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On selection in finite populations

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Abstract Two major forces shaping evolution are drift and selection. The standard models of neutral drift—the Wright–Fisher (WF) and Moran processes—can be extended to include selection. However, these standard models are not always applicable in practice, and—even without selection—many other drift models make very different predictions. For example, "generalised Wright–Fisher" models (so-called because their first two conditional moments agree with those of the WF process) can yield wildly different absorption times from WF. Additionally, evolutionary stability in finite populations depends only on fixation *probabilities*, which can be evaluated under less restrictive assumptions than those required to estimate fixation *times* or more complex population-genetic quantities. We therefore distill the notion of a selection process into a broad class of finite-population, mutationless models of drift and selection (including the WF and Moran processes). We characterize when selection favours fixation of one strategy over another, for *any* selection process, which allows us to derive finite-population conditions for evolutionary stability *independent* of the selection process. In applications, the precise details of the selection process are seldom known, yet by exploiting these new theoretical results it is now possible to make rigorously justifiable inferences about fixation of traits.

Keywords Selection · Drift · Fixation · Evolutionary stability · Evolutionary robustness

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1 Introduction

Two key determinants of the distribution of traits in a population are ***genetic drift*** (stochasticity in the temporal evolution of trait frequencies in finite populations) and ***selection*** (the process by which traits associated with higher fitness—i.e. greater expected lifetime reproductive output—increase in frequency over time (Ridley 2003; Hartl and Clark 2007; Ewens 2012). There are many mathematical models of neutral drift—when no variability in fitness is associated with the evolving traits (Moran 1962; Wright 1931; Fisher 1930; Cannings 1974; Chia and Watterson 1969; Karlin and McGregor 1964; Huillet and Möhle 2011; Sargsyan and Wakeley 2008)—but few that extend to traits involving variable fitness. In fact, almost all models in the literature involving both selection and drift are generalizations of the classical Moran (1962) and Wright–Fisher (WF; Wright 1931; Fisher 1930) processes (described in Appendices B.1 and B.2).

Even in the case of neutral drift, other models can behave very differently from the Moran and WF processes (Sargsyan and Wakeley 2008; Eldon and Wakeley 2006, 2008, 2009; Pitman 1999; Sagitov 1999; Schweinsberg 2003). For models including selection, as reviewed by Patwa and Wahl (2008), predictions about fixation probabilities are sensitive "to the specific effect of the beneficial mutation on [an organism's] life history" (e.g. increasing fecundity *vs.* decreasing generation time). As a case in point, Alexander and Wahl (2008) analyze a model in which mutations that affect life-history differently affect fixation probabilities differently, despite conferring identical Malthusian fitnesses (i.e. long-term growth rates). While diffusion approximations (Ewens 2012) have been useful in modelling both WF and non-WF populations, they apply only when both drift and selection are weak (Charlesworth 2009).

Motivated by this, and by the fact that not all biological populations satisfy the assumptions of the Moran and WF models relating to the mode of reproduction (e.g. Pacific Oysters, Hedgecock 1994; Eldon and Wakeley 2006), Der et al. (2011) and Der (2010) defined and analyzed Generalized Wright–Fisher (GWF) models (which include the Eldon–Wakeley process, Eldon and Wakeley 2006; Der et al. 2012). They showed that fixation probabilities, as well as other population-genetic quantities of interest, can vary substantially if the assumptions of the WF model are relaxed. Moreover, fitting alternative models of selection to empirical data on the dynamics of allele frequencies in fruit flies suggests that the alternative models have at least as much explanatory power as the WF model (Der et al. 2011). Greater understanding of more general selection processes in finite populations would be valuable.

The Moran and WF models have also recently been used to develop evolutionary game theory. In finite populations, strategies that yield lower expected payoffs (e.g. deleterious mutations) can have positive fixation probabilities, so evolutionarily stable strategies (ESSs) should be defined to be resistant to both invasion and fixation (Nowak et al. 2004; see Definition 5.2). Which strategies turn out to be ESSs may depend on the selection process: it has been shown by Ohtsuki et al. (2006) that different "updating rules" (i.e. the various processes by which variability in fitness can influence the

frequencies of strategies in the population) can yield different evolutionary dynamics. However, almost all results pertaining to evolutionary stability in finite populations obtained thus far have been based on either the Moran (Nowak et al. 2004; Lessard 2005; Ohtsuki 2010; Kurokawa and Ihara 2009; Wild and Taylor 2004) or WF (Imhof and Nowak 2006; Lessard 2005) processes. One exception is the analysis by Lessard and Ladret (2007) of a Cannings (1974) exchangeable allele model modified to include selection; however, this analysis is limited by the assumption of weak selection (as are many other studies applying only to the Moran or WF models). A promising approach to accommodating selection processes other than the WF and Moran models in evolutionary game theory consists of a framework for analyzing games with discrete strategies, a positive mutation rate (identical for all strategies), and an arbitrary updating rule, in the limit of weak selection , developed by Tarnita et al. (2009, 2011). This approach has been extended by Allen et al. (2013) to continuous strategy sets with small mutations and continuous time, in which case the assumption of weak selection can be relaxed. While these studies supply a useful framework in which to work, they involve calculating parameters that depend on the updating scheme and population structure (but independent of the game) in order to characterize when one strategy is favoured over another. This drawback may make results that are robust to the choice of selection process harder to obtain.

Many models of cultural change are also concerned with selection and drift of ideas or cultural traits, and are inspired by the Moran and WF models (e.g. the models of Aoki et al. 2011 and Acerbi and Bentley 2014; Bentley et al. 2004 are based on the former and latter, respectively).

A general theory of the population-level processes of drift and selection will promote progress in population genetics, evolutionary game theory and the theory of cultural evolution. Applications in evolutionary game theory often involve fixation probabilities only. It is therefore useful to relax some of the assumptions of the framework of GWF models, which facilitate analysis of continuum-limits and more complex population-genetic quantities such as fixation times (Der 2010; Der et al. 2011).

Here, we define a large class of biologically sensible models of selection in finite populations (which contains the Moran and WF processes), and a subclass of models of neutral drift. We study the probability of fixation of traits under these models and obtain an intuitive result whereby traits yielding a higher fitness regardless of their frequency in the population are more likely to fix than traits that do not confer a selective advantage. We then apply this result in the context of evolutionary games in finite populations, in which both the game payoffs and the fitnesses of individuals with a given payoff are stochastic. To our knowledge, these are the first results about evolutionary stability that apply to any n-player games (for any $n \geq 2$) and are robust to any of the particular details of life history, drift and selection. In addition, our results are independent of the intensity of selection.

A number of standard definitions and theorems from probability theory are stated using our notation in the Electronic Supplementary Material (ESM); references to equations, definitions and theorems from the ESM contain the prefix "S".

2 General selection processes

Consider an asexual population of N agents (i.e. individuals) comprised of two types, A and B. By *fitness* we mean, as usual, a (relative) measure of the reproductive success of agents in the population. Let $\overline{W}_A(i)$ and $\overline{W}_B(i)$ be the expected fitnesses of agents of type A and B, respectively, when there are i agents ($1 \leq i \leq N-1$) of type A in the population.[1] For discrete times $t \in \mathbb{N} = \{0, 1, 2, \ldots\}$, let $X(t)$ be the number of agents of type A at time t. We refer to $X(t)$ as the *state* of the population at time t, and to $X(0)$ as the *initial state* of the population.

Suppose that the population size remains constant and equal to N and that the population composition evolves according to a discrete-time Markov process with a stationary transition matrix P: the probability of the population state at time $t+1$ being $X(t+1) = j$ is dependent only on the population state $X(t)$ at time t (but not on the time t itself), and

$$P_{i,j} = \Pr\left(X(t+1) = j \mid X(t) = i\right). \tag{1}$$

The matrix $P = (P_{i,j})$ is row-stochastic, that is, $P_{i,j} \geq 0$ and $\sum_{j=0}^{N} P_{i,j} = 1$ for all i, $0 \leq i \leq N$. For example, the frequency dependent Moran and Wright–Fisher processes (Hartl and Clark 2007; Ewens 2012) specify how to construct the transition matrix $P_{i,j}$ from the fitnesses $\overline{W}_A(i)$ and $\overline{W}_B(i)$ (see Appendices B.1 and B.2).

We assume that there are no mutations, which also implies that if the entire population is composed of one type (A or B), then it will remain in that state forever (that is to say, the states in which the population is monomorphic are *absorbing*). By a *mixed-type state* we mean a population of As and Bs including at least one of each type.

2.1 Selection

Definition 2.1 We say that the transition matrix P defines a (mutationless) *selection process* $\mathscr{P}$ with respect to the expected fitnesses $\overline{W}_A(i)$ and $\overline{W}_B(i)$ ($1 \leq i \leq N-1$) if it satisfies the following biologically sensible properties:

H1 In any state $X(t) = i$, the fitness of individuals of one type is higher than that of the other, if and only if (*iff*) the expected number of individuals of the type having higher fitness in the next time step ($t+1$) is higher than their number at time t. Mathematically, for $1 \leq i \leq N-1$,

$$\overline{W}_A(i) > \overline{W}_B(i) \iff \mathbb{E}\left(X(t+1) \mid X(t) = i\right) = \sum_{j=0}^{N} j P_{i,j} > i = X(t), \tag{2a}$$

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[1] Fitnesses need not be defined for $i = 0$ or N, as in these extremes the population is homogeneous and there is no variability in fitness.

and

$$\overline{W}_B(i) > \overline{W}_A(i) \iff \mathbb{E}\left(X(t+1) \,\middle|\, X(t) = i\right) = \sum_{j=0}^{N} j P_{i,j} < i = X(t).$$

(2b)

H2 If at time τ, both types are present in the population (that is, the population is in a mixed-type state), then there is a positive probability of the population becoming monomorphic (i.e. reaching state 0 or N) in finite time. That is, if $1 \le i \le N-1$ then there exists $t > \tau$ (possibly dependent on i) such that

$$\Pr\left(X(t) = 0 \text{ or } X(t) = N \,\middle|\, X(\tau) = i\right) > 0.$$

(3)

H3 The states 0 and N are absorbing, that is, once reached, the population remains there forever: for all $\tau \ge 0$ and $t \ge \tau$,

$$\Pr\left(X(t) = 0 \,\middle|\, X(\tau) = 0\right) = 1,$$

(4a)

$$\Pr\left(X(t) = N \,\middle|\, X(\tau) = N\right) = 1.$$

(4b)

Remark 2.2 In general, *H1* does *not* imply that $X(t)$ is a sub- or supermartingale (Definition S2): if the fitter type at population state $X(t) = i$ varies with i, then at some states $\mathbb{E}\left(X(t+1) \,\middle|\, X(t) = i\right) > X(t)$ and at others $\mathbb{E}\left(X(t+1) \,\middle|\, X(t) = i\right) < X(t)$.

Remark 2.3 In this article, we analyze only selection processes without mutation; see Tarnita et al. (2009) for an analysis of selection processes that include mutation (at equal rates for all types, in the limit of weak selection).

