}}(u)$ and individual i was free to choose her strategy x_i from the strategy set X, and her goal was to maximize $u(x_i, \boldsymbol{x}_{-i}, \phi)$, then she would find it optimal to do the same as the others, that is, to choose $x_i = x$. Thus, the strategies in the set $X_{\mathrm{E}}(u)$ are precisely those that are compatible with all individuals behaving identically and as though each of them was choosing the strategy that maximizes her goal function.

The “as if” question

To state the “as if” question, and to make a link with the evolutionary model presented in the previous section, suppose that there is a one-to-one correspondence between an individual’s type and his or her strategy, i.e., an individual’s type uniquely determines his or her strategy, and it affects nothing beyond the strategy. Formally, let the set of types Θ, on which natural selection operates, be the same as the set X of strategies, from which individuals make their choices.

Then, the personal fitness writes $w(x_i, \boldsymbol{x}_{-i}, \phi)$, where $x_i \in X$ is individual i’s own strategy, $\boldsymbol{x}_{-i} \in X^{N-1}$ is the strategy profile among that individual’s patch neighbors, and $\phi \in \Delta\big(X^N\big)$ is the distribution of patch strategy-profiles in the population at large. In force of Result 1, a strategy $x \in X$ is then uninvadable if and only if

$$W(y, x) \leq W(x, x) \qquad \forall y \in X. \tag{14}$$

Let $X_{\mathrm{U}} \subseteq X$ denote the set of uninvadable strategies.

The "as if" question that we address in this paper is as follows. Does there exist a goal function u for which the set $X_{\mathrm{E}}\left(u\right)$ of (symmetric) Nash equilibrium strategies is the same as, or at least closely related to, the set X_{U} of uninvadable strategies?

At first sight, it may seem that the lineage fitness function, $W(x', x)$ (see eq. 6), would fit the bill. However, this is not true since lineage fitness is a multi-generational measure of fitness and is a function of only two strategies, x and x', whereas the "as if" question requires a goal function that depends on the whole population strategy-profile in a given generation. In fact, lineage fitness $W(x', x)$ can be thought of as the goal function of a focal "strategic gene" (Dawkins, 1978; Haig, 1997, 2012); that is, a gene attempting to maximize its own transmission across generations in a population where individuals behave according to the strategy of another gene, the focal's gene co-player. To see this, note that inequality 14 can be written as

$$x \in \arg\max_{x' \in X} W(x', x). \tag{15}$$

Strategy x is thus uninvadable if and only if the type pair (x, x) constitutes a Nash equilibrium in the symmetric two-player game in which strategies are elements of X and the game payoff to a strategy x', when played against a strategy x, is lineage fitness $W(x', x)$. This shows that we need to go beyond lineage fitness to establish a candidate individual-based goal function who's maximization will display uninvadability.

Uninvadability and maximizing behavior

We will start our analysis by considering two apparently natural individual-based goal functions. As will be seen presently, neither induces behavior that closely matches behavior that is uninvadable. To establish this negative result, it is sufficient to consider a canonical but simple case. In this section we thus assume that strategies x can be represented as real numbers in some open set X, and that all functions are twice continuously differentiable.

First, we consider individuals i with the goal function u_{A} defined by

$$u_{\mathrm{A}}(x_i, \boldsymbol{x}_{-i}, \phi) \;=\; w(x_i, \boldsymbol{x}_{-i}, \phi) + r(\bar{x}, \bar{x}) \sum_{j \neq i} w(x_j, \boldsymbol{x}_{-j}, \phi), \tag{16}$$

where $\bar{x} = \frac{1}{N} \int \left(\sum_{i=1}^{N} x_i \right) \mathrm{d}\phi(\boldsymbol{x})$ is the average strategy used in the population. This goal function is reminiscent of textbook interpretations of "inclusive fitness"; the individual's own personal fitness plus the personal fitness of all other individuals in the population weighted by their relatedness to the individual in question (e.g., Alcock, 2005). Note, however that this is different from the (population genetic) concept of inclusive fitness described in Hamilton (1964), which is the heritable part of the fitness of an average carrier of a particular allele and is thus identically transmitted from parent to offspring. This discrepancy emanates from the fact that u_{A} does also not take a population-statistical form like the lineage-fitness function W (see eq. 6), which characterizes uninvadability. We therefore introduce another individual-based goal function, which is closer to the lineage-fitness function.

To define this second goal function one needs an additional piece of notation. For any focal individual i consider the subset $X^N(i) \subset X^N$ of patch strategy-profiles $\boldsymbol{x}$ in which, for each patch neighbor j, the strategy is either x_i or x_j (for $j = i$ this leaves but one choice):

$$X^N(i) = \left\{ \boldsymbol{x} \in X^N : x_j \in \{x_i, x_j\} \quad \forall j \in I \right\}. \tag{17}$$

For each $k = 1, .., N$ write P_{ik} for the subset of $X^N(i)$ where strategy x_i appears exactly k times. Equipped with this notation, we turn to individuals with the goal function

$$u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi) \;=\; \sum_{k=1}^{N} \sum_{\boldsymbol{x}_{-i} \in P_{ik}} q_k\left(\bar{x}, \bar{x}\right) w(x_i, \boldsymbol{x}_{-i}, \phi), \tag{18}$$

where the q_k's are as defined in eq. 7. This goal function is the average personal fitness of individual i, where the weight attached to the event that $k-1$ neighbors use the same strategy as the individual herself is the probability that $k-1$ of a focal individual's neighbors belong to i's lineage, according to the experienced type-profile distribution in the evolutionary model.

Does maximizing behavior lead to uninvadability?

We are now in a position to relate the set of (symmetric) Nash equilibrium strategies, under each one of the two goal functions, to the set of strategies that are uninvadable. Since X is an open set and W is differentiable, Result 1 implies that any uninvadable strategy $x \in X$

must satisfy the first-order condition

$$\left.\frac{\partial W(y,x)}{\partial y}\right|_{y=x}=0, \tag{19}$$

where $\partial W(y,x)/\partial y$ is the usual selection gradient, that is, a first-order effect of selection on the fitness of an average carrier of the mutant "type" (here "strategy"). In the proof of Result 2 below, we show that

$$\left.\frac{\partial W(y,x)}{\partial y}\right|_{y=x}=w_1\big(x,\mathbf{x}^{(N-1)},1_x\big)+r(x,x)(N-1)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big), \tag{20}$$

where $w_j\big(x,\mathbf{x}^{(N-1)},1_x\big)$ is the (first-order) partial derivative of $w(x_i,\boldsymbol{x}_{-i},\phi)$ with respect to its j^{th} argument, for $j=1,...,N$. Note that owing to permutation invariance, $w_j=w_h$ for all $j,h>1$. The expression in eq. 20 is standard (Rousset, 2004, chapter 7) and is Hamilton's (1964) inclusive fitness effect: the first term represents the (direct) effect on a focal individual's personal fitness from an infinitesimal change of his or her own strategy, while the second term represents the (indirect) effect on the same focal individual's personal fitness from an infinitesimal change of the strategy of all her $N-1$ patch neighbors, weighted by pairwise relatedness in the neutral process.

We denote by $X_{\mathrm{D}}\subseteq X$ the set of strategies x that satisfy eq. 19. The next result establishes that the set X_{D} contains not only all uninvadable strategies, but also all strategies that meet the necessary first-order condition for symmetric Nash equilibrium in the population game $G_{\mathrm{A}}=(\mathbb{N},X,u_{\mathrm{A}})$ (see eq. 16), as well as in the population game $G_{\mathrm{B}}=(\mathbb{N},X,u_{\mathrm{B}})$ (see eq. 18):

Result 2 *For a strategy $x\in X$ to be uninvadable, or to be a symmetric Nash equilibrium strategy under any one of the two goal functions, u_{A} or u_{B}, it must satisfy (19). Formally:*

$$X_{\mathrm{U}}\cup X_{\mathrm{E}}(u_{\mathrm{A}})\cup X_{\mathrm{E}}(u_{\mathrm{B}})\subseteq X_{\mathrm{D}}. \tag{21}$$

If X_{D} is the empty set, no strategy is uninvadable and there exists no symmetric Nash equilibrium in G_{A} or G_{B}. Turning to the more interesting case in which X_{D} is non-empty, consider some strategy $x\in X_{\mathrm{D}}$. All we then know is that x may (but need not) be uninvadable, a symmetric Nash equilibrium strategy in G_{A}, and/or a symmetric Nash equilibrium strategy in G_{B}, or neither. As we show next, if a strategy is uninvadable it does not necessarily mean that it is also a Nash equilibrium strategy of G_{A} or G_{B}, or vice versa. Hence, it is not generally true that "evolution leads to maximizing behavior" in terms of the goal functions u_{A} and u_{B}. To establish this negative result, it is sufficient to focus on the simplest case, namely when X_{D} is a singleton set.

Writing x for the unique element of X_{D}, the second-order condition

$$\left.\frac{\partial^2 W(y,x)}{\partial y^2}\right|_{y=x} < 0 \tag{22}$$

is sufficient for $x \in X_{\mathrm{D}}$ to satisfy eq. 15. Comparing this second-order condition with that for symmetric Nash equilibrium, under u_{A} or u_{B}, one obtains conditions under which the sets on the left-hand side of eq. 21 indeed are nested. To state this result, we use the following definition: the strategies are (local) *strategic substitutes*, *strategically neutral* or *strategic complements* in terms of (personal) fitness at x, if $w_{ij}\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$ is negative, zero, or positive, respectively, for all $i, j \in \{1, .., N\}$ with $i \neq j$. Here, $w_{jh}\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$ is the second-order partial derivative of $w(x_i, \boldsymbol{x}_{-i}, \phi)$ with respect to its j^{th} and h^{th} arguments, evaluated at the monomorphic resident strategy-profile where all individuals play x (owing again to permutation invariance, $w_{1j} = w_{1h}$ for all $j, h > 1$, and $w_{jh} = w_{kl}$ for all $j, h, k, l > 1$ whenever $j \neq h$ and $k \neq l$).

The next result is divided into three parts, depending on the strategic character of the interaction at hand, as well as on the signs of $w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$ and $r_1(x,x) = \partial r(y,x)/\partial y|_{y=x}$, where the latter is the derivative of relatedness with respect to its first argument.

Result 3 *Suppose that x is the unique element of X_{D}.*
(a) If $r_1(x,x) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \geq 0$ and the strategies are strategic complements at x in terms of fitness, or $r_1(x,x) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) > 0$ and the strategies are strategically neutral at x in terms of fitness, then $X_{\mathrm{U}} \subseteq X_{\mathrm{E}}(u_{\mathrm{A}})$.
(b) If $r_1(x,x) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \leq 0$ and the strategies are strategic substitutes at x in terms of fitness, or $r_1(x,x) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \geq 0$ and the strategies are strategically neutral at x in terms of fitness, or $r_1(x,x) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) > 0$ and the strategies are strategically neutral at x in terms of fitness, then $X_{\mathrm{E}}(u_{\mathrm{A}}) \subseteq X_{\mathrm{U}}$.

(c) If $r_1(x,x)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)=0$ *and the strategies are strategically neutral at* x *in terms of fitness, then* $X_{\mathrm{E}}(u_{\mathrm{A}})=X_{\mathrm{U}}$*.*

Let us consider this result when $X_{\mathrm{U}}=X_{\mathrm{D}}$, that is, when the unique element x of X_{D} is uninvadable. If either of the two conditions in (a) is satisfied, then x is also a (symmetric) equilibrium strategy in the game G_{A}. In other words, under either condition in (a) an outside observer may interpret the behavior of the individuals in the population as maximizing with respect to the goal function u_{A}. Turning now to (b), if either of the two conditions therein is satisfied, then either x is a (symmetric) equilibrium strategy in G_{A} or else this game has no (symmetric) equilibrium strategy. In other words, under (b) an outsider who knows that G_{A} has at least one symmetric Nash equilibrium (and such existence may be proved from first principles for a wide class of games) may again interpret the evolutionarily selected behavior of the individuals in the population as maximizing behavior with respect to the goal function u_{A}. By contrast, if G_{A} has no equilibrium, then the outsider observing a strategy that is uninvadable cannot interpret it as being the outcome of maximizing u_{A}. Note that under (a) there may be other equilibrium behaviors than the unique strategy x, while under (b) there is no other equilibrium behavior.

Finally, we also note that Result 3 (c) establishes that the two sets $X_{\mathrm{E}}(u_{\mathrm{A}})$ and X_{U} are identical in the special case when $r_1(x,x)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)=0$ and the strategies are strategically neutral in terms of fitness. In particular, uninvadability is the same thing as maximizing behavior under the goal function u_{A} in pure decision problems, interactions in which the personal fitness only depends on the individual's own action (then $w_N=0$ and strategies are strategically neutral).

Our next result shows that maximizing behavior with respect to the goal function u_{B} has a closer tie than u_{A} with uninvadability. In particular, the strategic character of the interaction plays no role.

Result 4 *Suppose that* x *is the unique element of* X_{D}*.*
(a) If $r_1(x,x)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)>0$*, then* $X_{\mathrm{U}}\subseteq X_{\mathrm{E}}(u_{\mathrm{B}})$*.*
(b) If $r_1(x,x)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)<0$*, then* $X_{\mathrm{E}}(u_{\mathrm{B}})\subseteq X_{\mathrm{U}}$*.*

(c) If $r_1(x,x)w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)=0$*, then* $X_\mathrm{E}(u_\mathrm{B})=X_\mathrm{U}$.

The same comments applying to condition (a) and (b) under Result 3 (see paragraph following this result) also apply to Result 4, but comparing the conditions in Results 3 and 4, we see that an uninvadable strategy can be an equilibrium strategy in the game G_B without being an equilibrium strategy in the game G_A. By contrast, an uninvadable strategy cannot be an equilibrium strategy in G_A without also being an equilibrium strategy in G_B. Similarly, there are situations in which an equilibrium strategy in the game G_B is also uninvadable while not being an equilibrium strategy in the game G_A, while the reverse case cannot arise. Strategically neutral interactions constitute an important special case; then the set of equilibrium strategies in games G_A and G_B are related in the same way to uninvadability. Strategic neutrality means that the effect of an individual's action upon another individual's personal fitness is independent of what strategy the other takes. This is, arguably, a rare case in practice.

The link between natural selection, as expressed by uninvadability, and "as if" maximizing behavior, as expressed by symmetric Nash equilibrium, is hence in general tighter for the goal function u_B than for the goal function u_A. However, also the link between natural selection and the goal function u_B is, in general, not clear-cut, except when neutral pairwise relatedness is independent of the resident strategy, $r_1(x,x)=0$, or when an individual's personal fitness does not depend on the strategies of other individuals, $w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)=0$. In force of Result 4 one then has $X_\mathrm{E}(u_\mathrm{B})=X_\mathrm{U}$. In other words, then the result of natural selection is identical with individual "as if" maximization under goal function u_B.

Finally, note that if $m=1$ (the population is panmictic), then $q_k(\theta',\theta)=1$ for $k=1$ (hence zero for all other k), and $r\,(x,x)=0$, in which case u_A and u_B reduce to $w(x_i,\boldsymbol{x}_{-i},\phi)$. Maximizing personal fitness is then equivalent to maximizing lineage fitness (eq. 6). We conclude that in a panmictic population $X_\mathrm{E}(u_\mathrm{B})=X_\mathrm{E}(u_\mathrm{A})=X_\mathrm{U}$ (and this actually holds for general type spaces).

Example

As an illustration of the results, consider a simple example with fecundity effects and without survival effects. Suppose that $N = 2$ under a Moran reproductive process (eq. 1) with constant death rate and with fecundity linear-quadratic in the two players' strategies, $x \in \mathbb{R}$ (own strategy) and $y \in \mathbb{R}$ on a patch (and independent of strategies in other patches):

$$f(x, y) = f_{\mathrm{b}} \left[1 + \alpha x - \beta x y - \gamma x^2\right], \tag{23}$$

for parameters $\alpha, \beta, \gamma \in \mathbb{R}$ and for some (large) baseline fecundity $f_{\mathrm{b}} > 0$ common to every individual in the population. This fecundity function can be thought of as special case of the Cournot duopoly model (e.g., Fudenberg and Tirole, 1991). Substituting it into eq. 1 and then into eq. 20 along with eq. 5 shows that X_{D} is a singleton set with unique element

$$x^* = \frac{\alpha(3-m)}{2\left[\gamma(3-m) + \beta(m-2)\right]}. \tag{24}$$

For $\alpha = \beta = \gamma = 1$, this strategy x^* is uninvadable, $x^* \in X_{\mathrm{U}}$, and is also a symmetric Nash equilibrium strategy with respect to goal function u_{A}, $x^* \in X_{\mathrm{E}}(u_{\mathrm{A}})$, whereby $\{x^*\} = X_{\mathrm{E}}(u_{\mathrm{A}}) = X_{\mathrm{U}} = X_{\mathrm{D}}$ (see Fig. 1). In other words, maximizing behavior is equivalent with uninvadability for these parameter values. Suppose now that $\alpha = 1$, $\beta = 2$, and $\gamma = 0.01$. Then it is still true that x^* is uninvadable, $x^* \in X_{\mathrm{U}}$. However, for low values of $m > 0$, x^* is no longer a Nash equilibrium strategy (Fig. 1). One can then find a threshold value for $m \in (0, 1)$, above which $X_{\mathrm{E}}(u_{\mathrm{A}}) = X_{\mathrm{U}}$ and below which $x^* \notin X_{\mathrm{E}}(u_{\mathrm{A}})$ (in which case $X_{\mathrm{E}}(u_{\mathrm{A}}) = \varnothing$). Thus, relatedness-weighted fitness maximizing behavior is not equivalent to behavior that is uninvadable when m is small. Finally, let us consider the case $\alpha = 1$, $\beta = -1$, and $\gamma = 0.5$. Then x^* is a Nash equilibrium strategy, but for low values of m (low migration rates) it is not uninvadable (Fig. 1). One can then find a threshold value for $m \in (0, 1)$, above which $X_{\mathrm{E}}(u_{\mathrm{A}}) = X_{\mathrm{U}}$ and below which $x^* \notin X_{\mathrm{U}}$ (in which case $X_{\mathrm{U}} = \varnothing$). Thus, again, maximizing behavior with respect to the goal function u_{A} is not equivalent to behavior that is uninvadable when m is small, that is, when the population structure is strong.

Weak selection

We now turn to the study of uninvadability under weak selection and assume that types can only affect fecundity or survival, but not both simultaneously and also do not affect individuals' migration rate, which henceforth is constant. We further assume that the fecundity of any individual i can be written under the form

$$f(\theta_i, \boldsymbol{\theta}_{-i}, \phi) = f_{\mathrm{b}} \left[1 + \delta \pi(\theta_i, \boldsymbol{\theta}_{-i}, \phi)\right], \tag{25}$$

for some $\delta \geq 0$, and some function $\pi : \Theta^N \times \Delta\big(\Theta^N\big) \to \mathbb{R}_+$. The parameter δ measures the intensity of selection and if $\delta = 0$ every individual has exactly the same fecundity and hence same fitness, which entails that the evolutionary process is neutral. The function π can be thought of as the *expected material payoff* obtained during the stage of social interactions (stage (1) of the life cycle). The assumption behind eq. 25 is that fecundity can be normalized and expressed in terms of material payoff such that the outcome of the interaction affect reproduction only weakly, which can be justified by noting that fitness can depend on many other phenotypes such as morphology and physiology (which under the time span considered are taken to be fixed in the population).

If types affect the survival of adult individuals (e.g., eq. 1), one can posit a relationship between material payoff and individual survival in the same vein as in eq. 25, while if types affect the death risk like in eq. 1 (in which case we can write $h(\theta_i, \boldsymbol{\theta}_{-i}, \phi) = h_{\mathrm{b}} \left[1 + \delta \pi(\theta_i, \boldsymbol{\theta}_{-i}, \phi)\right]$), one must set $\delta \leq 0$. Irrespective of specification, most standard models of evolutionary population dynamics (e.g., Frank, 1998; Ewens, 2004; Rousset, 2004 and eq. 1) exhibit the following three canonical properties: (a) fitness is monotonically increasing in the fecundity (or survival) payoff to the individual, and therefore increasing in $\pi(x_i, \boldsymbol{x}_{-i}, \phi)$; (b) fitness is monotonically decreasing in the fecundity (or survival) to the individual's patch neighbors, and therefore the fitness of i is decreasing in $\pi(x_j, \boldsymbol{x}_{-j}, \phi)$ for $j \neq i$; (c) an individual's fitness is more sensitive to changes in own fecundity (or survival) payoff than to changes in any (individual) neighbor's material fecundity (or survival). In the subsequent analysis we will focus on the class of evolutionary dynamics that yield fitness functions with these properties.

Given these assumptions, a Taylor expansion of lineage fitness in δ, for δ near zero, yields

$$W(\theta', \theta) = 1 + \delta\eta \left[\Pi(\theta', \theta) - (1-\lambda)\pi(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta)\right] + O(\delta^2), \tag{26}$$

where $\eta > 0$ and $\lambda \in [0, 1]$ (see eq. A-46), and

$$\Pi(\theta', \theta) = \sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\theta', \theta)} q_k^\circ \left[\pi(\theta', \boldsymbol{\theta}_{-i}, 1_\theta) - \frac{\lambda}{N-1} \sum_{j \neq i} \pi(\theta_j, \boldsymbol{\theta}_{-i}, 1_\theta)\right] \tag{27}$$

is the *lineage payoff* to type θ' in a resident θ-population. Here, the profile distribution q_k° is eq. 7 evaluated under $\delta = 0$, which entails that the evolutionary process is neutral and is further independent of trait values. The coefficient λ is "the spatial scale of density-dependent competition" (Frank, 1998, p. 115), which quantifies the intensity of local competition for breeding spots between patch members. As shown in the Appendix (see eq.A-40), $\lambda \in [0, 1]$. In other words, an increase in the average payoff to the focal individual's patch neighbors by a small amount $\delta > 0$ increases the local density-dependent competition experienced by the focal individual (during stage (4) of the life cycle) by $\delta\lambda$. We show in the Appendix (eq. A-42) that in the Moran island model

$$\lambda = \frac{(N-1)(1-m)^2}{N - (1-m)^2} \tag{28}$$

for effects of types on fecundity (and $\lambda = 1$ for effects of types on death).

We will call a type $\theta \in \Theta$ *uninvadable under weak selection* if there exists a $\delta_0 > 0$ such that inequality (8) holds for all $\delta \in (0, \delta_0)$. Let $\Theta_{\mathrm{UW}} \subseteq \Theta_{\mathrm{U}}$ be the set of types that are uninvadable under weak selection.

Result 5 *A type $\theta \in \Theta$ is uninvadable under weak selection if and only if*

$$\Pi(\tau, \theta) \leq \Pi(\theta, \theta) \qquad \forall \tau \in \Theta. \tag{29}$$

The fact that attention may be restricted to a function that depends only on material payoffs (and not on fitness) is a consequence of the assumptions that fitness is monotonically increasing in material payoff, and that the migration probability is the same for all individuals. Indeed, under the latter assumption fitness depends on strategy only through the material payoff. Second, the fact that the weights in eq. 27 reflect the neutral population process is a consequence of weak selection: indeed, in the limit when $\delta = 0$, fitness is the same for everyone. Given these insights, it is straightforward to understand Result 5: any uninvadable type preempts entry by ensuring that there exists no mutant type that would beat carriers of the resident strategy in the competition for breeding spots in its own patch (by obtaining a higher material payoff).

Maximizing behavior

Turning now to maximizing behavior and the "as if" question, we focus on the case $\Theta = X$, as under strong selection. However, by contrast to the analysis under strong selection, here we do not make any structural assumption about the set X, or about differentiability. Let X_{UW} denote the set of uninvadable strategies under weak selection.