Note that in what follows, we leave the precise form of the expected fitnesses, $\overline{W}_A(i)$ and $\overline{W}_B(i)$ unspecified; we require only that at any population state, the trait with a higher fitness is expected to increase in frequency in the next time-step (H1).

2.2 Irreducibility

We will find the following definition from the theory of Markov processes useful:

Definition 2.4 We say that state j is ***accessible*** from state i (or that state i ***leads*** to state j) if, starting from state $X(0) = i$ it is possible to arrive at state j in finite time, i.e. there is a time $\tau \ge 0$ such that $\Pr\left(X(\tau) = j \,\middle|\, X(0) = i\right) > 0$.

Remark 2.5 Equivalently, the state j is accessible from state i *iff* there exists $n \ge 1$ such that $(P^n)_{i,j} > 0$.

Some selection processes (e.g. the Moran and WF processes; see Appendices B.1 and B.2) have an additional property, which is not strictly necessary for the analysis that follows, but is biologically sensible and simplifies some of the statements of our results:

Definition 2.6 We say that a selection process is ***mixed-irreducible*** if any two mixed-type states are accessible from one another.

A process being mixed-irreducible does not imply that the transition matrix P is an irreducible matrix. In fact, P cannot be irreducible because of the absorbing homogeneous states. However, the submatrix corresponding to the non-homogeneous (mixed-type) states ($\widetilde{P} = (P_{i,j})_{i,j=1}^{N-1}$) must be irreducible. Equivalently, a selection process is mixed-irreducible if and only if for any mixed-type states, $1 \le i \le N - 1$ and $1 \le j \le N - 1$, there is a time $\tau_{i,j} > 0$ such that

$$\Pr\left(X(t + \tau_{i,j}) = j \mid X(t) = i\right) > 0. \tag{5}$$

2.3 Fixation

Using Definition 2.4, hypothesis H2 of Definition 2.1 can be restated as: every state i leads to 0 or N. However, by a standard result in the theory of Markov processes, it is not only possible, but *certain*, that the process reaches one of the absorbing states in finite time:

Proposition 2.7 *A selection process reaches one of the absorbing states, 0 or N, in finite time: for any i, $0 \le i \le N$,*

$$\Pr\left(\exists t \in \mathbb{N} \text{ such that } X(t) \in \{0, N\} \mid X(0) = i\right) = 1. \tag{6}$$

Proposition 2.7 (proved in Appendix A.1) allows us to make the notions of absorption time and fixation probability precise.

Definition 2.8 (*Absorption time and fixation probability*) For any mutationless selection process,

1. the first time at which the population is in one of the absorbing states is the ***absorption time***, that is, $T_{\text{abs}} = \min\{t \mid X(t) = 0 \text{ or } N\}$.
2. for any i, $0 \le i \le N$, the probability of reaching the absorbing state N, i.e. the ***fixation probability*** of A from the initial state i, is

$$p_{\text{fix}}(i) = \Pr\left(\lim_{t \to \infty} X(t) = N \mid X(0) = i\right). \tag{7}$$

Because absorption is assured (Proposition 2.7), the probability of fixation of B starting from state i (defined similarly) is $1 - p_{\text{fix}}(i)$. Note that since the states $X = N$ and $X = 0$ are absorbing, $p_{\text{fix}}(0) = 0$ and $p_{\text{fix}}(N) = 1$. Also, Proposition 2.7 implies that the absorption time T_{abs} is a non-negative random variable satisfying $\Pr(T_{\text{abs}} < \infty) = 1$.

2.4 Drift

Intuitively, under neutral drift (absense of selection), the expected number of individuals of each type at time $t + 1$ should be equal to their numbers at time t, that is, if $X(t) = i$, then $\mathbb{E}\left(X(t+1)\right) = i = X(t)$. This motivates the following:

Definition 2.9 We say that the transition matrix P defines a ***neutral drift process*** if $X(t)$ satisfies H2, H3 and

$$\mathbb{E}\left(X(t+1) \,\big|\, X(t)\right) = X(t). \tag{8}$$

Alternatively, we say that $X(t)$ is a neutral drift process.

Remark 2.10 P defines a neutral drift process if and only if for any i, $0 \leq i \leq N$, $\sum_{j=0}^{N} j P_{i,j} = i$.

Since $X(t)$ is a bounded Markov process, if P defines a neutral drift process, Eq. (8) implies that $X(t)$ is also a ***martingale*** (see Definition S2).

3 Particular selection processes

In Appendix B, we discuss population processes from the literature and establish that apart from biologically absurd situations, they are selection or neutral drift processes according to Definitions 2.1 and 2.9. This amounts to verifying H2, H3 and either H1 or Eq. (8). In particular, Appendices B.1 and B.2 show that the frequency-dependent Moran and WF processes are mixed-irreducible selection processes (Definition 2.6). Moreover, when the fitnesses of types A and B are equal, both are neutral drift processes.

Appendix B.3 discusses the Eldon–Wakeley process—a generalization of the Moran process that allows for a skewed offspring distribution (Eldon and Wakeley 2006). We show that the Eldon–Wakeley process is a mixed-irreducible neutral drift process; adding viability selection to the Eldon–Wakeley process, as done by Der et al. (2012), also results in a selection process.

Appendix B.4 discusses GWF models (Der 2010; Der et al. 2011). We show that pure-drift GWF models are neutral drift processes (Definition 2.9), but that the method used by Der et al. (2011) to add selection to a pure-drift GWF model produces some models that are not selection processes (Definition 2.1).

In Appendix B.5, we consider Cannings (1974, exchangeable allele) models and a generalization of these by Lessard and Ladret (2007) that allows for selection. Although classical (neutral) Cannings models are neutral drift processes, some models in the generalization by Lessard and Ladret (2007) violate hypothesis H2; within the class of models that Lessard and Ladret (2007) define, those that satisfy the biologically sensible H2 are selection processes.

4 Fixation probabilities

4.1 Exact fixation probabilities under neutral drift

We begin by calculating the fixation probabilities $p_{\text{fix}}(i)$ for a neutral drift process, generalizing Theorem 2 of Der et al. (2011):

Proposition 4.1 (Fixation under neutral drift) *If $X(t)$ is a neutral drift process, then for $0 \leq i \leq N$, if $X(0) = i$, the fixation probability of A is*

$$p_{\text{fix}}(i) = \frac{i}{N}. \tag{9}$$

A formal proof of this proposition is given in Appendix A.2 [similar proofs exist in the literature, but they typically appear only in more restricted contexts, e.g. the Moran and WF models (Durrett 2008) or GWF models (Der et al. 2011)]. To understand the result intuitively, consider that if the population consists of N equally fit types (instead of two) a symmetry argument shows that all types are equally likely to fix. If absorption is assured, then each type fixes with probability $1/N$.

Now return to the scenario of only two segregating types. If initially (at time $t = 0$) there are no individuals of type A then A cannot fix (because we assume no mutation), so $p_{\text{fix}}(0) = 0$; similarly, $p_{\text{fix}}(N) = 1$.

If the initial number of individuals of type A satisfies $1 \leq X(0) = i \leq N - 1$, label these as individuals $1, \ldots, i$, and label the individuals of type B as $i + 1, \ldots, N$, so that all individuals are distinguishable. Define a heritable *"supertype"* as both the individual label, and the previously defined trait, A or B [e.g. individual 1 is now of type $(1, A)$, and individual $i + 1$ is now of type $(i + 1, B)$]. With this new definition, there are now N different supertypes segregating in the population: for $1 \leq j \leq i$, the descendants of an individual of supertype (j, A) are also of type (j, A), and for $i + 1 \leq j \leq N$ the descendants of an individual of type (j, B) are of type (j, B). If neither type A or B has a selective advantage, then the fixation probability of each supertype is $1/N$. The fixation probability of type A is then the sum of the fixation probabilities of supertypes (j, A) for $1 \leq j \leq i$, that is i/N.

4.2 Bounds on fixation probabilities under selection

Proposition 4.1 shows that fixation probabilities are identical for all neutral drift processes. Thus, fixation probabilities under neutral drift can be used as a baseline for comparing fixation probabilities under selection, motivating the following definition of selection favouring or opposing fixation of an invading mutant:

Definition 4.2 If there are i agents of type A and $N - i$ agents of type B in a population undergoing selection, we say that *selection favours fixation* of A if the probability of A fixing is $p_{\text{fix}}(i) > i/N$, and *selection opposes fixation* of A if $p_{\text{fix}}(i) < i/N$.

Remark 4.3 Because fixation is assured (Proposition 2.7), if selection favours fixation of A, then it opposes fixation of B.

Lemma 4.4 below (proved in Appendix A.3) gives intuitive sufficient conditions for selection opposing fixation: if type A is never fitter than type B, and is less fit in some state that is accessible from the initial one, then selection opposes fixation of A.

Lemma 4.4 (Sufficient conditions for selection opposing fixation) *Consider a population of constant size N in which there are two types, A and B, evolving under a selection process $\mathscr{P}$. Let $\overline{W}_A(i)$ and $\overline{W}_B(i)$ be the expected fitnesses of types A and B (respectively) when there are i individuals of type A in the population, and let $\mathcal{S}_i$ be the set of mixed-type states that are accessible from state i under $\mathscr{P}$ (so $\mathcal{S}_i \subset \{1, 2, \ldots, N-1\}$).*

If $X(0) = i$ denotes the initial state ($0 \leq i \leq N$), and an individual of type A is no fitter than *an individual of type B in any population state $j \in \mathcal{S}_i$, i.e. if*

$$\overline{W}_A(j) \leq \overline{W}_B(j), \quad \text{for each } j \in \mathcal{S}_i, \tag{10}$$

then the probabilities of A and B fixing satisfy

$$p_{\text{fix}}(i) \leq \frac{i}{N} \quad and \quad 1 - p_{\text{fix}}(i) \geq \frac{N-i}{N}, \tag{11}$$

respectively.

If, in addition, there exists a state $\hat{\imath} \in \mathcal{S}_i$ in which type A is strictly less fit than type B, i.e.

$$\overline{W}_A(\hat{\imath}) < \overline{W}_B(\hat{\imath}), \quad \text{for some } \hat{\imath} \in \mathcal{S}_i, \tag{12}$$

then selection opposes fixation of A, i.e. the probability of A fixing is strictly less *than under neutral drift and the probability of B fixing is* strictly greater *than under neutral drift, i.e.*

$$p_{\text{fix}}(i) < \frac{i}{N} \quad and \quad 1 - p_{\text{fix}}(i) > \frac{N-i}{N}, \tag{13}$$

respectively.

Note that Proulx (2000) and Proulx and Day (2002) found (without defining a selection process) that the fixation probability of a selectively advantageous mutation is *no less than* that of a neutral one. For a general selection process, we have identified and rigorously established conditions under which a selectively advantageous mutation fixes with probability *strictly larger* than neutral.

Under the hypotheses of Lemma 4.4, if the state $\hat{\imath}$ in which the A agents' fitness is lower than that of B agents is accessible from any other mixed-type state (for the selection process in question), then $p_{\text{fix}}(i) < i/N$ for all mixed-type states i. It follows that:

Corollary 4.5 *If the hypotheses of Lemma 4.4 hold, and the selection process is mixed-irreducible, then for any mixed-type initial state ($1 \leq i \leq N-1$), $p_{\text{fix}}(i) < i/N$, so selection opposes fixation of A.*

Corollary 4.5 generalizes Theorem 1 of Imhof and Nowak (2006), which applies only to the Wright–Fisher process. While the proof given by Imhof and Nowak (2006)

is easily extended to arbitrary mixed-irreducible selection processes, the proof of Lemma 4.4 given in Appendix A.3 is both more general, and renders the biological mechanism responsible for the reduced fixation probability compared to neutral drift processes more transparent: Under neutral drift processes, the expected number of individuals of each type *does not change* from one time step to the next. By contrast, under the conditions of Lemma 4.4, H1 implies only that the expected number of agents of type *A does not increase* over time. Moreover, if the process is in the state $\hat{\imath}$ (in which *A* is less fit), then the expected number of agents of type *A* decreases in the next generation. Because $\hat{\imath}$ is accessible from the initial population state, this increases the probability that *A* decreases in frequency over time (compared to neutral drift processes), which translates to a lower fixation probability.

4.3 Implications of existence of a fixation probability bound

Lemma 4.6 below (proved in Appendix A.4) is a partial converse to Lemma 4.4; together, Lemmas 4.4 and 4.6 show that Eqs. (15) and (16) characterize the situations in which selection opposes fixation irrespective of the selection process.

Lemma 4.6 (Necessary conditions for selection opposing fixation for any selection process) *Consider a population of constant size N in which there are two types, A and B. Let $\overline{W}_A(i)$ and $\overline{W}_B(i)$ be the expected fitnesses of types A and B (respectively) when there are i individuals of type A in the population.*

Suppose that the population is at a mixed-type initial state $X(0) = i$ ($1 \le i \le N - 1$) and, for any selection process, selection opposes fixation of A, that is,

$$p_{\text{fix}}(i) < i/N, \quad \text{for any selection process}. \tag{14}$$

Then:

- *The expected fitness of an individual of type A is* no larger *than that of an individual of type B in any mixed-type state, i.e.*

$$\overline{W}_A(j) \le \overline{W}_B(j), \quad \text{for all } j, \quad 1 \le j \le N - 1, \tag{15}$$

- *There exists a mixed-type state in which the expected fitness of type A is smaller than type B, i.e.*

$$\overline{W}_A(\hat{\imath}) < \overline{W}_B(\hat{\imath}), \quad \text{for some } \hat{\imath}, \quad 1 \le \hat{\imath} \le N - 1. \tag{16}$$

5 Application to evolutionary game theory in finite populations

Evolutionary game theory (Maynard Smith 1982; Hofbauer and Sigmund 1998) is concerned with a population of agents whose fecundity (or fitness) is determined by their payoffs in interactions modelled as games. The strategies in these games are heritable traits, and the payoffs are typically dependent on which strategies other agents play.

5.1 Concepts

A key concept in evolutionary game theory is evolutionary stability (Maynard Smith 1982; Nowak 2006). In an infinite population, a strategy s is **evolutionarily stable** (ES) if selection opposes the invasion of a population playing strategy s by a single individual playing any other strategy[2] s'. Typically, one says that selection opposes invasion of type s by type s' if the expected fitness of a single invader of type s' in a population otherwise composed of agents of type s is lower than the fitness of the agents of type s in this population (e.g. Nowak et al. 2004). In a finite population, we can use H1 to relate fitness to the expected change in the population state, yielding the following equivalent definition:

Definition 5.1 (*Selection Opposes Invasion*) For a selection process $\mathscr{P}$, we say that **selection opposes invasion** of $s = B$ by $s' = A$ if

$$\mathbb{E}\left(X(t+1) \mid X(t) = 1\right) = \sum_{j=1}^{N} j P_{1,j} < 1, \tag{17}$$

and **selection favours invasion** if

$$\mathbb{E}\left(X(t+1) \mid X(t) = 1\right) = \sum_{j=1}^{N} j P_{1,j} > 1. \tag{18}$$

However, due to the inherent stochasticity of finite populations, determining whether or not selection favours invasion of mutant strategies is no longer sufficient to determine evolutionary stability in finite-population games: in a population of constant size N, if a resident strategy is invaded by a single agent playing a different strategy that is equally fit, Proposition 4.1 implies that for any selection process, the invading strategy fixes with probability $1/N$. Moreover, the fixation probability of a strategy that is selected *against* when rare can be larger than $1/N$, if it is selected for when sufficiently common (Proulx and Day 2002; Nowak et al. 2004). Motivated by this, Nowak et al. (2004) have refined the definition of evolutionary stability of a strategy in a finite population to take into account the possibility of fixation of mutant strategies. Their definition, which they stated in the specific context of a Moran process, can be applied to general selection processes:

Definition 5.2 (*Evolutionary stability in a finite population*) A strategy s is **evolutionarily stable** (ESS$_N$) in a population of size N *iff*, when invaded by a single mutant playing a different strategy $s' \neq s$, selection opposes both invasion and fixation of s':

- The mutant's fitness is lower than the residents' (selection opposes invasion; Definition 5.1),

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[2] An invading strategy may appear in the population by immigration, mutation, or (in the case of cultural traits) innovation.

- The mutant's fixation probability is less than $1/N$
  (selection opposes fixation; Definition 4.2).

More recently, Stewart and Plotkin (2013) have referred to selection opposing invasion by a single mutant as "evolutionary robustness", on the grounds that the invasion dynamics are less important than which strategy fixes:

Definition 5.3 A resident strategy s is **evolutionarily robust** against an invading mutant strategy s' if selection opposes fixation of s' (i.e. the fixation probability of s' is less than $1/N$) when a population playing s is invaded by a single mutant playing s'.

5.2 Conditions for evolutionary robustness and stability

If the payoff obtained from a game with heritable strategies s and s' contributes linearly to individual fitness, Lemma 4.4 yields intuitive conditions for evolutionary robustness and stability in finite populations: if

- the expected payoff for strategy s is no less than the expected payoff for s' (in all population states to which the population can evolve from the initial one); and
- there is at least one state (to which the population can evolve from the initial state) where the expected payoff for s' is less than for s;

then s is evolutionarily robust to invasion by s'. If, additionally, the expected fitness of a mutant playing s' in a resident population otherwise playing s is lower than the residents' expected fitness, then s is evolutionarily stable (ESS_N). We formalize these statements in Corollary 5.4 and explain how the assumption of linearity can be relaxed in Remark 5.5.

Corollary 5.4 (Conditions for evolutionary robustness and stability) *Consider a population of constant, finite size N playing a game in which the two available strategies, s' and s, are heritable traits. For any mixed-type population state i ($1 \leq i \leq N - 1$), let the fitness of an agent obtaining payoff π in state i be a random variable, $W_i(\pi)$, with mean $\mathbb{E}(W_i(\pi) \mid \pi)$. Let the payoffs to agents playing strategy x ($x = s$ or s') when the population state is i be random variables, $\pi_x(i)$, with mean $\overline{\pi}_x(i)$. Denote the expected fitnesses of agents playing a strategy x in population state i by*

$$\overline{W}_x(i) = \mathbb{E}(W_i(\pi_x(i))), \tag{19}$$

the expectation being taken over all possible payoffs to an agent playing x in a population in state i. Suppose that the following conditions hold:

(I) *In any mixed-type population state, the expected payoff $\overline{\pi}_x(i)$ and the expected fitness $\overline{W}_x(i)$, of an agent playing strategy $x = s$ or s', are finite.*

(II) *The expected payoff of individuals playing s' is* never more than *those playing s, regardless of the number of individuals playing s' in the population ($\overline{\pi}_{s'}(i) \leq \overline{\pi}_s(i)$ for all mixed-type states i.*

(III) *There exists a mixed-type population state $\hat{i}$ accessible from the state $i = 1$ in which the expected payoff of an agent playing s' is less than the expected payoff of an agent playing s, i.e. $\overline{\pi}_{s'}\left(\hat{i}\right) < \overline{\pi}_s\left(\hat{i}\right)$.*

(IV) *The fitness of an agent obtaining payoff π in a mixed-type state i is*

$$W_i\left(\pi\right) = w_i\pi + V, \tag{20}$$

*where $w_i > 0$ represents the **intensity of selection** in state i (Nowak 2006), and V is a real-valued random variable with finite expectation $\mathbb{E}(V) < \infty$, representing the variability in the fitness of an individual with a given payoff. We further assume that $\mathbb{E}(V)$ is independent of the payoff π (although V may depend on π).*

Then strategy s is evolutionarily robust against invasion by s', for any selection process $\mathscr{P}$ (with respect to the frequency-dependent fitness $W_i\left(\pi\right)$, $1 \leq i \leq N - 1$). If (III) is satisfied for $\hat{i} = 1$, then strategy s is also an ESS$_N$.

Proof From (19), we have

$$\overline{W}_s\left(i\right) = \mathbb{E}\left(W_i\left(\pi_s\left(i\right)\right)\right) = w_i\overline{\pi}_s\left(i\right) + \mathbb{E}(V),$$

and similarly,

$$\overline{W}_{s'}\left(i\right) = w_i\overline{\pi}_{s'}\left(i\right) + \mathbb{E}(V).$$

Thus,

$$\overline{W}_s\left(i\right) - \overline{W}_{s'}\left(i\right) = w_i\left(\overline{\pi}_s\left(i\right) - \overline{\pi}_{s'}\left(i\right)\right) \geq 0, \tag{21}$$

with a strict inequality for $i = \hat{i}$. The conclusion that s is evolutionarily robust now follows immediately from Lemma 4.4 (with $s = B$ and $s' = A$). If, in addition, $\overline{\pi}_{s'}\left(1\right) < \overline{\pi}_s\left(1\right)$, then from Definition 5.2, s is an ESS$_N$. □

Remark 5.5 (Relaxing the linearity If assumption (II) of Corollary 5.4 is replaced by the stronger constraint on the game payoff distributions (rather than just their expectations), that for any $\phi \geq 0$,

$$\Pr(\pi_s\left(i\right) \geq \phi) \geq \Pr(\pi_{s'}\left(i\right) \geq \phi), \tag{22}$$

then assumption (IV) can be weakened to the expected fitness $\mathbb{E}\left(W_i\left(\pi\right) \mid \pi\right)$ being some increasing function of the payoff π. This follows because we have only used assumption (IV) in deducing $\overline{W}_s\left(i\right) - \overline{W}_{s'}\left(i\right) \geq 0$ [in inequality (21)]. But if inequality (22) holds, then since $\mathbb{E}\left(W_i\left(\pi\right) \mid \pi\right)$ is increasing,

$$\mathbb{E}\left(W_i\left(\pi\right) \mid \pi = \pi_s\left(i\right)\right) - \mathbb{E}\left(W_i\left(\pi\right) \mid \pi = \pi_{s'}\left(i\right)\right) \geq 0, \tag{23}$$

so $\overline{W}_s\left(i\right) - \overline{W}_{s'}\left(i\right) \geq 0$ still holds, with a strict inequality for $i = \hat{i}$.