We now consider the goal function u_{C} defined by

$$u_{\mathrm{C}}(x_i, \boldsymbol{x}_{-i}, \phi) \;=\; \sum_{k=1}^{N} \sum_{\boldsymbol{x}_{-i} \in P_{ik}} q_k^{\circ} \left[\pi(x_i, \boldsymbol{x}_{-i}, \phi) - \frac{\lambda}{N-1} \sum_{j \neq i} \pi(x_j, \boldsymbol{x}_{-j}, \phi) \right], \qquad (30)$$

which has a close resemblance with the function Π in eq. 27. The only difference is the set of type profiles over which summation takes place. We show in the Appendix that uninvadability is equivalent with maximizing behavior with respect to this goal function. Formally:

Result 6 $X_{\mathrm{E}}(u_{\mathrm{C}}) = X_{\mathrm{UW}}$.

In sum, we have shown in a model with minimal assumptions on the specifics of the social interaction, that under weak selection evolution selects behaviors that are "as if" individuals strived to maximize their expected relatedness-weighted payoff advantage over their patch neighbors, where the expectation is taken with respect to their experienced local lineage distribution, and where the payoff advantages is based on a comparison of own material payoff to the average material payoff of others in the patch depends on the degree of local competition, λ, which in turn depends on patch size and the migration rate.

Our analysis permits the fecundity (or survival) of an individual to depend not only on his or her own type/strategy but also on the types/strategies of the other individuals in the patch and the population at large. The special case when fecundity is independent of others' types (or strategies), one may view material payoff as a function of the individual's own strategy only. In that special case, behavior driven by maximization of u_{C} is identical with behavior driven by maximization of own material payoff, $\pi(x_i)$, irrespective of y, the patch neighbor's strategy. Hence, in this special case, Result 6 takes a particularly simple and stark form; natural selection (as expressed by uninvadability) will drive individuals to behave as if their goal always was to maximize their own material payoff.

Example

Consider again the Moran process with $N = 2$. For an individual i who plays $x_i = y$ while her patch neighbor plays $x_{-i} = x$, eq. 30 can be written as

$$u_{\mathrm{C}}(y, x, \phi) = (1-\lambda)\left[(1-r)\,\pi(y, x, \phi) + r\pi(y, y, \phi)\right] + \lambda\,(1-r)\left[\pi(y, x, \phi) - \pi(x, y, \phi)\right]. \quad (31)$$

where (from eq. 5), we have $r = (1-m)/(1+m)$ and (from eq. 28) $\lambda = (1-m)^2 / \left[2-(1-m)^2\right]$. In other words, the goal function u_{C} is then the weighted sum of two terms, with weight $\lambda\,(1-r)$ to the individual's "payoff advantage" over her patch neighbor, and weight $1-\lambda$ to a convex combination of own payoff and the payoff that both individuals would obtain had the other individual used the same strategy. When the material payoff does not depend on the behavior of individuals in other patches, this convex combination is the goal function of a *homo moralis* individual (Alger and Weibull, 2013) with degree of morality $r \in [0, 1]$.

Returning to the example in eq. 23, let the material payoff be

$$\pi(y, x, \phi) = \alpha y - \beta x y - \gamma y^2. \quad (32)$$

Then, substituting into eq. 31 shows that a unique strategy satisfies the first-order condition $\partial u_{\mathrm{C}}(y, x, \phi)/\partial y|_{y=x} = 0$ and that it is given by eq. 24. Hence, if this strategy also satisfies the second-order condition $\partial^2 u_{\mathrm{C}}(y, x, \phi)/\partial y^2|_{y=x} < 0$, then this strategy is the unique symmetric Nash equilibrium strategy in the game $G_{\mathrm{A}} = (\mathbb{N}, X, u_{\mathrm{A}})$. Hence, by Result 6, this strategy is then also the unique uninvadable strategy. In this example, the above second-order condition boils down to

$$(1-m)\,(2-m)\,\beta+(3-m)\gamma>0. \tag{33}$$

Constrained behavior

We formulated the relationship between maximizing behavior and uninvadability in terms of individuals (freely) choosing their strategies, where a strategy is a complete plan of action for all possible contingencies (see section 2.2). As is well-known in game-theory (see e.g., van Damme, 1987), a (behavior) strategy profile is a Nash equilibrium if and only if it prescribes optimal (in terms of the player's goal function) continuation play from every information set that is reached with positive probability (while actions, or continuation play, at unreached information sets need not be optimal).

Consider a social interaction in which each participant has a behavior rule that implements a behavior strategy for that individual. A situation in which each action in the continuation play from any information set onwards can evolve to optimality entails that the set $\mathcal{S}$ of states of an individual is very large. This has been used in models without social interactions in behavioral ecology (i.e., decision problems where individuals interact with their exogenous environment, e.g., McNamara and Houston, 1999). But it is rarely (if ever) considered in biological models of social interactions, as the set $\mathcal{S}$ of states is usually taken to be of small dimension, a modeling choice often following from the observation that most animal (including human) decision-making is cognitively bounded (Fawcett et al., 2012). A low-dimensional state space cannot represent the whole history of actions $\mathcal{H}$, and the behavior rule itself is further usually assumed to depend only a low-dimensional evolvable type θ. A low-dimensional behavior rule can thus fundamentally constrain the flexibility of behavior in social interactions, and this curtails the possibility to have actions that are all optimal along the path of play.

We will now discuss how such mechanistic constraints change the interpretation of maximizing behavior. To that end, we will consider a multi-move game where individuals have a memory of step one, and stay with the Moran process under $N = 2$. A typical example is a infinitely repeated prisoner's dilemma where individuals can only react to the past action of their partner (e.g., McNamara et al., 1999; Killingback and Doebeli, 2002; Taylor and Day, 2004; André and Day, 2007). The simplest setting therein is maybe provided by the so-called continuous prisoner's dilemma with linear reactive "strategies," where $a_i(t) \geq 0$ is the level of investment in cooperation by individual i in social period t of the repeated game, and is given by

$$\begin{cases} a_1(t) = \alpha + \theta_1 a_2(t-1) \\ a_2(t) = \alpha + \theta_2 a_1(t-1) \end{cases} \qquad \text{for } t = 1, 2, ..., \tag{34}$$

where $\alpha > 0$ is an exogenous initial donation, and $a_1(0) = a_2(0) = \alpha$. Here $\theta_i \in \Theta = (0, 1)$ represents the evolvable response slope of individual i on the level of investment of its partner in the previous round. For this model, the decision rule is

$$d_i(s_i(t)) = \alpha + \theta_i s_i(t) \text{ with } s_i(t) = a_{-i}(t-1) \text{ and } s_i(0) = 0. \tag{35}$$

Given some material payoffs in each round $t = 0, 1, 2, ...$ uninvadability of θ can be evaluated, for example, in terms of the long-run average material payoff. This average is well-defined, since both individuals' actions increase monotonically over social time and converge to the within-period action pair

$$\begin{cases} a_1^* = \alpha(1 + \theta_1)/(1 - \theta_1\theta_2) \\ a_2^* = \alpha(1 + \theta_2)/(1 - \theta_1\theta_2). \end{cases} \tag{36}$$

Hence, if the material payoffs in each time period of the repeated interaction are given by $\psi\,(a, a')$, where z is own action and z' the other individual's action, then the long-run average material payoff within the demographic time period to an individual with trait θ' interacting with an individual with trait θ is

$$\pi(\theta', \theta, \phi) = \psi\left[\frac{\alpha + \alpha\theta'}{1 - \theta'\theta}, \frac{\alpha + \alpha\theta}{1 - \theta'\theta}\right]. \tag{37}$$

For the sake of illustration, suppose the function ψ is linear-quadratic: $\psi\,(a, a') = \beta a a' - \gamma a^2$ for some $\beta, \gamma > 0$. Substituting the resulting payoff function into lineage payoff (eq. 27) and computing the first-order condition for a type $\theta \in (0, 1)$ to be a locally uninvadable shows that X_{UW} is a singleton set with unique element

$$\theta^* = \frac{1-(2-m)\,(\beta/\gamma-1)}{1+(2-m)\,(\beta/\gamma-1)}. \tag{38}$$

The necessary second-order condition for uninvadability is $\gamma \leq \beta$ for a panmictic population ($m=1$), and $m(2\beta-\gamma)^5/(\beta-\gamma)^3 \leq 0$ for m close to zero (see Appendix). The second-order condition is complicated for intermediate values of m. But since a necessary condition for $\theta^* \in (0,1)$ is that $\gamma < \beta$, the two boundary cases are sufficient to illustrate the fact that limited dispersal tends to destabilize the candidate uninvadable point; θ^* is uninvadable in a panmictic population, while for strong population structures θ^* is invadable.

By Result 6, the locally uninvadable type θ^* is also the unique symmetric Nash equilibrium strategy x^* when individuals' goal function is u_{C} and $X = \Theta = (0,1)$. But is it behaviorally/biologically reasonable to interpret the reaction slope as a strategy x^*, chosen by individuals? Under the infinitely repeated prisoners' dilemma (eqs. 34–37), the reaction slope θ determines the decision rule of individuals (eq. 35). From a game-theoretic viewpoint, this constrained repeated prisoners' dilemma is a one-shot game, where each player only has one choice, namely what reaction slope $x \in X = \Theta = (0,1)$ to use throughout the whole social interaction. Hence, the reaction slope is now the player's *strategy* in a simultaneous-move one-shot game with material payoff from playing strategy x' against strategy x given by eq. 37 with θ' replaced by x' and θ by x. The interpretation in terms of maximizing behavior is then that individuals choose how strongly to react to the other player's last action, within the given class of affine functions.

In other words, the parameters determining the mechanism that generates actions (the behavior rule) are optimal for each individual, in terms of the goal function u_{C} when these parameters take the values that are uninvadable, and can thus be interpreted as being the results of maximizing behavior. This reasoning applies to any trait affecting any behavior rule, such as traits affecting cognitive properties such as memory size, learning speed, or internal reward systems involved in decision making. In sum, the interpretation in terms of maximizing behavior can be applied to both flexible and constrained behavior, and any evolvable phenotype determining a proximate mechanism that generates actions can be interpreted as a strategy in a corresponding game.

Discussion

We have examined the question whether in a patch structured population strategies that are uninvadable can be interpreted as chosen by each individual in order to maximize some goal function for the individual (a proximate cause), while what is really being maximized is the strategy's lineage fitness (the ultimate cause). For the purpose of analyzing this "as if" question, we have examined goal functions that are linear combinations of personal fitness or personal material payoff. These are goal functions of a form often used in evolutionary biology and economics. They are analytically relatively simple and transparent in the sense that they explicitly depend on the fitnesses of, or material payoffs to, the individual and (potentially) its partners engaged in the social interaction at hand, weighted by some "population-structural" coefficients.

We analyzed the connection between uninvadability and such individual goal functions under two different selective regimes. Our results can be summarized as follows.

- *Arbitrary selection strength.* Individual goal functions producing "as if" behavior with population-structural coefficients independent of selection and/or given by relatedness obtains only for certain classes of social interactions, in particular, it obtains for strategically neutral interactions. In other words, although lineage fitness is maximized by natural selection, individuals can in general not be regarded as if they would maximize their individual or inclusive fitness, with "inclusive fitness" taking the textbook interpretation.

- *Weak selection.* Regardless of the complexity and strategic nature of the social interaction, an individual goal function producing "as if" behavior with weights independent of selection can be found. This turns out to be a function (eq. 30) that represents a certain weighted average of material payoff, which can be interpreted as a combination of selfishness (own material payoff), Kantian morality or righteousness (what the individual would like all individuals to do), and rivalry or local competitiveness (material payoff differences).

We will now discuss more in detail the scope of these results, the interpretation of our model of strategy evolution, and how this relates to previous formalization of maximizing behavior in evolutionary biology.

Patches, families, and panmictic populations

Without any assumptions on the strength of selection, we found no individual-based goal function whose maximization lead to the behavior favored by natural selection, with population-structural coefficients independent of selection, not even when the trait space is one-dimensional (see Result 3 and 4). Hence, even in situations in which a concept of invasion fitness maximization applies (lineage fitness in our formalization), the "as if" notion of individuals as maximizing agents, equipped with goal functions such as "inclusive fitness" does not generally obtain. This stems from the fact that lineage fitness, generally depends on the full distribution of types that a carrier of the mutant trait is exposed to, and this distribution in turn depends on the expression of the mutant and resident type in past generations. Hence, lineage fitness is a complex multi-generational measure of invasion fitness, where the distribution of types is endogenously determined and thus depends on selection. Since this dependency is endogenous by nature, a goal function representing lineage fitness cannot in general be written as a linear combination of personal fitness functions, with coefficients that are independent of the fitness of the different types and thus of selection.