6 Conclusions

We have defined a large class of biologically sensible models of selection acting on two traits in populations of N agents in the absence of mutation (Definition 2.1), and a sub-class of models of neutral drift (Definition 2.9). Our primary result (Lemma 4.4) is a set of simple sufficient conditions for selection favouring or opposing fixation of a trait for *any* selection process. From an entirely mathematical perspective, our analysis identifies conditions under which the inequality in the optional stopping theorem for supermartingales (theorem S6) can be made strict.

We used Lemma 4.4 to obtain sufficient conditions for evolutionary robustness and stability in a finite population (corollary 5.4). In fact, Lemma 4.6 implies that the conditions of corollary 5.4 *characterize* the games for which evolutionary robustness and stability are independent of the selection process. The proof of corollary 5.4 is simple, but the result has important implications; in particular, it is a critical component used by Molina and Earn (in prep.) to develop criteria for evolutionary and convergent stability that are independent of the selection process and apply to any continuous-strategy symmetric n-player game played in a (possibly structured) population. Thus, by appropriately abstracting the notion of fitness, we obtain predictions about fixation probabilities that are robust to the details of an organism's life history. More broadly, since models such as the Wright–Fisher process seldom describe realistic populations exactly, characterizing when selection favours fixation regardless of the selection process can reinforce qualitative conclusions about fixation and evolutionary robustness in applications in which the population process is uncertain.

Focusing on fixation probabilities (as opposed to fixation times or properties of the continuum limit) allows us to maintain more generality compared to the formulation of Generalized Wright–Fisher (GWF) models (Der 2010; Der et al. 2011), both in removing the assumption on the second moment of the drift process [Eq. (67b) or Der et al. 2011, Eq. (5)], and changing the class of non-drift processes that are included.[3] The importance of the latter generalization is highlighted by the fact that, as noted by Der (2010, p. 36), the classical Wright–Fisher process with selection is *not* a GWF process, whereas (excluding mutation) it is a selection process according to Definition 2.1 (see Appendix B.2).

Our treatment was limited to two-trait models for simplicity, but the framework can be extended to a larger number of interacting strategies in the population (at the expense of increasing the complexity of the analysis; see Tarnita et al. 2011). The presence of only two competing strategies in the population at any time is a common assumption in many evolutionary models: for instance, both the standard formulation of adaptive dynamics (Metz et al. 1996) and its extension to structured populations (Allen et al. 2013), rely on the assumption of "trait substitution". Under this assumption, mutants arise and either vanish or fix before a new mutation occurs. In practice, multiple mutant strategies may be present in a population at the same time if fixation rates are slow compared to mutation rates; this is especially true in the context of cultural change (e.g. there are more than two competing religions in the world). It would therefore be

---

[3] In fact, not all GWF models with selection satisfy our definition of selection processes (Definition 2.1); see Appendix B.4.

useful, on the one hand, to construct a framework that relaxes the assumptions of trait substitution and, on the other hand, to identify conditions under which models based on trait substitution are valid [by comparing two-type and several-type populations subject to stronger assumptions on the selection process that allow bounds on fixation times to be obtained, e.g. GWF models (Der 2010; Der et al. 2011)].

While we confined our analysis to asexual populations, extensions that allow for genetic inheritance in sexual populations would be useful. Such extensions, however, might depend on the particulars of the genetic system. For example, in diploid populations, the fitnesses of the two homozygotes and the heterozygote may differ. Moreover, if the allele for trait A is dominant over trait B, then populations with identical phenotypes may have vastly different genetic make-ups, which may have different transition probabilities to other states, e.g. when the entire population displays the phenotype A, one cannot know how many individuals are heterozygotes. But if all individuals are homozygotic for A, then A has fixed and the transition probability to any other state is 0, which is not the case if all individuals are heterozygotes. Thus, for sexual diploid populations, the state space will likely contain information on the different genetic types in the population, rather than just the phenotypic types. Additional extensions of our framework that may prove fruitful include accounting for mutation between the two strategies, considering populations of variable size, and evolution in continuous time.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Appendix

A Proofs

A.1 Proof of Proposition 2.7

If $X(0) = 0$ or $X(0) = N$, nothing remains to be shown.

Let $C = \{1, 2, \ldots, N - 1\}$ and consider $i \in C$. Suppose, in order to derive a contradiction, that the absorption probability starting from state i is

$$\Pr\left(\exists t \in \mathbb{N} \text{ such that } X(t) \in \{0, N\} \mid X(0) = i\right) < 1. \tag{24}$$

Then,

$$\Pr\left(X(t) \in C \text{ for all } t \in \mathbb{N} \mid X(0) = i\right) > 0. \tag{25}$$

If $X(t)$ takes values in C for all times $t \geq 0$, then since C is finite, at least one index $j, 1 \leq j \leq N - 1$ is visited infinitely often, that is, for some $j, 1 \leq j \leq N - 1$,

$$\Pr\left(\text{for any } T \geq 0, \text{ there exists } t > T \text{ such that } X(t) = j \mid X(0) = i\right) > 0. \tag{26}$$

Now note that H1 implies that C is a set of inessential, and therefore nonrecurrent states (see Appendix D.2 in the ESM and Theorem I.4.4 of Chung 1967), which cannot be visited infinitely often (Theorem I.4.3 of Chung 1967), contradicting inequality (26).

□

A.2 Proof of Proposition 4.1

Define the random variable $T_A = \min\{t \mid X(t) = N\}$, that is, T_A is the fixation time of A ($T_A = \infty$ if A never fixes). Similarly, let $T_B = \min\{t \mid X(t) = 0\}$ be the fixation time of B. Both T_A and T_B are stopping times (see Definition S3), and hence the absorption time $T_{\text{abs}} = \min\{T_A, T_B\}$ is also a stopping time (Karlin and Taylor 1975, p. 256).

Since either A or B must fix (Proposition 2.7),

$$\Pr(T_{\text{abs}} < \infty) = 1, \tag{27}$$

so

$$p_{\text{fix}}(i) = \Pr\left(\lim_{t \to \infty} X(t) = N \,\Big|\, X(0) = i\right) = \Pr\left(X(T_{\text{abs}}) = N \mid X(0) = i\right), \tag{28}$$

and

$$\begin{aligned}
\mathbb{E}\left(X(T_{\text{abs}}) \mid X(0) = i\right) &= \Pr\left(X(T_{\text{abs}}) = 0 \mid X(0) = i\right) \cdot 0 \\
&\quad + \Pr\left(X(T_{\text{abs}}) = N \mid X(0) = i\right) \cdot N = p_{\text{fix}}(i) \cdot N.
\end{aligned} \tag{29}$$

For any t, we have $0 \le X(t) \le N$, so it follows that for any stopping time T,

$$\mathbb{E}\left(\sup_{t \ge 0} X(\min\{T, t\})\right) < \infty. \tag{30}$$

Thus, since $X(t)$ is a martingale and T_{abs} is a stopping time satisfying Eqs. (27) and (30) the optional stopping theorem (theorem S5) implies that

$$i = X(0) = \mathbb{E}\left(X(0) \mid X(0) = i\right) = \mathbb{E}\left(X(T_{\text{abs}}) \mid X(0) = i\right), \tag{31}$$

and hence

$$\begin{aligned}
p_{\text{fix}}(i) &= \Pr\left(\lim_{t \to \infty} X(t) = N \,\Big|\, X(0) = i\right) \\
&= \Pr\left(X(T_{\text{abs}}) = N \mid X(0) = i\right) = i/N.
\end{aligned} \tag{32}$$

□

Remark A.1 Feller (1968, p.399) gives an alternative proof of Proposition 4.1 that does not rely on the optional stopping theorem.

A.3 Proof of Lemma 4.4

Observe that $X(t)$ is a non-negative supermartingale (Definition S2). Thus, for any stopping time S, with $\Pr(S < \infty) = 1$, a version of the optional stopping theorem for supermartingales (theorem S6) states that

$$\mathbb{E}\left(X(S)\right) \leq \mathbb{E}\left(X(0)\right). \tag{33}$$

Using a constant stopping time $S = \tau \geq 0$, inequality (33) gives

$$\mathbb{E}\left(X(\tau) \mid X(0) = i\right) \leq X(0) = i. \tag{34}$$

Letting T_{abs} be the absorption time for the system, by Proposition 2.7 we can apply inequality (33) and Eq. (29) to show that for any initial state $X(0) = i$ for $(0 \leq i \leq N)$ the fixation probability of A satisfies

$$p_{\text{fix}}(i) N = \mathbb{E}\left(X(T_{\text{abs}}) \mid X(0) = i\right) \leq X(0) = i, \tag{35}$$

so $p_{\text{fix}}(i) \leq i/N$, and the fixation probability of B is $1 - p_{\text{fix}}(i) \geq (N - i)/N$.

Similarly, if we use H1 as well then

$$p_{\text{fix}}\left(\hat{i}\right) N = \mathbb{E}\left(X(T_{\text{abs}}) \mid X(0) = \hat{i}\right) \leq \mathbb{E}\left(X(1) \mid X(0) = \hat{i}\right) < \hat{i}, \tag{36}$$

so $p_{\text{fix}}\left(\hat{i}\right) < \hat{i}/N$.

Denoting the probability of reaching state j at time $\tau \geq 0$ starting from state $X(0) = i$ by

$$P_{i,j}^{(\tau)} = \Pr\left(X(\tau) = j \mid X(0) = i\right), \tag{37}$$

we have $P_{i,j}^{(\tau)} = (P^\tau)_{i,j}$.

If i leads to $\hat{i}$, then for some time $\tau \geq 0$, the probability of reaching state $\hat{i}$ from state i is nonzero, $P_{i,\hat{i}}^{(\tau)} > 0$. Conditioning on the state arrived at in the τ-th time-step, we have

$$p_{\text{fix}}(i) = \sum_{j=0}^{N} P_{i,j}^{(\tau)} p_{\text{fix}}(j) = \sum_{\substack{j=0 \\ j \neq \hat{i}}}^{N} P_{i,j}^{(\tau)} p_{\text{fix}}(j) + P_{i,\hat{i}}^{(\tau)} p_{\text{fix}}\left(\hat{i}\right) < \frac{1}{N} \sum_{j=0}^{N} P_{i,j}^{(\tau)} j$$

$$= \frac{1}{N} \mathbb{E}\left(X(\tau) \mid X(0) = i\right). \tag{38}$$

Using Eq. (34), we obtain

$$p_{\text{fix}}(i) < \frac{1}{N} X(0) = \frac{i}{N}, \tag{39}$$

and the probability of B fixing is $1 - p_{\text{fix}}(i) > \frac{N-i}{N}$. $\square$

A.4 Proof of Lemma 4.6

Suppose, in order to derive a contradiction, that inequality (16) does not hold: for all states $1 \leq j \leq N - 1$

$$\overline{W}_A(j) \geq \overline{W}_B(j). \tag{40}$$

Then for any selection process, from Lemma 4.4 (with the roles of A and B reversed), $p_{\text{fix}}(i) \geq i/N$, contradicting inequality (14). Thus inequality (16) holds.

Now suppose, in order to derive a contradiction, that inequality (15) does not hold: there exists a state $\hat{j}$ for which

$$\overline{W}_A(\hat{j}) > \overline{W}_B(\hat{j}). \tag{41}$$

We will construct a transition matrix P for a selection process $\mathscr{P}$ (consistent with the fitnesses $\overline{W}_A(j)$ and $\overline{W}_B(j)$, $1 \leq j \leq N - 1$) such that $p_{\text{fix}}(i) \geq i/N$, which contradicts inequality (14) holding for all selection processes.

To find such a selection process $\mathscr{P}$, we can restrict attention to processes with the property that at any time and any mixed-type state, the number of individuals of type A must change by exactly 1. Thus, for any mixed-type state k, $P_{j,k} \neq 0$ if and only if $j = k \pm 1$. The matrix P then defines a "birth-death" process, for which the fixation probabilities starting from state $X(0) = i$ satisfy (see Appendix C):

$$p_{\text{fix}}(i) = \frac{1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}}}{1 + \sum_{k=1}^{N-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}}}. \tag{42}$$

Let $\mathcal{A}_>$, $\mathcal{A}_<$ and $\mathcal{A}_=$ be the sets of states in which the expected fitness of individuals of type A is higher than, lower than or equal to that of B individuals (respectively). Note that $\hat{j} \in \mathcal{A}_>$ and $\hat{i} \in \mathcal{A}_<$. We then specify the ratios of the non-vanishing transition probabilities by

$$\frac{P_{j,j-1}}{P_{j,j+1}} = \begin{cases} r_+ & j \in \mathcal{A}_>, \\ r_- & j \in \mathcal{A}_<, \\ 1 & j \in \mathcal{A}_=, \end{cases} \tag{43}$$

where r_+ and r_- are constants—independent of j—that satisfy $0 < r_+ < 1 < r_-$.

Observe that P defines a mixed-irreducible selection process $\mathscr{P}$:

- If $X(t) = j$, then

$$\mathbb{E}\big(X(t+1) \,\big|\, X(t) = j\big) = (j+1)P_{j,j+1} + (j-1)P_{j,j-1} = j + P_{j,j+1} - P_{j,j-1}, \tag{44}$$

  so H1 is satisfied.
- As for the Moran process [see Eq. (54a)], for any j and k such that $1 \leq j \leq N-1$, $0 \leq k \leq N$ and $j \neq k$, there is a positive probability of transitioning from state j

to state k in $d = |j - k|$ steps: setting $\sigma = \text{sign}(k - j)$, we have

$$\Pr\left(X(t + d) = k \mid X(t) = j\right) = \prod_{m=1}^{d} P_{(j+\sigma(m-1)),(j+\sigma m)} > 0, \tag{45a}$$

$$\Pr\left(X(t + 2) = j \mid X(t) = j\right) = P_{j,j+1} P_{j+1,j} + P_{j,j-1} P_{j-1,j} > 0, \tag{45b}$$

so all states can be reached from state $X(t) = i$ in finite time. Thus, P is mixed-irreducible. Moreover, the probability of B fixing at a future time $t + \tau$ ($\tau \geq 0$) is positive, so H2 is satisfied.

• The states 0 and N are absorbing, so H3 is trivially satisfied.

For $1 \leq j \leq N - 1$, we define the number of states k ($1 \leq k \leq j$) in which the expected fitness of A individuals is higher than that of B individuals,

$$\alpha_+(j) = \left| \left\{ k \mid 1 \leq k \leq j \text{ and } k \in \mathcal{A}_> \right\} \right|, \tag{46}$$

and similarly,

$$\alpha_-(j) = \left| \left\{ k \mid 1 \leq k \leq j \text{ and } k \in \mathcal{A}_< \right\} \right|. \tag{47}$$

Lastly, let a_+ be the smallest number of individuals of type A in the population for which type A's expected fitness is higher than type B's, that is,

$$a_+ = \min \mathcal{A}_> \geq 1. \tag{48}$$

Note that $a_+ \leq \hat{\jmath} < N$, and that $\alpha_+(j) = 0$ for all $j < a_+$.

From Eq. (42), the fixation probability $p_{\text{fix}}(i)$ is a rational function of r_+ and r_-,

$$p_{\text{fix}}(i) = \frac{1 + \sum_{k=1}^{i-1} r_+^{\alpha_+(k)} r_-^{\alpha_-(k)}}{1 + \sum_{k=1}^{N-1} r_+^{\alpha_+(k)} r_-^{\alpha_-(k)}}, \tag{49}$$

and is continuous because the denominator is positive for any $r_-, r_+ > 0$.

If $i \geq a_+$, then $p_{\text{fix}}(i) \to 1$ as $r_+ \to 0$. If $i < a_+$, then

$$\lim_{r_+ \to 0} p_{\text{fix}}(i) = \frac{1 + \sum_{k=1}^{i-1} r_-^{\alpha_-(k)}}{1 + \sum_{k=1}^{a_+-1} r_-^{\alpha_-(k)}} \xrightarrow{r_- \to 1} \frac{i}{a_+} > \frac{i}{N}. \tag{50}$$

It is thus possible to choose r_- sufficiently close to 1 and r_+ sufficiently close to 0 to ensure that $p_{\text{fix}}(i) > i/N$, which completes the proof. □

B Examples

B.1 The Moran process

If the population evolves according to the Moran process (Moran 1962; Hartl and Clark 2007; Ewens 2012), then exactly one agent is replaced at each time step. In detail, at each time step:

- An agent is chosen for death, with equal probability for all agents;
- An agent is chosen for reproduction, with probability proportional to its fitness[4];
- The agent chosen for death is replaced with a clone of the agent chosen for reproduction.

Note that sampling of agents is done with replacement, so that an agent can be chosen for both death and reproduction (in which case the population remains unchanged).

When the population consists of i mutants (individuals of type A) and $N - i$ residents (individuals of type B), the probabilities of choosing a mutant or a resident for death are i/N and $(N - i)/N$, respectively. The probabilities of choosing a mutant or a resident for reproduction are

$$\frac{i \overline{W}_A(i)}{i \overline{W}_A(i) + (N - i) \overline{W}_B(i)}, \tag{51a}$$

and

$$\frac{(N - i) \overline{W}_B(i)}{i \overline{W}_A(i) + (N - i) \overline{W}_B(i)}. \tag{51b}$$

Because the death and reproduction events are independent, the transition probabilities are simply

$$P_{i,i+1} = \frac{i \overline{W}_A(i)}{i \overline{W}_A(i) + (N - i) \overline{\overline{W}}_B(i)} \times \frac{N - i}{N} > 0, \tag{52a}$$

$$P_{i,i-1} = \frac{(N - i) \overline{W}_B(i)}{i \overline{W}_A(i) + (N - i) \overline{\overline{W}}_B(i)} \times \frac{i}{N} > 0, \tag{52b}$$

and (since at each time step at most one individual is replaced)

$$P_{i,i} = 1 - P_{i,i+1} - P_{i,i-1} = \frac{i^2 \overline{W}_A(i) + (N - i)^2 \overline{W}_B(i)}{N(i \overline{W}_A(i) + (N - i) \overline{W}_B(i))} > 0. \tag{52c}$$

Lastly, $P_{0,0} = P_{N,N} = 1$ and $P_{0,i} = P_{N,N-i} = 0$ for all $1 \leq i \leq N$ (the states where the resident or mutant have fixed are absorbing, so H3 is trivially satisfied).

---

[4] We assume here that the fitnesses $\overline{W}_A(j)$ and $\overline{W}_B(j)$ are positive for $1 \leq j \leq N - 1$.

For any $1 \leq i \leq N - 1$, if $X(t) = i$, we have

$$
\begin{aligned}
\mathbb{E}\left(X(t+1) - X(t) \mid X(t) = i\right) &= -i + \sum_{j=0}^{N} j P_{i,j} \\
&= -i + \left[(i-1)P_{i,i-1} + i P_{i,i} + (i+1)P_{i,i+1}\right] \\
&= -i + \left[i + P_{i,i+1} - P_{i,i-1}\right] \\
&= \frac{i(N-i)\left(\overline{W}_A(i) - \overline{W}_B(i)\right)}{N\left(i\overline{W}_A(i) + (N-i)\overline{W}_B(i)\right)}.
\end{aligned}
\tag{53}
$$

The expected number of individuals of type A (respectively B) in the next time-step is larger than in the current time-step, if and only if $\overline{W}_A(i) > \overline{W}_B(i)$ (respectively $\overline{W}_B(i) > \overline{W}_A(i)$), so H1 is satisfied.

To see that H2 is satisfied, and moreover, that P defines a mixed-irreducible selection process, consider i and j such that $1 \leq i \leq N-1$, $0 \leq j \leq N$ and $j \neq i$, and observe that there is a positive probability of changing from state i to state j in $d = |j - i|$ steps: setting $\sigma = \mathrm{sign}(j - i)$, we have

$$
\Pr\left(X(t+d) = j \mid X(t) = i\right) = \prod_{k=1}^{d} P_{(i+\sigma(k-1)),(i+\sigma k)} > 0
\tag{54a}
$$

$$
\Pr\left(X(t+1) = i \mid X(t) = i\right) = P_{i,i} > 0,
\tag{54b}
$$

so all states can be reached from state $X(t) = i$ in finite time, and in particular, the probability of B fixing at a future time $t + \tau$ ($\tau \geq 0$) is positive.

If neither type has a selective advantage over the other, regardless of their frequencies in the population, then for all $1 \leq i \leq N-1$, $\overline{W}_A(i) = \overline{W}_B(i)$, so from Eq. (53), $\mathbb{E}\left(X(t+1)\right) = X(t)$, and P defines a neutral drift process.

B.2 The Wright–Fisher process

If the population evolves according to the Wright–Fisher process (Hartl and Clark 2007; Ewens 2012) then all individuals are replaced at each time step (generations do not overlap). At each time step, the entire population of N individuals is replaced by a new generation constructed using binomial sampling: in each of the N Bernoulli trials, the probability of drawing any type represented in the current generation is proportional to its present mean fitness and to the present number of individuals of that type. Thus, the probability that an individual in the next generation will be of type A is

$$
\frac{i\overline{W}_A(i)}{i\overline{W}_A(i) + (N-i)\overline{W}_B(i)},
\tag{55}
$$

and

$$
\begin{aligned}
P_{i,j} &= \Pr\left(X(t+1) = j \mid X(t) = i\right) \\
&= \binom{N}{j}\left(\frac{i\,\overline{W}_A(i)}{i\,\overline{W}_A(i) + (N-i)\overline{W}_B(i)}\right)^j \left(\frac{(N-i)\overline{W}_B(i)}{i\,\overline{W}_A(i) + (N-i)\overline{W}_B(i)}\right)^{N-j},
\end{aligned}
\tag{56}
$$

where $P_{0,0} = P_{N,N} = 1$ (so the states $X = 0$ and $X = N$ are absorbing and H3 is satisfied). Note that if A is not present at some time τ, B has fixed and the population remains in state $X(t) = 0$ for all $t \geq \tau$, and similarly if B is not present at some time τ, then $X(t) = N$ for all $t \geq \tau$.