This argument applies regardless of the dimensionality of the type space. Hence, our Result 3 and Result 4 establish the fact that, in general, no full correspondence between the set of Nash equilibria induced by maximizing behavior and the set of uninvadable strategies exists. But there are exceptions to these negative results. For instance, in evolutionary biology and evolutionary game theory the canonical model of social interactions is symmetric pairwise interactions in a panmictic population (e.g., Maynard Smith, 1982; Eshel, 1983), which, by definition, is a situation where there is no local competition. In this case, lineage fitness is proportional to personal fitness, which in turn is an affine increasing function of material payoff. Then, an individual-based goal function that produces "as if maximizing" behavior can be readily found, and is directly given by the material payoff function of the social interaction, which implies that uninvadability is equivalent with equilibrium play in the social interaction. Our model allows for a direct extension of this case to multi-player interactions within groups of any size $N > 1$ in a panmictic population, a case that has been extensively studied in evolutionary biology (e.g., the "haystack" model, Maynard Smith, 1964, or the "group-selection" and "founder effect" models, Wilson, 1975; Cohen and Eshel, 1976). This is a general result, regardless of the game being played between group members.

Other general cases of maximizing behavior can be found by considering interactions among family members in a panmictic population, like for instance interactions among siblings (or parent-offspring interactions) before the round of complete dispersal, and where the kinship structure is determined in a single episode of reproduction and does not depend on the type distribution when mutants are rare. For this case, invasion fitness is $W(y,x) \propto r\pi(y,y) + (1-r)\pi(y,x)$ for a constant pairwise relatedness $r \in [0,1]$ (Day and Taylor, 1998), which does thus not depend on the types. In this case, the individual-based goal function $u_F(y,x) = r\pi(y,y) + (1-r)\pi(y,x)$ (introduced in Alger and Weibull, 2013) results in "as if" maximizing behavior since $X_{\mathrm{E}}(u_F) = X_{\mathrm{U}}$. Hence, in family-structured populations maximizing behavior can obtain for all games under the condition that relatedness is not affected by selection. More generally, it is due to the fact that population's genetic structure generally depends on selection (in our model the $q_k(y,x)$-distribution depends on both mutant and residents types, and is different from the distribution $q_k(x,x)$ evaluated under the neutral process), that a general "as if maximizing" representation is unlikely. It would thus be useful in future research to delineate the instances of family (or spatially) structured populations where invasion fitness depends on population-structural coefficients that are independent of selection.

Weak selection

Under weak selection, all earlier events of selection can be summarized by a neutral distribution of types, which quantifies the effects of the kinship structure induced by limited dispersal on an individual's goal function [the distribution $q_k(\theta,\theta)$ is independent of the mutant, see eq. 27]. Hence, an individual goal function, with population-structural coefficients independent of selection, can be found. We showed that, regardless of the complexity of social interactions, individuals who maximize their average scaled payoff would choose, in equilibrium, strategies that are uninvadable (our Result 6). We note that this result is nevertheless not fully general as it applies only to traits affecting survival or reproduction, but not migration rates or other trait modifying the genetic system (i.e., modifier traits).

While we rule out modifier traits by assumption, we impose virtually no restrictions on the games individuals play. Our weak-selection result covers maximizing behavior for games with strategic substitutes, complements, and the special case of strategically neutral games. A special case of strategically neutral games are those in which the payoff function is additive separable in the strategies used by different group members. In such games, a goal function that takes the same form as the relatedness-weighted fitness goal function (eq. 16), but were fitness is replaced by payoff, would also produce "as if maximizing" behavior. This is analogous to the situation considered in Grafen (2006), so our results matches his results about "optimization of inclusive fitness" with constant environmental states. Strategically neutral games can be viewed as independent decision problems, one for each player, and so the concept of Nash equilibrium to characterize maximizing behavior is not needed in this special situation. This is probably the reason why this fundamental concept does not appear previously in the literature in evolutionary biology on maximizing behavior in the context of interactions between relatives, a literature that usually deals only with strategically neutral games (e.g., Grafen, 2006; Gardner and Welch, 2011). This previous work also endorses a concept of stability of a resident type evaluated from the action of natural selection over only a single demographic time period, the initial period where the mutant arises (e.g., Grafen, 2006, p. 553), and which is in general dynamically insufficient to ascertain the stability of a resident type when interactions occur between relatives (Lehmann and Rousset, 2014). By contrast, uninvadability in our analysis is ascertained from a multi-generational measure of invasion fitness (lineage fitness), which is consistent with standard evolutionary analysis (Ferrière and Gatto, 1995; Rousset, 2004; Metz and Gyllenberg, 2001).

Finally, it is worth noting that since different goal functions can produce the same behavior, the goal functions introduced in the "as if" approach are not uniquely defined. For instance, any strictly increasing transformation of a given goal function returns a new goal function with the same set of maximands. Nevertheless, the goal function producing "as if" behavior that we have identified (u_{C}, eq. 30) combines three features, which are likely to be generic and general. These are (i) "selfishness", which ultimately results from fitness depending on the individual's own material payoff; (ii) "Kantian morality", whereby individuals do what they would like everybody to do, which results from identity-by-descent within patches and cause individuals to express identical strategies and; (iii) "competitiveness" or "rivalry", which results from local competition in a spatially structured population, which makes the fitness of an individual decrease in the others' material payoffs. These last two features are direct consequences of limited dispersal and can in general not be separated from each other. They are the goal-oriented behavioral consequences of kin-selected benefits (or costs) and kin competition, the two fundamental and general additional components of the selection pressure on any social behavior induced by limited dispersal (e.g., Grafen, 1984; Queller, 1994; West et al., 2002; Rousset, 2004). As such we conjecture that the three qualitative features of the u_{C} goal function will also emerge under more realistic demographics, like class or demographically structured populations, something that could be detailed in future work.

Evolutionary selection of goal functions

Our "as if" question led us to posit three alternative goal functions, and to compare the strategies that would result from maximization of these goal functions to those being selected for by way of natural selection. However, in cognitively sophisticated organisms selection may act directly at the level of goal functions, and so to speak delegate the (free) choice of action(s) to the organism. One may then ask which goal functions will be selected for (hence the goal function itself becomes an evolving "strategy"). This question is distinct from the "as if" question addressed here and has been analyzed previously by economists (Alger and Weibull, 2012, 2013 and references therein) and biologists (Akçay and Van Cleve, 2009, 2012). The present modeling framework could be applied to such an analysis, in which case each type would define a goal function, and the set of types would be all the goal functions that the organism's cognition and physiology could implement. In such an analysis it will matter if organisms can recognize each others' type or not, and we conjecture (by extrapolating from the analysis in Alger and Weibull, 2013) that the u_{C} goal function (eq. 30) will be uninvadable under weak selection when goal function evolution occurs and organisms cannot recognize each others' type.

Conclusion

Since in our model there are no genetic constraints, evolvable traits can be thought of as being coded by a one-locus genetic basis (i.e., our set of alternative alleles). Our model thus provides a setting where the conditions are ideal for identifying maximizing behavior under evolutionary dynamics. Our results show that when social interactions are modeled as games between population members, lineage fitness can in general not be translated into individual fitness, and this in turn suggest that lineage fitness maximization will in general not make individuals appear as if they were maximizing an individual-based goal function. But individuals can still be the instruments of the gene's goal, and our model is consistent with the view that this is the level at which adaptation and thus maximizing behavior can be conceived in complete generality (Dawkins, 1978; Haig, 2012).

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Appendix A: proof of Results 1–6

Result 1

We here prove that a mutant type τ appearing initially as a single copy on a single focal island of the population, which is otherwise fixed for the resident θ, will go extinct with probability one if, and only if, $W(\tau,\theta) \leq W(\theta,\theta)$. Our proof below follows the line of arguments developed in Mullon et al. (in preparation) and that builds on Wild (2011).

Denote by $M_i(t)$ the random number of patches in the population with $i \in I = \{1, 2, ..., N\}$ mutants at demographic time t, and let $\mathbf{M}(t) = (M_1(t), \dots, M_N(t))$ be the associated random vector. Starting with a single initial mutant in the focal patch at time $t = 0$, i.e., $\mathbf{M}(0) = (1, 0, \dots, 0)$, we are interested in finding an operational necessary and sufficient condition for the mutant type to go extinct in finite time with probability one; formally, a condition for $\Pr[\mathbf{M}(t) = \mathbf{0} \text{ for some } t \in \mathbb{N} \mid \mathbf{M}(0) = (1, 0, \dots, 0)] = 1$. To that end, we first note that our assumption that there is an infinite number of islands implies that the stochastic process $\{\mathbf{M}(t)\}_{t\in\mathbb{N}}$ is a multi-type branching process (Wild, 2011), which is equivalent to assuming that only residents immigrate to the focal patch when the mutant is globally rare. Such a process can be summarized by a matrix $\mathbf{A}(\tau,\theta)$ whose (i,j) entry is the expected number of patches with $i \in I$ mutants (of type τ) that are produced over one demographic time period by the focal patch when this has $j \in I$ mutants and when the population is otherwise monomorphic for type θ. It follows from standard results on multi-type branching processes (Karlin and Taylor, 1975, p. 412) that $\Pr[\mathbf{M}(t) = \mathbf{0} \text{ for some } t \mid \mathbf{M}(0) = (1, 0, \dots, 0)] = 1$ if and only if the leading eigenvalue of $\mathbf{A}(\tau,\theta)$ is less than or equal to 1, i.e., if, and only if $\rho(\mathbf{A}(\tau,\theta)) \leq 1$ where $\rho(\mathbf{A}(\tau,\theta))$ denotes the spectral radius of $\mathbf{A}(\tau,\theta)$. It thus remains to (a) find an expression for $\mathbf{A}(\tau,\theta)$ under our biological assumptions, and (b) show that $\rho(\mathbf{A}(\tau,\theta)) \leq 1$ is equivalent to $W(\tau,\theta) \leq W(\theta,\theta)$.

Following our life-cycle assumptions, one can write

$$\mathbf{A}(\tau,\theta) = \mathbf{Q}(\tau,\theta) + \mathbf{E}(\tau,\theta), \tag{A-1}$$

where $\mathbf{Q}(\tau,\theta)$ is the matrix for which the component in row i and column j is the probability that the focal patch with $j \in I$ mutants turns into a patch with $i \in I$ mutants, and where the transition probabilities are independent of the state $\mathbf{M}$. Thus, $\mathbf{Q}(\tau, \theta)$ is the transient matrix of the Markov chain, describing the subpopulation of mutants in the focal patch, with state space $\{0, 1, 2, ..., N\}$. This Markov chain has the local extinction of the mutant type as its unique absorbing state. We also have that,

$$\mathbf{E}(\tau, \theta) = \begin{pmatrix} \epsilon_1(\tau, \theta) & \epsilon_2(\tau, \theta) & \dots & \epsilon_N(\tau, \theta) \\ 0 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 0 \end{pmatrix}, \tag{A-2}$$

where $\epsilon_j(\tau, \theta)$ is the expected number of patches with one mutant that are produced by mutant emigration from the focal patch, when the focal patch is in state j. All other entries of matrix $\mathbf{E}(\tau, \theta)$ equal zero since when the number of islands is infinite, the probability that two or more offspring from the same patch settle on the same island through dispersal is zero. To see this, note that if the number of patches would be finite, then the probability that a given breeding spot on a given patch is settled through dispersal by an offspring of an individual from the focal patch is of order $O(m/(ND))$, where D is the number of patches. The probability that two or more such offspring settle in the same patch is of order $O(m^2/(ND)^2)$ or smaller. Summing over all patches, the probability that two or more offspring from the same individual settle on the same patch through dispersal is thus at most of order $m^2/(N^2 D)$, and hence goes to zero as $D \to \infty$. Therefore, the focal patch with j mutants can only turn a patch with zero mutants into one with a single mutant.