The mean of a binomial random variable defined by n trials with success probability p is np, so for any $0 \leq i \leq N$, we have

$$
\begin{aligned}
\mathbb{E}\left(X(t+1) \mid X(t) = i\right) - i &= N\frac{i\,\overline{W}_A(i)}{i\,\overline{W}_A(i) + (N-i)\overline{W}_B(i)} - i \\
&= i(N-i)\frac{\overline{W}_A(i) - \overline{W}_B(i)}{i\,\overline{W}_A(i) + (N-i)\overline{W}_B(i)},
\end{aligned}
\tag{57}
$$

so H1 is satisfied. H2 is trivially satisfied because for any $1 \leq i \leq N - 1$, $P_{i,0} > 0$. Thus, P defines a selection process, which is, moreover, mixed-irreducible, because for any $1 \leq i \leq N - 1$, $P_{i,j} > 0$ also for any $1 \leq j \leq N - 1$.

If neither type has a selective advantage over the other, $\overline{W}_A(i) = \overline{W}_B(i)$ for all $1 \leq i \leq N - 1$, and Eq. (57) becomes $\mathbb{E}\left(X(t+1) \mid X(t) = i\right) = i = X(t)$, so $X(t)$ is a neutral drift process.

B.3 The Eldon–Wakeley process with viability selection

The Eldon–Wakeley (EW) process (Eldon and Wakeley 2006; Der et al. 2012) is a variation on the neutral Moran process that allows for a skewed (rather than uniform) offspring distribution. It has been used to interpret genetic data from Pacific Oysters (Eldon and Wakeley 2006; Der et al. 2012).

The EW process describes neutral drift in a population of constant size N, consisting of two types, A and B. At each time step, a single agent is randomly drawn from the population with uniform probability, and produces a random number of offspring $U - 1$. The parent agent survives to the next generation and its $U - 1$ offspring replace $U - 1$ randomly chosen members of the remainder of the population. In the special case that exactly one offspring is always produced, i.e. $\Pr(U = 2) = 1$, the EW process is similar (but not identical) to the classical Moran process (Ewens 2012; Moran 1962): in both processes, the parent always produces one offspring, which increases the number of individuals of the parent's type in the next generation *iff* the agent chosen to be replaced is not of the parent's type. In the EW process, the parent is guaranteed to survive, and one additional offspring replaces another randomly chosen

member of the population, so if there are i agents of type A, the probability that the population state remains the same is

$$\frac{i}{N}\frac{i-1}{N-1} + \frac{N-i}{N}\frac{N-i-1}{N-1} = \frac{i^2 + (N-i)^2 - N}{N(N-1)}.$$ (58)

By contrast, in the Moran process, this probability is given by $\frac{i^2+(N-i)^2}{N^2}$ [see Eq. (52c)]. Thus, whenever the population is in a mixed-type state (i.e. $1 \leq i \leq N-1$), the probability that the population state remains unchanged is larger for the Moran model than for the EW model. However, for both models, the probability of increase in type A is the same as the probability of increase in type B (this probability does depend on the population composition). Thus, in effect, the neutral (i.e. selectionless) EW process with $U = 2$ is a slightly "sped up" version of the neutral Moran process, with fewer time-steps in which the population state is unchanged.[5]

Letting $X(t) = i$ be the number of individuals of type A at some time $t \geq 0$, then the probabilities that an agent of type A and B are chosen for reproduction are i/N and $(N-i)/N$, respectively. If an agent of type A is chosen for reproduction and produces $U-1 = u-1$ offspring, then the number of B agents chosen for replacement is hypergeometrically distributed with sample size $N-1$, initial configuration $N-i$ and $u-1$ draws (Der et al. 2012), so the probability of k agents of type B ($0 \leq k \leq u-1$) being replaced by agents of type A is

$$\frac{\binom{N-i}{k}\binom{i-1}{u-1-k}}{\binom{N-1}{u-1}},$$ (59)

which has mean $(u-1)\frac{N-i}{N-1}$. Similarly, the mean number of agents of type A to be replaced, given that a B agent is chosen for reproduction and produces $u-1$ offspring is $(u-1)\frac{i}{N-1}$. Thus, by the law of total expectation (theorem S1, conditioning on the type of agent chosen for reproduction), the expected number of individuals of type A in the next generation, given their present number, is:

$$
\begin{aligned}
\mathbb{E}\left(X(t+1) \mid X(t) = i\right) &= \frac{i}{N}\mathbb{E}\left(i + (U-1)\frac{N-i}{N-1}\right) \\
&\quad + \frac{N-i}{N}\mathbb{E}\left(i - (U-1)\frac{i}{N-1}\right) \\
&= i + \frac{i}{N}\frac{N-i}{N-1}\mathbb{E}(U-1) - \frac{N-i}{N}\frac{i}{N-1}\mathbb{E}(U-1) \\
&= i.
\end{aligned}
$$ (60)

---

[5] In the original version of the EW process (Eldon and Wakeley 2006), the fitnesses of both types were equal, and the parent agent was guaranteed to survive to the next generation. Der et al. (2012) generalized the original model to types with different fitnesses, but in their version of the EW process, it is possible for the parent to be chosen for replacement. Here, we reformulate Der et al's extended model while retaining the original condition that the reproducing agent cannot be chosen for replacement. In contrast to our version of the EW process, setting $U = 2$ in Der et al's version yields the Moran process exactly.

Der et al. (2012) have generalized the neutral EW process (Eldon and Wakeley 2006) by adding a deterministic "viability selection" step: for $s \in \mathbb{R}$, given the population state $X(t)$ at time t, an intermediate, pre-selection offspring population state at time $t + 1$ is generated according to the EW model without selection (described above). The population state $X(t + 1)$ at time $t + 1$ is then obtained by transforming the pre-selection offspring state according to standard (deterministic) logistic growth:

$$i \mapsto v(i) = \left\lfloor \frac{(1 + s/N)i}{(1 + s/N)i + (N - i)} N \right\rfloor = \left\lfloor \frac{N + s}{N + s(i/N)} i \right\rfloor, \tag{61}$$

where $\lfloor x \rfloor$ is the largest integer smaller than x. This corresponds to selection acting on the offspring before reaching reproductive age ($X(t)$ represents the state of the reproductively-mature population).

Now observe that for any $1 \leq i \leq N - 1$, if $s > 0$ then

$$v(i) \geq i, \tag{62}$$

if $s < 0$

$$v(i) \leq i, \tag{63}$$

and if $s = 0$, $v(i) = i$ (so the original EW process is recovered). Note also that because $\frac{(1+s/N)i}{(1+s/N)i+(N-i)} N < N$, fixation cannot occur in the selection step.

For any s, the selection step and neutral EW process above define a Markov process. Equations (60) and (62) imply that H1 is satisfied for this Markov process.

To verify H2 for any $s \geq 0$, choose any i ($1 \leq i \leq N - 1$) and $u \geq 2$ such that $\Pr(U = u) = p_u > 0$ (such u must exist because otherwise no offspring are ever created). The probability of an individual of type A reproducing is $\frac{i}{N}$. Using Eq. (59), the probability of increasing the number of As in the population given that an individual of type A reproduces and that $U = u$ is

$$p_+(i) = 1 - \frac{\binom{N-i}{0}\binom{i-1}{u}}{\binom{N-1}{u}}, \tag{64}$$

and $p_+(i) > 0$ because $i < N$. Hence, the probability of increasing the number of agents of type A in the population in the next generation is no less than

$$\Pr\left(X(t+1) > i \mid X(t) = i\right) \geq \frac{i}{N} p_u p_+(i) > 0, \tag{65}$$

[recall that the selection step cannot decrease the number of As in the population; see inequality (62)]. Now, starting from state i, if the number of agents of type A in the population is increased at each step, fixation of A is attained in at most $N - i$ steps. Since the probability of increasing the number of A's in the population is positive for $1 \leq i < N$, the probability of A fixing in i steps is positive,

$$\Pr\left(X(t+i) = N \mid X(t) = i\right) > 0. \tag{66}$$

Verifying H2 for $s < 0$ is similar.

As in Appendices B.1 and B.2, H3 is satisfied because there is no mutation, and consequently the EW process with viability selection defines a selection process.

Note that Eq. (60) implies that in the absence of selection, the EW process is a neutral drift process. Moreover, a similar method to that used in Appendix B.1 shows that the EW process without selection is mixed-irreducible.

B.4 Generalized Wright–Fisher models

Generalized Wright–Fisher (GWF) models are "a broad class of forward-time population models that share the same mean and variance of the Wright–Fisher model, but may otherwise differ"(Der et al. 2011). GWF models can allow for selection and mutation, but the general construction builds on pure-drift GWF models.

Mathematically, a pure-drift GWF model is Markov processes $X(t)$ such that

$$\mathbb{E}\left(X(t+1) \mid X(t) = i\right) = X(t), \tag{67a}$$

$$\mathrm{Var}\left(X(t+1) \mid X(t) = i\right) = \frac{N\sigma^2}{N-1} X(t) \left(1 - \frac{X(t)}{N}\right). \tag{67b}$$

If $\sigma^2 = 0$ then $\mathrm{Var}\left(X(t+1) \mid X(t) = i\right) = 0$ and the transition matrix for the corresponding Markov process is the identity matrix; this case, in which the population state never changes, is biologically absurd, so $\sigma^2 > 0$ is assumed hereafter.

Pure-drift GWF models are neutral drift processes (Definition 2.9):

Neutrality: Equation (8) is satisfied by assumption [Eq. (67a)], i.e. neither type is expected to increase in frequency from one time-step to the next.

H2: This hypothesis stipulates that starting from a mixed-type state i $(0 < i < N)$, the fixation of at least one the types (A or B) must be possible. Equation (67b) implies that for any mixed-type state $X(t) = i \notin \{0, N\}$,

$$\mathrm{Var}\left(X(t+1) \mid X(t) = i\right) > 0. \tag{68}$$

From Eq. (67a), it follows that

$$\Pr\left(X(t+1) < i \mid X(t) = i\right)) > 0, \tag{69}$$

Thus, starting at any mixed-type state i $(0 < i < N)$, it is possible to reach the state 0 in i or fewer steps in which A decreases in frequency, each of which occurs with positive probability, so A can fix with positive probability, and H2 holds. A similar argument shows that B can also fix with positive probability.

H3: This hypothesis stipulates that the states at which the population is composed only of one type (A or B) are absorbing. Pure-drift GWF processes satisfy H3,

because if $X(t) = 0$ then from Eq. (67b), $\text{Var}\left(X(t+1) \mid X(t) = 0\right) = 0$ so from Eq. (67a), if $X(t) = 0$, then

$$X(t+1) = \mathbb{E}\left(X(t+1) \mid X(t) = 0\right) = X(t) = 0, \tag{70}$$

and similarly, if $X(t) = N$, then $X(t+1) = N$.