Since

$$\rho(\mathbf{A}(\tau, \theta)) \leq 1 \iff \rho(\mathbf{A}(\tau, \theta) - \mathbf{I}) \leq 0. \tag{A-3}$$

Using eq. (A-1), we have

$$\rho(\mathbf{A}(\tau, \theta) - \mathbf{I}) \leq 0 \iff \rho\left(\mathbf{E}(\tau, \theta) - (\mathbf{I} - \mathbf{Q}(\tau, \theta))\right) \leq 0. \tag{A-4}$$

The matrix $\mathbf{I} - \mathbf{Q}(\tau, \theta)$ is non-negative, since all components of $\mathbf{Q}$ are between zero and one. In addition, $\mathbf{A}(\tau, \theta) - \mathbf{I}$ has non-negative off-diagonal entries, and $\mathbf{E}(\tau, \theta)$ is non-negative. Therefore, we can apply the first-generation-theorem (Thieme, 2009, Theorem 2.1) to obtain the equivalence

$$\rho(\mathbf{A}(\tau,\theta)-\mathbf{I}) \leq 0 \iff \rho\left(\mathbf{E}(\tau,\theta)(\mathbf{I}-\mathbf{Q}(\tau,\theta))^{-1}\right) \leq 1. \tag{A-5}$$

By construction of $\mathbf{E}(\tau,\theta)$, the matrix $\mathbf{E}(\tau,\theta)(\mathbf{I}-\mathbf{Q}(\tau,\theta))^{-1}$ is upper triangular, and all its diagonal elements except the first are zero. Since the eigenvalues of a triangular matrix equal its diagonal entries, the leading eigenvalue of $\mathbf{E}(\tau,\theta)(\mathbf{I}-\mathbf{Q}(\tau,\theta))^{-1}$ equals its first diagonal element. This is given by $\sum_{k=1}^{N} \epsilon_k(\tau,\theta)t_k(\tau,\theta)$, where $t_k(\tau,\theta)$ is the expected number of time steps that a patch that started with a single mutant spends with k mutants (owing to the fact that the component (i,j) of matrix $(\mathbf{I}-\mathbf{Q}(\tau,\theta))^{-1}$ corresponds to the expected sojourn time of the Markov chain in state i when initially starting the process in state j and excluding mutant immigration, Grinstead and Snell, 1997). Therefore,

$$\rho(\mathbf{A}(\tau,\theta)) \leq 1 \iff \sum_{k=1}^{N} \epsilon_k(\tau,\theta)t_k(\tau,\theta) \leq 1. \tag{A-6}$$

We now proceed to re-write condition (A-6) in terms of fitness. The expected number of descendants of a single mutant (τ) individual in the focal patch in state $k \in K$ (that is, the personal fitness of a mutant in a patch with k mutants), conditional on the rest of the population being monomorphic for θ, can be written as

$$w_k(\tau,\theta) = \phi_k(\tau,\theta) + \epsilon_k(\tau,\theta)/k, \tag{A-7}$$

where $\phi_k(\tau,\theta)$ denotes the expected number of descendants in the focal patch produced through philopatry by a single mutant in the focal patch in state $k \in K$, conditional on the rest of the population being monomorphic for θ, while $\epsilon_k(\tau,\theta)/k$ is the corresponding expected number of emigrant offspring produced by a single mutant. Then, because $\sum_{k=1}^{N} kt_k(\tau,\theta)$ counts the total local number of mutants during the lifespan of the lineage, and this is equal to $1+\sum_{k=1}^{N}\phi_k(\tau,\theta)kt_k(\tau,\theta)$ (the founding mutant plus the total number of local descendants, Mullon and Lehmann, 2014), we have, from eq. (A-7), the equality

$$\sum_{k=1}^{N} \epsilon_k(\tau,\theta)t_k(\tau,\theta) - 1 = \sum_{k=1}^{N} \left[w_k(\tau,\theta)-1\right] kt_k(\tau,\theta). \tag{A-8}$$

Setting

$$\Lambda(\tau,\theta) = \sum_{k=1}^{N} \left[w_k(\tau,\theta)-1\right] kt_k(\tau,\theta), \tag{A-9}$$

we have

$$\rho(\mathbf{A}(\tau,\theta)) \leq 1 \iff \Lambda(\tau,\theta) \leq 0. \tag{A-10}$$

Since we assume no class structure (no roles) within patches, individuals of a given type are exchangeable within patches and types can be allocated randomly to neighbors of a focal individual. Because of the symmetry of the personal fitness function $w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta)$, we can write

$$w_k(\tau,\theta) = \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\tau,\theta)} \binom{N-1}{k-1}^{-1} w(\tau, \boldsymbol{\theta}_{-i}, 1_\theta), \tag{A-11}$$

where S_{k-1} is the set of all subsets of $\{\tau,\theta\}^{N-1}$ with exactly $k-1$ individuals having type τ. Substituting into eq. A-9, and recalling the notation $\bar{t}(\theta',\theta) = \sum_{k=1}^{N} k t_k(\theta',\theta)$, we have

$$\begin{aligned}
\Lambda(\tau,\theta) &= \sum_{k=1}^{N} \left[\sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\tau,\theta)} \frac{w(\tau, \boldsymbol{\theta}_{-i}, 1_\theta)}{\binom{N-1}{k-1}} - 1 \right] k t_k(\tau,\theta) \\
&= \sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\tau,\theta)} \left[w(\tau, \boldsymbol{\theta}_{-i}, 1_\theta) \frac{k t_k(\tau,\theta)}{\binom{N-1}{k-1}} \right] - \sum_{k=1}^{N} k t_k(\tau,\theta) \\
&= \bar{t}(\tau,\theta) \left[\sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}(\tau,\theta)} w(\tau, \boldsymbol{\theta}_{-i}, 1_\theta) q_k(\tau,\theta) - 1 \right].
\end{aligned} \tag{A-12}$$

Using (6), we finally obtain

$$\Lambda(\tau,\theta) = \bar{t}(\tau,\theta) \left[W(\tau,\theta) - 1 \right]. \tag{A-13}$$

Since $W(\theta,\theta) = 1$, and since $\bar{t}(\tau,\theta) \geq 1$, it follows that

$$\Lambda(\tau,\theta) \leq 0 \iff W(\tau,\theta) \leq W(\theta,\theta). \tag{A-14}$$

Result 2

As noted in the main text, Result 1 implies that for x to be uninvadable it must be that, given x, $y = x$ is a local maximum of

$$W(y,x) = \sum_{k=1}^{N} \sum_{\boldsymbol{x}_{-i} \in S_{k-1}(y,x)} q_k(y,x) w(y, \boldsymbol{x}_{-i}, 1_x). \tag{A-15}$$

The first step of the proof consists in showing that the expression for $\partial W(y,x)/\partial y|_{y=x}$ in (20) obtains. We begin by noting that thanks to the permutation invariance of w with respect to the components of $\boldsymbol{x}_{-i}$, for any $\boldsymbol{x}_{-i} \in S_{k-1}(y,x)$ we can write $\boldsymbol{x}_{-i} = \big(\mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}\big)$, where $\mathbf{y}^{(k-1)}$ is the $(k-1)$-dimensional vector whose components all equal y, and $\mathbf{x}^{(N-k)}$ is the $(N-k)$-dimensional vector whose components all equal x. By a slight abuse of notation, we drop the parentheses around $\mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}$, and write

$$w(y, \boldsymbol{x}_{-i}, 1_x) = w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\,. \tag{A-16}$$

Using this notation,

$$W(y,x) = \sum_{k=1}^{N} \binom{N-1}{k-1} q_k(y,x)\, w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\,. \tag{A-17}$$

Writing w_j for the partial derivative of w with respect to its j-th argument, where $j = 1, ..., N$, we have

$$\begin{aligned}\frac{\partial W(y,x)}{\partial y} &= \sum_{k=1}^{N} \left[\binom{N-1}{k-1} \frac{\partial q_k(y,x)}{\partial y} w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right] + \\ &\sum_{k=1}^{N} \left[\binom{N-1}{k-1} q_k(y,x) \sum_{j=1}^{k} w_j\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right].\end{aligned} \tag{A-18}$$

Noting that for $y = x$, $w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big) = w\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$, which is independent of k so that it can be factored out in the first term, and using the definition of $p_k(y,x)$, we obtain

$$\begin{aligned}\left.\frac{\partial W(y,x)}{\partial y}\right|_{y=x} &= w\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \sum_{k=1}^{N} \left[\left.\frac{\partial p_k(y,x)}{\partial y}\right|_{y=x}\right] + \\ &\left.\sum_{k=1}^{N} \left[p_k(y,x) \sum_{j=1}^{k} w_j\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]\right|_{y=x}.\end{aligned} \tag{A-19}$$

This expression can be further simplified by noting that

$$\sum_{k=1}^{N} \left[\left.\frac{\partial p_k(y,x)}{\partial y}\right|_{y=x}\right] = \left.\frac{\partial \left[\sum_{k=1}^{N} p_k(y,x)\right]}{\partial y}\right|_{y=x} = \left.\frac{\partial}{\partial y}(1)\right|_{y=x} = 0. \tag{A-20}$$

Hence,

$$\left.\frac{\partial W(y,x)}{\partial y}\right|_{y=x} = \left.\sum_{k=1}^{N} \left[p_k(y,x) \sum_{j=1}^{k} w_j\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]\right|_{y=x}. \tag{A-21}$$

Permutation invariance further implies that for any $j \geq 2$, $w_j\big(x, \mathbf{x}^{(N-1)}, 1_x\big) = w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$ (it's as if the individual whose marginal type change is under consideration were systematically labeled to appear as the last component in the vector $\mathbf{x}^{(N-1)}$). Noticing also that $\sum_{k=1}^{N} \left[p_k(y,x) w_1\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]\big|_{y=x} = w_1\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$, we can write:

$$\begin{aligned}
\left.\frac{\partial W(y,x)}{\partial y}\right|_{y=x} &= w_1\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + \left.\sum_{k=2}^{N} \left[p_k(y,x) \sum_{j=2}^{k} w_j\left(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\right)\right]\right|_{y=x} \\
&= w_1\left(x, \mathbf{x}^{(N-1)}, 1_x\right) + \sum_{k=2}^{N} \left[p_k(x,x)\,(k-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\right] \\
&= w_1\left(x, \mathbf{x}^{(N-1)}, 1_x\right) + \\
&\quad (N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \sum_{k=2}^{N} \left[\frac{(k-1)\, p_k(x,x)}{(N-1)}\right] \\
&= w_1\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + r(x,x)(N-1) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\,, \qquad \text{(A-22)}
\end{aligned}$$

which is the expression provided in eq. 20.

Turning now to the goal functions, we start with the u_{A} function defined in eq. 16 of the main text. A necessary condition for a strategy x to be a symmetric Nash equilibrium strategy of $G_{\mathrm{A}} = (\mathbb{N}, X, u_{\mathrm{A}})$ is that, if all the other players except player i use strategy x, strategy x satisfy the first-order condition for a local maximum for individual i:

$$\left.\frac{\partial u_{\mathrm{A}}(x_i, \mathbf{x}^{(N-1)}, \phi)}{\partial x_i}\right|_{x_i = x} = 0. \qquad \text{(A-23)}$$

Note that in the second term in eq. 16, x_i appears exactly once in $\boldsymbol{x}_{-j}$, for each j. By permutation invariance, we can without loss of generality assume that x_i appears as the last component in each $\boldsymbol{x}_{-j}$, so that, for each j, the partial derivative of $w(x_j, \boldsymbol{x}_{-j}, \phi)$ with respect to x_i writes $w_N(x_j, \boldsymbol{x}_{-j}, \phi)$. Moreover, since $\bar{x} = x$ if all other individuals uses strategy x, we immediately obtain

$$\left.\frac{\partial u_{\mathrm{A}}(x_i, \mathbf{x}^{(N-1)}, \phi)}{\partial x_i}\right|_{x_i = x} = w_1(x, \mathbf{x}^{(N-1)}, 1_x) + r(x,x)\,(N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\,, \qquad \text{(A-24)}$$

an expression which coincides with eq. 20.