For a population of size N, pure selection (i.e. mutationless) GWF models are constructed by modifying a pure-drift GWF model[6]: starting with a pure-drift process with transition matrix $Q^{(N)}$ selection is represented by a second $(N+1) \times (N+1)$ row-stochastic matrix $S^{(N)}$, and the transition matrix for the pure selection process is defined by $S^{(N)} Q^{(N)}$. When choosing how to construct selection matrices $S^{(N)}$, the only requirement is that in the limit $N \to \infty$, if $Q^{(N)} \to I$ (which means that the offspring variance approaches 0 as $N \to \infty$), the dynamics converge to Haldane's classical theory of deterministic evolution (Haldane 1932). This amounts to requiring that

$$\lim_{N \to \infty} N\left(S^{(N)} - I\right) u_N = \gamma x (1-x) \frac{\mathrm{d}u}{\mathrm{d}x}, \tag{71}$$

where u is any smooth function and

$$u_N = \left(u(0), u\left(\frac{1}{N}\right), \ldots, u\left(\frac{N-1}{N}\right)\right), \tag{72}$$

and γ is type B's selective advantage (Der 2010; Der et al. 2011).

Because of the generality of the method in which Der et al. allow for selection, GWF models with selection are not necessarily selection processes acorrding to Definition 2.1. To see that this is possible, observe that there is no restriction on the selection matrix, $S^{(N)}$ for any specific population size N (other than it being row-stochastic); only the infinite-population limit of a sequence of such selection matrices is restricted. Thus, let Q be the transition matrix for a pure-drift GWF model. Let the selection matrix S be any row-stochastic matrix with first and last columns composed of zeros other than the top and bottom (respectively) entries, which are taken to be 1. The transition matrix $P = SQ$ defines a Markov process for which fixation from any mixed-type state is impossible (violating H2).

B.5 Neutral and non-neutral Cannings (exchangeable) models

B.5.1 Neutral Cannings models

An important class of models arising in population genetics are due to Cannings (1974). In the most basic formulation, a population of N individuals is considered, each of which can be of either type A or B. The reproduction of each of these individuals (regardless of its type) is assumed to be equivalent in the sense that the numbers of offspring left by each individual are ***exchangeable random variables***.

---

[6] GWF processes also allow for mutation which is not discussed here; see Der (2010); Der et al. (2011).

Mathematically, for any time $t \geq 0$ and population state, $X(t) = i$ (that is, i is the number of individuals of type A), let v_k ($1 \leq k \leq N$) be a random variable describing the number of offspring of the kth individual in the population (that is, its contribution to the next generation, at time $t + 1$). Without loss of generality, we label the individuals of type A as $1, \ldots, i$ and the individuals of type B as $i + 1, \ldots, N$ (where one of these sets of indices is empty if $i = 0$ or $i = N$). The population state at time $t + 1$ given that $X(t) = i$ is then

$$X(t+1) = \sum_{k=1}^{i} v_k. \tag{73}$$

The assumption of exchangeability of the offspring variables is then that $\{v_k\}_{k=1}^{N}$ is a set of exchangeable random variables and independent of the population state, i, that is, the joint probability distribution of $\{v_k\}_{k=1}^{N}$ is invariant to the order of these random variables: for any permutation σ of the indices $1, \ldots, N$, and numbers of offspring $(\xi_1, \ldots, \xi_N) \in \{0, \ldots, N\}^N$,

$$\Pr\left(v_k = \xi_k; \ 1 \leq k \leq N\right) = \Pr\left(v_{\sigma(k)} = \xi_k; \ 1 \leq k \leq N\right), \tag{74}$$

Because the population size is constant, the offspring variables $\{v_k\}_{k=1}^{N}$ must also satisfy

$$N = \sum_{k=1}^{N} v_k, \tag{75}$$

so the variables $\{v_k(i)\}_{k=1}^{N}$ are in general not independently distributed.[7]

Any Cannings process is a pure-drift GWF process (Appendix B.4), and thus a neutral drift process (Definition 2.9). To prove this, we must show that the first and second conditional moments of a Cannings process conform to Eq. (67). The exchangeability of the offspring variables implies that the expected number of offspring of all individuals are equal (regardless of their type),

$$\mathbb{E}(v_k) = \mathbb{E}(v_j) \quad \text{for all } k, j \text{ such that } 1 \leq k \leq N, 1 \leq j \leq N. \tag{76}$$

Using Eq. (75),

$$N = \sum_{k=1}^{N} \mathbb{E}(v_k) = N \mathbb{E}(v_1), \tag{77}$$

so $\mathbb{E}(v_k) = \mathbb{E}(v_1) = 1$ for any k such that $1 \leq k \leq N$. It follows that,

$$\mathbb{E}(X(t+1)) \mid X(t) = i) = \mathbb{E}\left(\sum_{k=1}^{i} v_k\right) = i \mathbb{E}(v_k) = i = X(t) \tag{78}$$

---

[7] Taking $\{v_k\}_{k=1}^{N}$ to be exchangeable multinomial variables yields the neutral WF process (Cannings 1974).

so $X(t)$ is a martingale and Eq. (67a) is satisfied. The following Lemma shows that Eq. (67b) also holds.

Lemma B.1 *The conditional variance of a Cannings process with offspring variance* σ^2 *is*

$$\text{Var}\left(X(t+1) \mid X(t) = i\right) = \sigma^2 X(t)\frac{N - X(t)}{N - 1}. \tag{79}$$

Proof Our derivation follows that of Ewens (2012). Using Eq. (75),

$$0 = \text{Var}(N) = \text{Var}\left(\sum_{k=1}^{N} v_k\right) = \sum_{k=1}^{N} \text{Var}(v_k) + \sum_{\substack{j,k=1 \\ j \neq k}}^{N} \text{Cov}(v_j, v_k), \tag{80}$$

By symmetry, for any $k \neq j$ such that $1 \leq j \leq N$ and $1 \leq k \leq N$, we have

$$0 = N\,\text{Var}(v_k) + N(N - 1)\,\text{Cov}(v_j, v_k), \tag{81}$$

and hence,

$$\text{Cov}(v_j, v_k) = -\frac{\sigma^2}{N - 1}. \tag{82}$$

It follows that

$$
\begin{aligned}
\text{Var}\left(X(t+1) \mid X(t) = i\right) &= \text{Var}\left(\sum_{k=1}^{i} v_k\right) \\
&= \sum_{k=1}^{i} \text{Var}(v_k) + \sum_{\substack{j,k=1 \\ j \neq k}}^{i} \text{Cov}(v_j, v_k), \\
&= i\sigma^2 - i(i - 1)\frac{\sigma^2}{N - 1} \\
&= \sigma^2 i \frac{N - i}{N - 1} = \sigma^2 X(t)\frac{N - X(t)}{N - 1}.
\end{aligned}
\tag{83}
$$

$\square$

B.5.2 Cannings models with selection

Lessard and Ladret (2007) introduced an extension of Cannings models that includes selection. Here, we show that although not all of the models in the class defined by Lessard and Ladret (2007) are selection processes, this is due to some biologically absurd models belonging to this class; under minimal biologically reasonable assumptions, such models are selection processes.

Following Lessard and Ladret (2007, with slightly modified notation), we consider a population of N individuals, each of which can be of either type A or B. In contrast to neutral Cannings models, in which all individuals are exchangeable, we now suppose

individuals can be exchanged only with others of their own type (so an A can be exchanged with any other A but not a B).

Mathematically, for any time $t \geq 0$ and population state, $X(t) = i$ (that is, i is the number of individuals of type A), let $v_k(i)$ ($1 \leq k \leq N$) be a random variable describing the number of offspring of the kth individual in the population. Without loss of generality, we label the individuals of type A as $1, \ldots, i$ and the individuals of type B as $i+1, \ldots, N$. The population state at time $t+1$ given that $X(t) = i$ is then

$$X(t+1) = \sum_{k=1}^{i} v_k(i).$$
(84)

We assume that the offspring variables for each type, $\{v_k(i)\}_{k=1}^{i}$ and $\{v_k(i)\}_{k=i+1}^{N}$ are both sets of exchangeable random variables, that is the joint probability distributions of $\{v_k(i)\}_{k=1}^{i}$ and $\{v_k(i)\}_{k=i+1}^{N}$ are invariant to the order of these random variables: for any permutations σ_A and σ_B of the indices $1, \ldots, i$ and $i+1, \ldots, N$, respectively, and numbers of offspring $(\xi_1, \ldots, \xi_N) \in \{0, \ldots, N\}^N$,

$$\Pr\left(v_k(i) = \xi_k; \ 1 \leq k \leq i\right) = \Pr\left(v_{\sigma_A(k)}(i) = \xi_k; \ 1 \leq k \leq i\right),$$
(85a)

and

$$\Pr\left(v_k(i) = \xi_k; \ i+1 \leq k \leq N\right) = \Pr\left(v_{\sigma_B(k)}(i) = \xi_k; \ i+1 \leq k \leq N\right).$$
(85b)

Because the population size is constant, the offspring variables $\{v_k(i)\}_{k=1}^{N}$ must also satisfy

$$N = \sum_{k=1}^{N} v_k(i).$$
(86)

Let the expected number of offspring of individuals of type A be

$$\mu_A(i) = \mathbb{E}(v_k(i)) \quad \text{for } 1 \leq k \leq i,$$
(87)

and the expected number of offspring of individuals of type B be

$$\mu_B(i) = \mathbb{E}(v_k(i)) \quad \text{for } i+1 \leq k \leq N.$$
(88)

Equation (86) then implies

$$N = \sum_{k=1}^{N} \mathbb{E}(v_k(i)) = i\mu_A(i) + (N-i)\mu_B(i).$$
(89)

Differential fitnesses for the two types can then be introduced by allowing $\mu_A(i)$ and $\mu_B(i)$ to differ, and defining the fitness of each type in a manner consistent with hypothesis H1 of Definition 2.1 (for example, Wrightian fitness can be used, i.e. define

the expected fitness of each type $t = A$ or B as $\overline{W}_t (i) \triangleq \mu_t (i)$; see for example Wu et al. 2013). In particular, frequency dependent selection is obtained by allowing the expected numbers of offspring to depend on the population state i.

Lessard and Ladret's extension of Cannings' model (described above) defines a discrete time Markov chain with transition matrix

$$P_{i,j} = \mathrm{Pr}\left(\sum_{k=1}^{i} v_k (i) = j \right). \tag{90}$$

Not all models in the class defined by Lessard and Ladret are selection processes. For example, suppose that $\{v_k (i)\}_{k=1}^{i}$ and $\{v_k (i)\}_{k=i+1}^{N}$ are sets of exchangeable random variables with means $\mu_A (i) = \mu_B (i) = 1$. Then,

$$\sum_{k=1}^{i} v_k (i) = i, \tag{91a}$$

and

$$\sum_{k=i+1}^{N} v_k (i) = N - i. \tag{91b}$$

that, is, each type evolves independently according to a (neutral) Cannings model.[8] The joint probability distribution of $\{v_k (i)\}_{k=1}^{i}$ is then

$$\mathrm{Pr}\left(v_k (i) = \xi_k;\ 1 \le k \le i \right) = \begin{cases} 1/i & \text{if } o_k = i\delta_{k\hat{k}} \text{ for some } \hat{k} \in \{1, \ldots, i\}, \\ 0 & \text{otherwise}, \end{cases} \tag{92}$$

with an analogous expression for $\{v_k (i)\}_{k=i+1}^{N}$ (where we have used Kronecker's delta notation: $\delta_{mn} = 1$ if $m = n$ and $\delta_{mn} = 0$ otherwise). The resulting transition matrix $P = I$ defines a neutral process in the sense that $\mathbb{E} (X(t + 1) \mid X(t)) = X(t)$. However, any state is an absorbing state of this Markov process, and in particular, hypothesis H2 of Definition 2.1 is violated.[9]

It is thus natural to ask which of Lessard and Ladret's models are selection processes? To answer this question, we consider the three hypotheses of Definition 2.1:

H1: This hypothesis asserts that the type that has higher fitness at time t is expected to increase in frequency in the next time step. While fitness as such is not part of the definition of Lessard and Ladret's models, one may define the expected fitness of each type $t = A$ or B as the expected number of offspring of individuals of that type (as suggested above),

$$\overline{W}_t (i) \triangleq \mu_t (i). \tag{93}$$

---

[8] This occurs when the two types effectively make up two sub-populations that reproduce and evolve independently.