Next, we turn to the goal function u_{B} defined in eq. 18 of the main text. A necessary condition for a strategy x to be a symmetric Nash equilibrium strategy of $G_{\mathrm{B}} = (\mathbb{N}, X, u_{\mathrm{B}})$

is that, if all the other players except player i use strategy x, i.e., if $\boldsymbol{x}_{-i} = \mathbf{x}^{(N-1)}$, strategy x satisfy the first-order condition for a local maximum for individual i:

$$\left.\frac{\partial u_{\mathrm{B}}(x_i, \mathbf{x}^{(N-1)}, \phi)}{\partial x_i}\right|_{x_i = x} = 0. \tag{A-25}$$

Permutation invariance implies

$$u_{\mathrm{B}}(x_i, \mathbf{x}^{(N-1)}, \phi) \; = \; \sum_{k=1}^{N} q_k(\bar{x}, \bar{x}) \binom{N-1}{k-1} w\Big(x_i, \mathbf{x}_i^{(k-1)}, \mathbf{x}^{(N-k)}, \phi\Big). \tag{A-26}$$

Supposing now that everyone in the population except individual i uses strategy x, and applying observations made earlier in this proof, we obtain

$$\begin{aligned}
\left.\frac{\partial u_{\mathrm{B}}\big(x_i, \mathbf{x}^{(N-1)}, \phi\big)}{\partial x_i}\right|_{x_i = x} &= \left.\left[\sum_{k=1}^{N} q_k(x, x) \binom{N-1}{k-1} \sum_{j=1}^{k} w_j\Big(x_i, \mathbf{x}_i^{(k-1)}, \mathbf{x}^{(N-k)}, \phi\Big)\right]\right|_{x_i = x} \\
&= w_1\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + (N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \sum_{k=2}^{N} \frac{(k-1)\, p_k(x, x)}{(N-1)} \\
&= w_1\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + r(x, x)(N-1) w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big), \qquad \text{(A-27)}
\end{aligned}$$

which is an expression which coincides with the one provided in eq. 20.

Result 3

Suppose that $X_{\mathrm{D}} = \{x\}$, for some $x \in X$. We have

$$\begin{aligned}
\frac{\partial^2 W(y, x)}{\partial y^2} = &\sum_{k=1}^{N} \left[\binom{N-1}{k-1} \frac{\partial^2 q_k(y, x)}{\partial y^2} w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right] + \\
&2 \sum_{k=1}^{N} \left[\binom{N-1}{k-1} \frac{\partial q_k(y, x)}{\partial y} \sum_{j=1}^{k} w_j\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right] + \\
&\sum_{k=1}^{N} \left[\binom{N-1}{k-1} q_k(y, x) \sum_{j=1}^{k} \sum_{\ell=1}^{k} w_{j\ell}\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]. \qquad \text{(A-28)}
\end{aligned}$$

As noted above, we need to evaluate this expression at $y = x$. Since $w\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\big|_{y=x} = w\big(x, \mathbf{x}^{(N-1)}, 1_x\big)$, which is independent of k, and given the definition of $q_k(y, x)$, when evaluated at $y = x$, the first line in eq. A-28 may be written as

$$\begin{aligned}
&w\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \sum_{k=1}^{N} \left.\frac{\partial^2 p_k(y,x)}{\partial y^2}\right|_{y=x} \\
&= w\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \frac{\partial^2}{\partial y^2} \sum_{k=1}^{N} p_k(y,x)\big|_{y=x} \\
&= w\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \frac{\partial^2}{\partial y^2} (1) = 0. \qquad \text{(A-29)}
\end{aligned}$$

Next, and disregarding the constant 2, the second line in (eq. A-28) may be rewritten as follows:

$$\begin{aligned}
&\sum_{k=1}^{N} \left.\left[\binom{N-1}{k-1} \frac{\partial q_k(y,x)}{\partial y} w_1\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]\right|_{y=x} + \\
&\sum_{k=2}^{N} \left.\left[\binom{N-1}{k-1} \frac{\partial q_k(y,x)}{\partial y} \sum_{j=2}^{k} w_j\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big)\right]\right|_{y=x} \\
&= w_1\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}, 1_x\big) \frac{\partial}{\partial y} \left.\sum_{k=1}^{N} p_k(y,x)\right|_{y=x} + \\
&+ \sum_{k=2}^{N} \left.\left[\binom{N-1}{k-1} \frac{\partial q_k(y,x)}{\partial y} (k-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\right]\right|_{y=x}. \qquad \text{(A-30)}
\end{aligned}$$

The first term on the right-hand side of this equality equals zero (see eq. A-20). Turning now to the second term, by factoring out $w_N\left(x, \mathbf{x}^{(N-1)}, 1_x\right)$, by multiplying and dividing by $(N-1)$, and by using the definition of q_k, this term writes

$$\begin{aligned}
&(N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \sum_{k=2}^{N} \left.\left[\frac{\partial p_k(y,x)}{\partial y} \frac{(k-1)}{(N-1)}\right]\right|_{y=x} \\
&= (N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big) \frac{\partial}{\partial y} \sum_{k=2}^{N} \left.\left[\frac{(k-1)\, p_k(y,x)}{(N-1)}\right]\right|_{y=x} \\
&= (N-1)\, w_N\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\; r_1(y,x)\big|_{y=x}. \qquad \text{(A-31)}
\end{aligned}$$

Finally, we proceed to rewriting the third line in the original expression (eq. A-28). Using permutation invariance, we obtain the following expression:

$$\begin{aligned}
&w_{11}\big(x,\mathbf{x}^{(N-1)},1_x\big)+\\
&(N-1)\,w_{1N}\big(x,\mathbf{x}^{(N-1)},1_x\big)\sum_{k=1}^{N}\left[\frac{(k-1)\,p_k(y,x)}{(N-1)}\right]\Bigg|_{y=x}+\\
&(N-1)\,w_{N1}\big(x,\mathbf{x}^{(N-1)},1_x\big)\sum_{k=1}^{N}\left[\frac{(k-1)\,p_k(y,x)}{(N-1)}\right]\Bigg|_{y=x}+\\
&(N-1)\,w_{NN}\big(x,\mathbf{x}^{(N-1)},1_x\big)\sum_{k=1}^{N}\left[\frac{(k-1)\,p_k(y,x)}{(N-1)}\right]\Bigg|_{y=x}+\\
&(N-2)\,(N-1)\,w_{2N}\big(x,\mathbf{x}^{(N-1)},1_x\big)\sum_{k=1}^{N}\left[\frac{(k-2)\,(k-1)\,p_k(y,x)}{(N-2)\,(N-1)}\right]\Bigg|_{y=x}.
\end{aligned}\tag{A-32}$$

Using the coefficient of pairwise relatedness, $r(y,x)$, as well as the coefficient of *triplet relatedness*,

$$\tilde{r}(y,x)=\sum_{k=1}^{N}\frac{(k-2)(k-1)}{(N-2)(N-1)}p_k(y,x),\tag{A-33}$$

and recalling that $w_{1N}=w_{N1}$, the third line expression in eq. A-28 may thus be written:

$$\begin{aligned}
&w_{11}\big(x,\mathbf{x}^{(N-1)},1_x\big)+2\,(N-1)\,w_{1N}\big(x,\mathbf{x}^{(N-1)},1_x\big)\,r(x,x)+\\
&(N-1)\,w_{NN}\big(x,\mathbf{x}^{(N-1)},1_x\big)\,r(x,x)+\\
&(N-2)\,(N-1)\,w_{2N}\big(x,\mathbf{x}^{(N-1)},1_x\big)\,\tilde{r}(x,x).
\end{aligned}\tag{A-34}$$

Collecting the expressions for the second and third lines in eq. A-28 (respectively in eq. A-31 and eq. A-34), and writing $r_1\,(x,x)$ for $r_1\,(y,x)|_{y=x}$, the expression in eq. A-28 writes:

$$\begin{aligned}
\frac{\partial^2 W(y,x)}{\partial y^2}\bigg|_{y=x}&=w_{11}\big(x,\mathbf{x}^{(N-1)},1_x\big)+r(x,x)\,(N-1)\,w_{NN}\big(x,\mathbf{x}^{(N-1)},1_x\big)+\\
&\quad r(x,x)2\,(N-1)\,w_{1N}\big(x,\mathbf{x}^{(N-1)},1_x\big)+\\
&\quad \tilde{r}(x,x)\,(N-2)\,(N-1)\,w_{2N}\big(x,\mathbf{x}^{(N-1)},1_x\big)+\\
&\quad r_1(x,x)2\,(N-1)\,w_N\big(x,\mathbf{x}^{(N-1)},1_x\big)\,.
\end{aligned}\tag{A-35}$$

We now turn to the goal function u_{A} (eq. 16). By Result 2, and given that X_{D} is a singleton, $X_{\mathrm{D}}=\{x\}$, a necessary condition for x to be a symmetric Nash equilibrium strategy in the population game $G_{\mathrm{A}} = (\mathbb{N}, X, u_{\mathrm{A}})$ is $\partial^2 u_{\mathrm{A}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} \leq 0$, and a sufficient condition is that this inequality hold strictly. By permutation invariance, we can without loss of generality assume that x_i appears as the last component in each $\boldsymbol{x}_{-j}$ in the expression for u_{A} (see eq. 16), so that, for each j, the partial derivative of $w(x_j, \boldsymbol{x}_{-j}, \phi)$ with respect to x_i writes $w_N(x_j, \boldsymbol{x}_{-j}, \phi)$, and the second-order partial derivative with respect to x_i writes $w_{NN}(x_j, \boldsymbol{x}_{-j}, \phi)$. Moreover, since $\bar{x} = x$ if all other individuals use strategy x in eq. 16, we immediately obtain

$$\left.\frac{\partial^2 u_{\mathrm{A}}(x_i, \boldsymbol{x}_{-i}, \phi)}{\partial x_i^2}\right|_{x_i=x} = w_{11}\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + r(x,x)\,(N-1)\,w_{NN}\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\,. \qquad \text{(A-36)}$$

Suppose now that $x \in X_{\mathrm{U}}$; then $\partial^2 W(y,x)/\partial y^2|_{y=x} \leq 0$. By comparing eq. A-35 and eq. A-36, it immediately follows that if the sum of the three last terms in eq. A-35 is strictly positive, $\partial^2 u_{\mathrm{A}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} < 0$, in which case $x \in X_{\mathrm{E}}(u_{\mathrm{A}})$. The conditions stated in part (a) of the result are sufficient for the sum of the three last terms in eq. A-35 to be strictly positive.

Suppose now that $x \in X_{\mathrm{E}}(u_{\mathrm{A}})$; then $\partial^2 u_{\mathrm{A}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} \leq 0$. By comparing eq. A-35 and eq. A-36, it immediately follows that if the sum of the three last terms in eq. A-35 is strictly negative, $\partial^2 W(y,x)/\partial y^2|_{y=x} < 0$, in which case $x \in X_{\mathrm{U}}$. The conditions stated in part (b) of the result are sufficient for the sum of the three last terms in eq. A-35 to be strictly negative.

Finally, if the sum of the three last terms in eq. A-35 equals zero,

$$\left.\frac{\partial^2 W(y,x)}{\partial y^2}\right|_{y=x} = \left.\frac{\partial^2 u_{\mathrm{A}}\left(x_i, \boldsymbol{x}_{-i}, \phi\right)}{\partial x_i^2}\right|_{x_i=x}, \qquad \text{(A-37)}$$

in which case $X_{\mathrm{E}}(u_{\mathrm{A}}) = X_{\mathrm{U}}$. The conditions stated in part (c) of the result are sufficient for the sum of the three last terms in eq. A-35 to equal zero.

Result 4

The proof is qualitatively similar to the previous one. By Result 2, and given that X_{D} is a singleton, $X_{\mathrm{D}} = \{x\}$, a necessary condition for x to be a symmetric Nash equilibrium strategy in the population game $G_{\mathrm{B}} = (\mathbb{N}, X, u_{\mathrm{B}})$ is $\partial^2 u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} \leq 0$, and a sufficient condition is that this inequality hold strictly. By permutation invariance, we can without loss of generality assume that x_i appears as the last component in each $\boldsymbol{x}_{-j}$ in the expression for u_{B} (see eq. 18), so that, for each j, the partial derivative of $w(x_j, \boldsymbol{x}_{-j}, \phi)$ with respect to x_i writes $w_N(x_j, \boldsymbol{x}_{-j}, \phi)$, and the second-order partial derivative with respect to x_i writes $w_{NN}(x_j, \boldsymbol{x}_{-j}, \phi)$. Moreover, since $\bar{x} = x$ if all other individuals use strategy x, we immediately obtain

$$\begin{aligned}\frac{\partial^2 u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi)}{\partial x_i^2} &= w_{11}\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + r(x,x)\,(N-1)\,w_{NN}\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + \\ &\quad r(x,x) 2\,(N-1)\,w_{1N}\big(x, \mathbf{x}^{(N-1)}, 1_x\big) + \\ &\quad \tilde{r}(x,x)(N-2)(N-1) w_{2N}\big(x, \mathbf{x}^{(N-1)}, 1_x\big)\,. \end{aligned} \tag{A-38}$$

Suppose now that $x \in X_{\mathrm{U}}$; then $\partial^2 W(y,x)/\partial y^2|_{y=x} \leq 0$. By comparing eq. A-35 and eq. A-38, it immediately follows that if the last term in eq. A-35 is strictly positive, i.e., if the condition stated in part (a) of the result is satisfied, $\partial^2 u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} < 0$, in which case $x \in X_{\mathrm{E}}(u_{\mathrm{B}})$.

Suppose now that $x \in X_{\mathrm{E}}(u_{\mathrm{B}})$; then $\partial^2 u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x} \leq 0$. By comparing eq. A-35 and eq. A-38, it immediately follows that if the last term in eq. A-35 is strictly negative, i.e., if the condition stated in part (b) of the result is satisfied, $\partial^2 W(y,x)/\partial y^2|_{y=x} < 0$, in which case $x \in X_{\mathrm{U}}$.

Finally, if the last term in eq. A-35 equals zero, i.e., if the condition stated in part (c) of the result is satisfied, $\partial^2 W(y,x)/\partial y^2|_{y=x} = \partial^2 u_{\mathrm{B}}(x_i, \boldsymbol{x}_{-i}, \phi)/\partial x_i^2|_{x_i=x}$, in which case $X_{\mathrm{E}}(u_{\mathrm{B}}) = X_{\mathrm{U}}$.

Result 5

In order to prove this result, we start by evaluating individual fitness under weak selection. By using a first-order Taylor expansion of the fitness of a focal individual i in a focal patch, with respect to δ and evaluated at $\delta = 0$, we can write

$$w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) = 1 + \delta \left[a_{\mathrm{f}} \Big(\pi(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) - \pi(\boldsymbol{\theta}^{(N)}, 1_\theta) \Big) - a_{\mathrm{n}} \sum_{j \neq i} \left(\frac{\pi(\theta_j, \boldsymbol{\theta}_{-j}, 1_\theta) - \pi(\boldsymbol{\theta}^{(N)}, 1_\theta)}{N-1} \right) \right] + O(\delta^2), \quad \text{(A-39)}$$

where a_{f} and a_{n} are coefficients that depend on structural demographic parameters, such as patch size and migration rate. This expansion for fitness follows from four facts about $w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta)$: (i) to the first order in δ, fitness is necessarily an affine (linear plus constant) function in the payoff of each individual in the population; (ii) each individual $j \in I$ with $j \neq i$ has the same effect on the fitness of the focal individual i (permutation invariance of payoff effects of neighbors); (iii) each individual from each patch different from the focal patch has the same effect on the fitness of focal i (permutation invariance of payoff effects of individuals in different patches when they all carry x); and (iv) total selective effects (here total effects of payoff on fitness) must sum to zero in a monomorphic population, as the expected change in type number or frequency is necessarily nil (Lehmann and Rousset, 2009, p. 38).

Owing to the assumption (introduced in section 2.3) that the fitness of an individual is monotonic increasing in its payoff and bounded by it, we have $0 < a_{\mathrm{f}} \leq 1$. Owing to the assumption that the fitness of an individual is monotonic decreasing in the payoff of its patch neighbors, and that the negative effect on fitness of a single patch neighbor having its payoff varied is not larger than the positive effect of the focal having its own payoff varied, we have $0 \leq a_{\mathrm{n}} \leq a_{\mathrm{f}}$. Letting

$$\lambda = a_{\mathrm{n}}/a_{\mathrm{f}}, \quad \text{(A-40)}$$

we conclude that $0 \leq \lambda \leq 1$. Factoring out $a_{\mathrm{f}} > 0$ from eq. A-39, we obtain:

$$w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) = 1 + \delta a_{\mathrm{f}} \left[\pi(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) - \lambda \sum_{j \neq i} \frac{\pi(\theta_j, \boldsymbol{\theta}_{-j}, 1_\theta)}{N-1} - (1-\lambda)\pi(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta) \right] + O(\delta^2). \quad \text{(A-41)}$$

This shows that the coefficient λ quantifies the proportion of density-dependent competition that is local, among patch members, and thus defines the spatial scale of density-dependent competition (Frank, 1998, p. 115).

As an illustration, in the Moran island model, and thus using the fitness function for the main text (eq. 1) along with the fecundity function (eq. 25) (our corresponding risk-factor), a Taylor expansion and subsequent rearrangement yields

$$\lambda = \begin{cases} \frac{(N-1)(1-m)^2}{N-(1-m)^2} & \text{for fecundity effects} \\ 1 & \text{for survival effects.} \end{cases} \tag{A-42}$$

We now note that when types only affect material payoff, vital rates (fecundity and survival) are the same for all types when $\delta = 0$. Hence, also fitness is then type independent and thus equal to 1 (set $\delta = 0$ in eq. 1 when fecundity is given by eq. 25). All these quantities are then exchangeable variables between individuals; the population is monomorphic and the resulting evolutionary process is neutral (Crow and Kimura, 1970; Gillespie, 2004; Ewens, 2004). Under this neutral process, that is independent of resident type θ, the experienced lineage-size distribution (eq. 3) takes a value determined solely by local sampling drift (see e.g., in Crow and Kimura, 1970; Ewens, 2004; Rousset, 2004 for an explicit example). We denote by q_k° the associated type-profile distribution, where the superscript $\circ$ signifies that the quantity is evaluated at the neutral process when $\delta = 0$. Hence, we can write

$$q_k(\theta', \theta) = q_k^\circ + O(\delta), \tag{A-43}$$

where $O(\delta)$ is the deviation (relative to the neutral process) of the type profile distribution induced by selection (i.e., $\delta > 0$) that is at most of order δ.

From eq. A-39 and eq. A-43 we have

$$\begin{aligned} &w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) q_k(\theta', \theta) = q_k(\theta', \theta) \\ &\quad + \delta a_{\mathrm{f}} \left[\pi(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) - \lambda \sum_{j \neq i} \frac{\pi(\theta_j, \boldsymbol{\theta}_{-j}, 1_\theta)}{N-1} - (1-\lambda) \pi(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta) \right] q_k^\circ + O(\delta^2). \end{aligned} \tag{A-44}$$

Substituting this into lineage fitness (eq. 6) produces

$$\begin{aligned} W(\theta', \theta) &= \sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}} w(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) q_k(\theta', \theta) = 1 \\ &+ \delta a_{\mathrm{f}} \sum_{k=1}^{N} \sum_{\boldsymbol{\theta}_{-i} \in S_{k-1}} \left[\pi(\theta_i, \boldsymbol{\theta}_{-i}, 1_\theta) - \lambda \sum_{j \neq i} \frac{\pi(\theta_j, \boldsymbol{\theta}_{-j}, 1_\theta)}{N-1} - (1-\lambda) \pi(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta) \right] q_k^\circ + O(\delta^2). \end{aligned} \tag{A-45}$$

Hence, to the first order in selection intensity δ, the expectation of fitness is taken over the neutral experienced lineage-size distribution, which is a common result of evolutionary dynamics that applies both to finite and infinite populations (Roze and Rousset, 2003; Rousset, 2004; Lehmann and Rousset, 2009; Lessard, 2009)

From the definition of Π in eq. 27 combined with eq. A-45, we can write lineage fitness as

$$W(\theta', \theta) = 1 + \delta a_{\mathrm{f}} \left[\Pi\left(\theta', \theta\right) - (1-\lambda)\pi(\theta, \boldsymbol{\theta}^{(N-1)}, 1_\theta) \right] + O(\delta^2), \tag{A-46}$$

Neglecting higher order terms in δ in this equation allows us to write the condition for uninvadability $W(\tau, \theta) \leq W\left(\theta, \theta\right)$ given in eq. 8 for weak selection as

$$\Pi(\tau, \theta) \leq \Pi(\theta, \theta). \tag{A-47}$$

Result 6

In order to save on notation in this proof, we let

$$\pi_{\mathrm{R}}(x_i, \boldsymbol{x}_{-i}, \phi) = \pi(x_i, \boldsymbol{x}_{-i}, \phi) - \frac{\lambda}{N-1} \sum_{j \neq i} \pi(x_j, \boldsymbol{x}_{-j}, \phi). \tag{A-48}$$

From eq. A-47 a necessary and sufficient condition for x to be uninvadable under weak selection is

$$x \in \arg\max_{y \in X} \Pi(y, x), \tag{A-49}$$

where

$$\Pi(y, x) = \sum_{k=1}^{N} \sum_{\boldsymbol{x}_{-i} \in S_{k-1}(y,x)} q_k^{\circ}\, \pi_{\mathrm{R}}(y, \boldsymbol{x}_{-i}, \phi). \tag{A-50}$$

Thanks to the permutation invariance of π with respect to the components of $\boldsymbol{x}_{-i}$, for any $\boldsymbol{x}_{-i} \in S_{k-1}\left(y, x\right)$ we can write $\boldsymbol{x}_{-i} = \left(\mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}\right)$, where $\mathbf{y}^{(k-1)}$ is the $(k-1)$-dimensional vector whose components all equal y, and $\mathbf{x}^{(N-k)}$ is the $(N-k)$-dimensional vector whose components all equal x. By a slight abuse of notation, we drop the parentheses around $\mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}$, and write:

$$\pi_{\mathrm{R}}(y, \boldsymbol{x}_{-i}) = \pi_{\mathrm{R}}\left(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}\right). \tag{A-51}$$

Using this notation,

$$\Pi(y,x) = \sum_{k=1}^{N} \binom{N-1}{k-1} q_k^{\circ}\, \pi_{\mathrm{R}}\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}\big)\,. \tag{A-52}$$

Hence, (A-49) writes

$$x \in \arg\max_{y\in X} \sum_{k=1}^{N} \binom{N-1}{k-1} q_k^{\circ}\, \pi_{\mathrm{R}}\big(y, \mathbf{y}^{(k-1)}, \mathbf{x}^{(N-k)}\big)\,. \tag{A-53}$$

We turn now to the goal function u_{C} defined in eq. 30, which, using eq. A-48, can be written

$$u_{\mathrm{C}}(x_i, \boldsymbol{x}_{-i}, \phi) = \sum_{k=1}^{N} \sum_{\boldsymbol{x}_{-i}\in P_{ik}} q_k^{\circ}\, \pi_{\mathrm{R}}(x_i, \boldsymbol{x}_{-i}). \tag{A-54}$$

A strategy x is a symmetric Nash equilibrium strategy of $G_{\mathrm{C}} = (\mathbb{N}, X, u_{\mathrm{C}})$ if and only if it is optimal for each individual i to play x if all the other players also play x. Thus, and noting that if all the other players except player i use strategy x we can write $\boldsymbol{x}_{-i} = \mathbf{x}^{(N-1)}$, the necessary and sufficient condition for x to be a symmetric Nash equilibrium strategy of $G_{\mathrm{C}} = (\mathbb{N}, X, u_{\mathrm{C}})$ writes:

$$x \in \arg\max_{x_i\in X} u_{\mathrm{C}}\big(x_i, \mathbf{x}^{(N-1)}, 1_x\big)\,. \tag{A-55}$$

By permutation invariance,

$$u_{\mathrm{C}}\big(x_i, \mathbf{x}^{(N-1)}, 1_x\big) \;=\; \sum_{k=1}^{N} \binom{N-1}{k-1} q_k^{\circ}\, \pi_{\mathrm{R}}\Big(x_i, \mathbf{x}_i^{(k-1)}, \mathbf{x}^{(N-k)}\Big) \tag{A-56}$$

so eq. A-55 is identical with eq. A-53, which establishes Result 6.