[9] Importantly, note that assuming equal mean numbers of offspring in Lessard and Ladret's model, $\mu_A (i) = \mu_B (i) = 1$, does not recover Cannings' original (neutral) model.

Under this definition of fitness,

$$\mathbb{E}(X(t+1) \mid X(t)=i) = \mathbb{E}\left(\sum_{k=1}^{i} v_k(i)\right) = i\mu_A(i) = i + \frac{i}{N}(N\mu_A(i) - N)$$

$$= i + \frac{i}{N}\left[N\mu_A(i) - (i\mu_A(i) + (N-i)\mu_B(i))\right]$$

$$= i + i\frac{N-i}{N}(\mu_A(i) - \mu_B(i)), \tag{94}$$

so H1 is satisfied.

H2: This hypothesis stipulates that starting from a mixed-type state i (where both types are present in the population), the fixation of at least one the types (A or B) must be possible. We are not aware of a simple sufficient condition on the exchangeable sets $\{v_k(i)\}_{k=1}^{i}$ and $\{v_k(i)\}_{k=i+1}^{N}$ ensuring that H2 holds. However, models violating this hypothesis seem to us biologically unreasonable.

H3: This hypothesis stipulates that the states at which the population is composed only of one type (A or B) are absorbing. Any process in the class defined by Lessard and Ladret satisfies H3, because if $X(t) = 0$, then from Eq. (84)

$$X(t+1) = \sum_{k=1}^{0} v_k(i) = 0, \tag{95}$$

and similarly, if $X(t) = N$, then $X(t+1) = N$.

C Fixation probabilities for birth–death processes

Suppose that individuals in a population of constant size N can possess one of two traits, A and B. Let the state of the population (i.e. the number of individuals of type A) evolve according to a discrete-time **birth–death process** in which a trait that has disappeared cannot re-emerge. That is, the population state may change by at most one at any given time-step (individuals change their type one at a time), and the states 0 and N are absorbing. In this Appendix, we find $p_{\text{fix}}(i)$, the fixation probability of the trait A, when there are initially i individuals of type A in the population. We do this following the method presented by Nowak (2006).

Mathematically, the time evolution of the population composition follows a Markov process with transition matrix P satisfying

$$P_{k,k} = 1 - P_{k,k+1} - P_{k,k-1}, \tag{96}$$

and $P_{k,j} = 0$ for all $0 \leq j < k - 1$ and $k + 1 < j \leq N$, where $P_{k,k+1}$ and $P_{k,k-1}$ are the transition probabilities from the state in which there are k individuals of type A, to the ones in which the population contains $k + 1$ or $k - 1$ individuals of type A, respectively. Note also that $P_{0,0} = P_{1,1} = 1$ and $P_{0,k} = P_{N,N-k} = 0$ for all $1 \leq k \leq N$ (the states corresponding to homogeneous populations are absorbing).

Let $p_{\text{fix}}(i)$ be the probability of reaching state N (fixation of A) when starting from state i. It follows that $p_{\text{fix}}(0) = 0$, $p_{\text{fix}}(N) = 1$ and for $1 \leq i \leq N - 1$,

$$p_{\text{fix}}(i) = P_{i,i-1} p_{\text{fix}}(i-1) + P_{i,i+1} p_{\text{fix}}(i+1) + P_{i,i} p_{\text{fix}}(i). \tag{97}$$

Consequently,

$$(P_{i,i+1} + P_{i,i-1}) p_{\text{fix}}(i) = (1 - P_{i,i}) p_{\text{fix}}(i) = P_{i,i-1} p_{\text{fix}}(i-1) + P_{i,i+1} p_{\text{fix}}(i+1),$$

so

$$P_{i,i-1}(p_{\text{fix}}(i) - p_{\text{fix}}(i-1)) = P_{i,i+1}(p_{\text{fix}}(i+1) - p_{\text{fix}}(i)),$$

or, defining $y_i = p_{\text{fix}}(i) - p_{\text{fix}}(i-1)$ for $1 \leq i \leq N$,

$$y_{i+1} = \frac{P_{i,i-1}}{P_{i,i+1}} y_i.$$

Thus,

$$y_1 = p_{\text{fix}}(1) - p_{\text{fix}}(0) = p_{\text{fix}}(1),$$
$$y_2 = \frac{P_{1,0}}{P_{1,2}} y_1 = \frac{P_{1,0}}{P_{1,2}} p_{\text{fix}}(1),$$
$$y_3 = \frac{P_{2,1}}{P_{2,3}} y_2 = \frac{P_{2,1}}{P_{2,3}} \frac{P_{1,0}}{P_{1,2}} p_{\text{fix}}(1),$$
$$\vdots$$
$$y_{i+1} = \prod_{j=1}^{i} \frac{P_{j,j-1}}{P_{j,j+1}} p_{\text{fix}}(1) \tag{98}$$

for $2 \leq i \leq N - 1$.

Summing y_k for $1 \leq k \leq i \leq N$ gives

$$\sum_{k=1}^{i} y_k = \sum_{k=1}^{i} \left(p_{\text{fix}}(k) - p_{\text{fix}}(k-1) \right) = p_{\text{fix}}(i) - p_{\text{fix}}(0) = p_{\text{fix}}(i). \tag{99}$$

From Eqs. (98) and (99),

$$p_{\text{fix}}(i) = y_1 + \sum_{k=1}^{i-1} y_{k+1} = p_{\text{fix}}(1) \left(1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}} \right). \tag{100}$$

Since $p_{\text{fix}}(N) = 1$, substituting $i = N$ in Eq. (100) gives

$$p_{\text{fix}}(1) = \frac{1}{1 + \sum_{k=1}^{N-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}}}. \tag{101}$$

Thus, from Eqs. (101) and (100), the fixation probability of A when there are initially i individuals of type A in the population is

$$p_{\text{fix}}(i) = \frac{1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}}}{1 + \sum_{k=1}^{N-1} \prod_{j=1}^{k} \frac{P_{j,j-1}}{P_{j,j+1}}}. \tag{102}$$

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Electronic Supplementary Material

for

On selection in finite populations

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D   Definitions and theorems from probability theory

In this appendix, we collect definitions and theorems from probability theory necessary for the proofs in the main text, but that are not necessary to follow the flow of the paper when proofs are omitted. These are collected here to aid readers who are already sufficiently familiar with probability theory so as to require only a brief reminder of the relevant concepts. For a comprehensive exposition of the relevant theory, see the references cited for each definition and theorem.

All random variables are assumed to be real-valued.

D.1   Total expectation

Theorem S1 (Law of total expectation; equation 1.14 of Karlin and Taylor, 1975). *If X and Y are random variables and g is a function such that $\mathbb{E}\big(g(X)\big) < \infty$, then*

$$\mathbb{E}_X\big(g(X)\big) = \mathbb{E}_Y\big(\mathbb{E}_X(g(X)\,|\,Y)\big). \tag{S1}$$

D.2   Markov Chains

Let $X(t)$ be a discrete-time Markov chain with stationary transition matrix P. We say that the states i and j **communicate** if state i leads to state j, and *vice-versa* (see definition **??**). A state that communicates with all the states it leads to is called **essential**; otherwise, it is **inessential**. Lastly, a state i is called **recurrent** if, when starting from $X(0) = i$ the process is guaranteed to return to state i (at least once), that is

$$\Pr\big(\exists \tau > 0 \text{ such that } X(\tau) = i \,\big|\, X(0) = i\big) = 1. \tag{S2}$$

Comprehensive discussions of the classification of states of Markov chains can be found in the books by Chung (1967); Seneta (2006).

D.3   Martingale theory

Definition S2 (Martingales; chapter 6 of Karlin and Taylor, 1975). *Let $X(t)$ be a bounded, discrete-time Markov process.*

- *$X(t)$ is a martingale iff for all $t \geq 0$,*

$$\mathbb{E}\big(X(t+1)\,\big|\,X(t)\big) = X(t). \tag{S3}$$

- *$X(t)$ is a supermartingale iff for all $t \geq 0$,*

$$\mathbb{E}\big(X(t+1)\,\big|\,X(t)\big) \leq X(t). \tag{S4}$$

- $X(t)$ *is a submartingale* iff *for all* $t \geq 0$,

$$\mathbb{E}\left(X(t+1) \mid X(t)\right) \geq X(t).\tag{S5}$$

Definition S3 (Stopping time; definition 3.1 in chapter 6 of Karlin and Taylor, 1975). *Let $X(t)$ be a discrete-time Markov process. A random variable T taking values in $\{0, 1, 2, \ldots, \infty\}$ such that the indicator function of the event $T = n$, $I_{T=n}$, is a function of $X(0), \ldots, X(n)$, is called a* **stopping time** *(with respect to $X(t)$).*

Thus, a random variable T is a stopping time *iff* the event "stopped at time n" ($T = n$) depends only on the states $X(t)$ that have occurred up to time n. A stopping time can be interpretted as a rule for deciding whether or not to stop a process, based only on events that have already occurred (not on any knowledge of the future).

Remark S4. *Martingales, supermartingales and stopping times can be defined more generally. We use these restricted definitions for simplicity.*

The following is a version of the optional stopping theorem given in theorem 3.1 in chapter 6 in the book by Karlin and Taylor (1975):

Theorem S5 (Optional stopping theorem). *Let X be a martingale and T a stopping time that is almost surely finite $(\Pr(T < \infty) = 1)$ and*

$$\mathbb{E}\left(\sup_{t \geq 0}\left|X(\min\{T, t\})\right|\right) < \infty.\tag{S6}$$

Then, $\mathbb{E}\left(X(T)\right) = \mathbb{E}\left(X(0)\right)$.

Condition (S6) means that the expected supremum (least upper bound) of the magnitude of the state before a stopping time is finite.

Theorem S6 (Optional stopping for supermartingales; theorem 4.2 in chapter 6 of Karlin and Taylor, 1975). *Let X be a supermartingale and T a stopping time. Then,* $\mathbb{E}\left(X(T)I_{\{T<\infty\}}\right) \leq \mathbb{E}\left(X(0)\right)$, *where $I_{\{T<\infty\}}$ is the indicator function for the event $\{T < \infty\}$.*

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