Appendix B: Moran process calculations

Sojourn times

We here evaluate the different results for our examples based on the Moran process (along similar lines as in Mullon and Lehmann, 2014). The key is to obtain an expression for $t_i(\tau,\theta)$, which is obtained from the (transient) transition matrix $\mathbf{Q}(\tau,\theta)$ (see eq. A-1) with element $q_{ij}(\tau,\theta)$ giving the probability that the focal patch with $j \in I = \{1, 2, ..., N\}$ mutants turns into a patch. Since for a Moran process only one individual in a patch can be replaced per unit of demographic time, the Markov chain describing local lineage is a birth-death process (e.g, Karlin and Taylor, 1975), whose transition probabilities for transient states are

$$q_{ij}(\tau,\theta) = \begin{cases} b_j(\tau,\theta), & \text{if } i = j+1 \text{ (``birth'' of a mutant)} \\ \mu_j(\tau,\theta), & \text{if } i = j-1 \text{ (``death'' of a mutant)} \\ 1-(b_j(\tau,\theta)+\mu_j(\tau,\theta)) & \text{if } j = i \text{ (``no change'')} \\ 0 & \text{otherwise.} \end{cases} \tag{B-1}$$

Standard results on birth-death processes (e.g., Ewens, 2004, eq. 2.160) show that when the initial state of the chain is one mutant, we have

$$t_i(\tau,\theta) = \frac{1}{\mu_1(\tau,\theta)} \prod_{k=1}^{i-1} \frac{b_k(\tau,\theta)}{\mu_{k+1}(\tau,\theta)}. \tag{B-2}$$

In order to evaluate the b_k's and μ_k's explicitly in terms of model parameter, we start to denote by $f_k(\theta',\theta)$ and $d_k(\theta',\theta)$, respectively, the fecundity and risk-factor of a single type $\theta' \in \{\tau,\theta\}$ individual when there are exactly k mutants among its patch neighbors. Then, for the Moran process (1) we have:

$$b_k(\tau,\theta) = \frac{(N-k)d_k(\theta,\theta)}{kd_{k-1}(\tau,\theta)+(N-k)d_k(\theta,\theta)} \left[\frac{(1-m)kf_{k-1}(\tau,\theta)}{(1-m)\left[kf_{k-1}(\tau,\theta)+(N-k)f_k(\theta,\theta)\right]+mNf_0(\theta,\theta)}\right], \tag{B-3}$$

where the first factor is the probability that a resident is chosen to die and thus vacates a breeding spot and the second factor (term in square brackets) is the probability that this vacated breeding spot is occupied by a mutant. Hence, we have

$$\mu_k(\tau,\theta) = \left[1 - \frac{(N-k)d_k(\theta,\theta)}{kd_k(\tau,\theta)+(N-k)d_k(\theta,\theta)}\right] \left[1 - \frac{(1-m)kf_k(\tau,\theta)}{(1-m)\left[kf_k(\tau,\theta)+(N-k)f_k(\theta,\theta)\right]+mNf_0(\theta,\theta)}\right]. \tag{B-4}$$

It now remains to express the f_k's and d_k's in terms of the fecundity and risk-factor functions $f(\theta_i,\boldsymbol{\theta}_{-i},\phi)$ and $d(\theta_i,\boldsymbol{\theta}_{-i},\phi)$. Owing to permutation invariance (and recalling the argument leading to eq.A-11), we have

$$f_k(\theta', \theta) = \sum_{\boldsymbol{\theta}_{-i} \in S_k(\tau,\theta)} \binom{N-1}{k}^{-1} f(\theta', \boldsymbol{\theta}_{-i}, 1_\theta), \text{ for } k = 0, 2, ..., N-1$$

$$d_k(\theta', \theta) = \sum_{\boldsymbol{\theta}_{-i} \in S_k(\tau,\theta)} \binom{N-1}{k}^{-1} d(\theta', \boldsymbol{\theta}_{-i}, 1_\theta), \text{ for } k = 0, 2, ..., N-1. \tag{B-5}$$

On substitution of eqs. B-2–B-4 into lineage fitness (eq. 6) along with the fitness function of the Moran process (eq. 1), we have all the elements to compute lineage fitness exactly under the Moran process for games of arbitrary complexity.

Neutral distribution

Setting $\tau = \theta$ in eqs. B-2–B-4, we can compute the full neutral distribution of types (eq. 3), which gives

$$p_k(\theta, \theta) = \frac{kmN}{m+N-1} \prod_{i=1}^{k-1} \frac{(1-m)i(N-i)}{(i+1)(N-(i+1)(1-m))}, \tag{B-6}$$

and on substitution into eq. 4 (by setting $\theta' = \theta$) produces eq. 5. The same result can be obtained by using a standard (and simpler) identity-by-descent argument (e.g., Karlin, 1968; Rousset, 2004), implying that relatedness satisfies $r(\theta,\theta) = (1-m)\left(1/N + [(N-1)/N]r(\theta,\theta)\right)$, whose solution results again in eq. 5.

Cournot game example

We here evaluate the second order conditions for the Cournot game (eq. 23) under a Moran process when $N = 2$ and with constant death rate. Substituting the functionals of the Moran process,eq. 1 and eqs. B-2–B-5 into lineage fitness (eq. 6) along with the game payoff function eq. 23, allows us to readily compute (using Wolfram Mathematica 10) the second order condition (eq. 22), which can be simplified to

$$\left.\frac{\partial^2 W(y,x)}{\partial y^2}\right|_{y=x} = -\frac{m\left[\beta(1-m)(2-m)+\gamma(3-m)\right]A}{(1+m)\left(A+\alpha^2(3-m)\left[\beta(1-m)+\gamma(3-m)\right]\right)}, \tag{B-7}$$

where $A = 4\left[\beta(2-m)+\gamma(3-m)\right]^2 \geq 0$.

Substituting eq. 1 and eq. 23 into eq. A-36 yields

$$\left.\frac{\partial^2 u_{\mathrm{A}}\big(x_i, \mathbf{x}^{(N-1)}, 1_x\big)}{\partial x_i^2}\right|_{x_i=x} = -B\,\big[-2\alpha^2\beta^2(1-m)^3$$

$$+\gamma(3-m)\left(\gamma(3-m)^2\left(\alpha^2+4\gamma\right)+4\beta^2(2-m)^2+\beta(3-m)C\right)\big]\,, \quad \text{(B-8)}$$

where

$$B = \frac{4m\left[\gamma(3-m)+\beta(2-m)\right]^2}{(m+1)\left[(3-m)\left[\gamma(3-m)\left(\alpha^2+4\gamma\right)+\beta C\right]+4\beta^2(2-m)^2\right]^2} \geq 0, \quad \text{(B-9)}$$

and $C = 8\gamma(2-m)+\alpha^2(1-m) \geq 0$.

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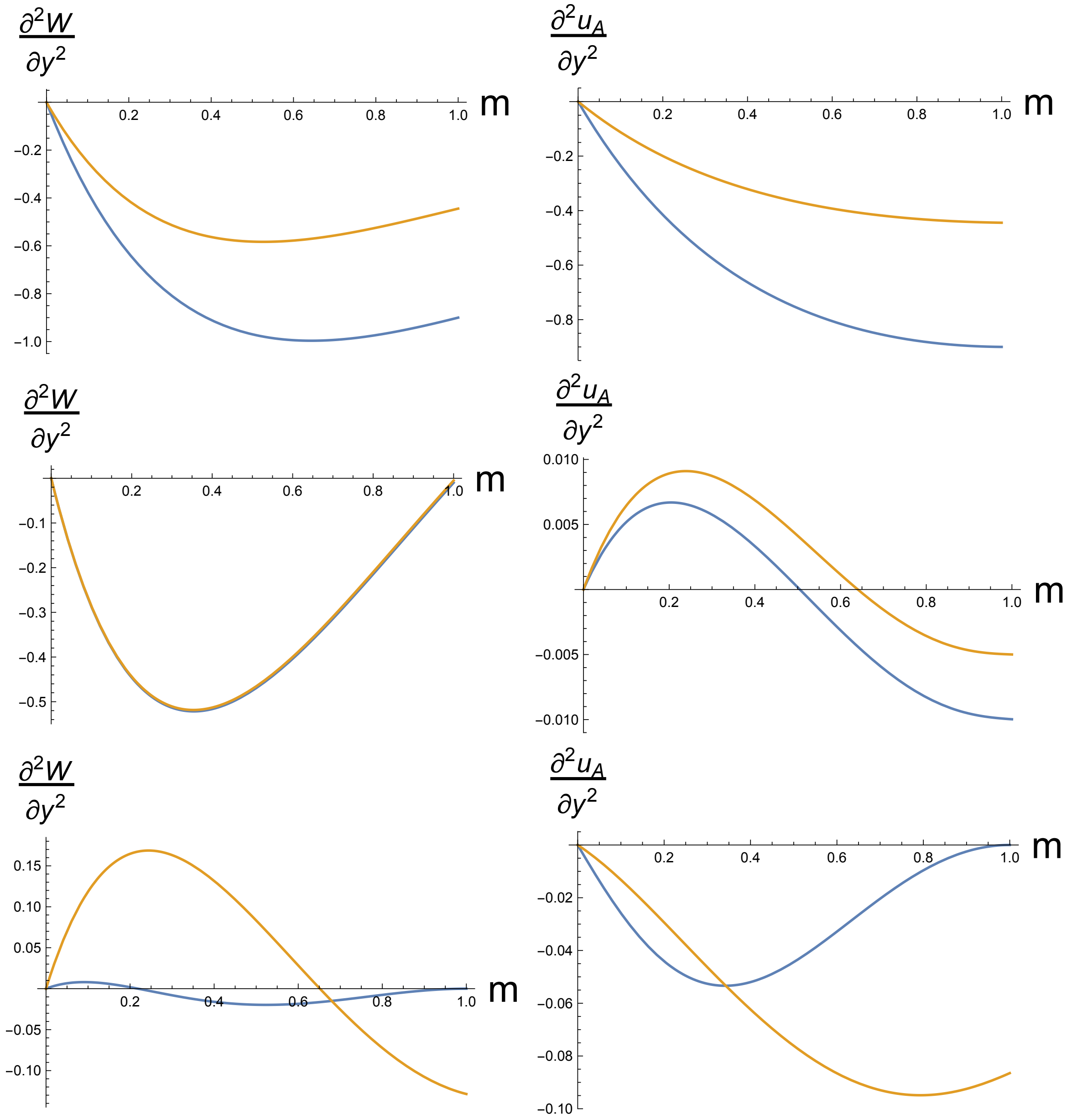

Figure 1: Graphs of $\partial^2 W(y,x)/\partial y^2\big|_{y=x=x^*}$ (as given by eq. B-7 in the Appendix) and $\partial^2 u_{\mathrm{A}}\left(y, \mathbf{x}^{(N-1)}, 1_x\right)/\partial y^2\big|_{y=x=x^*}$ (eq. B-8) as functions of migration m. These are thus the second order conditions evaluated at x^* (eq. 24) for the Cournot game (23) under a Moran process when $N = 2$. The first row of panels is for $\alpha = \beta = 1$, and $\gamma = 1$ ($\gamma = 0.5$) for the blue (yellow) line. The second row of panels if for $\alpha = 1$, $\beta = 2$, and $\gamma = 0.01$ ($\gamma = 0.005$) for the blue (yellow) line. The third row of panels if for $\alpha = 1$, $\beta = -1$, and $\gamma = 0.5$ ($\gamma = 0.2$) for the blue (yellow) line.