Disentangling eco-evolutionary effects on trait fixation

Peter Czuppon[1] and Chaitanya S. Gokhale[1]
[1]*Department of Evolutionary Theory,*
Max Planck Institute for Evolutionary Biology,
August-Thienemann-Straße 2, 24306 Plön, Germany

In population genetics, fixation of traits in a demographically changing population under frequency-independent selection has been extensively analyzed. In evolutionary game theory, models of fixation have typically focused on fixed population sizes and frequency-dependent selection. However, combining ecological fluctuations with frequency-dependent interactions such as Lotka-Volterra dynamics and thus the analysis of eco-evolutionary fixation has received comparatively little attention. Here, we consider a two-type stochastic competitive Lotka-Volterra model with higher order interactions. The emerging individual based model allows for stochastic fluctuations not just in the frequencies of the two types but the total population size as well. Assuming weak selective differences between the traits we approximate the fixation probability for differing competition coefficients. We find that it resembles qualitatively the corresponding evolutionary deterministic dynamics within a population of fixed size. Furthermore, we analyze and partially disentangle the selection effects into their ecological and evolutionary components. Concretely, we show that the evolutionary selection intensity has a larger effect on the predictive power of our approximation than the ecological selection. However, the fixed points themselves are also affected by the selection intensity which implies that a clean separation of the ecological and evolutionary impacts on the evolutionary outcome of the model is not possible. The entanglement of eco-evolutionary processes in a co-evolutionary system is thus a reality which needs to be considered when determining the fixation properties in populations of fluctuating size.

Keywords: eco-evolution; fixation probability; social dilemma; stochastic diffusion; evolutionary game theory; competitive Lotka-Volterra model

I. INTRODUCTION

The theoretical study of fixation or extinction of an allele or a trait in a population has a long history in the context of population genetics [24, 37, 48, 94]. It has since then served as a basic theory in a huge variety of fields in evolutionary biology [63]. While traditionally the focus is on the evolutionary dynamics of a trait in a fixed or infinitely large population size under frequency-independent selection, there are also models including deterministic population size changes [23, 49, 70, 89, 92].

Additionally, also evolutionary game dynamics has been utilized in biological and social contexts since its inception [55, 58]. This framework allows for an easy interpretation and implementation of frequency-dependent selection processes which can lead to coexistence or bistable dynamics. Amongst others, evolutionary games have provided insights into evolution of cooperation [65], evolution of sex [57], host-parasite-dynamics [50] and more recently, the evolution of cancer [71]. The introduction of stochasticity albeit within fixed population sizes, allows the study of quantities such as fixation probabilities or mean fixation times [2, 3, 31]. The main focus of this discipline, has been on evolutionary dynamics [45, 64], mainly neglecting ecological effects.

In real biological systems, as it is becoming increasingly clear from epidemiological as well as experimental studies, the interaction of ecology and evolution is crucial in determining the joint eco-evolutionary trajectory of a system [26, 36, 78]. Evolutionary dynamics of two traits, e.g. cooperators and cheaters, has been studied in evolutionary models inspired by microbial experiments [1, 12, 16, 17, 35]. Ecology, and in particular fluctuating population sizes, often dictate the dynamics of these experiments.

In this study we take inspiration from population genetics, theoretical ecology and evolutionary game theory and develop a mechanistic eco-evolutionary model with higher order interaction terms. Focusing on finite populations we explicitly calculate the fixation probability where the population size can fluctuate stochastically over time.

The analysis of evolutionary games in finite populations has garnered a lot of attention in the past decade [2, 6, 86]. Besides adding realism, models of finite populations can even provide results qualitatively different from the deterministic estimates [9, 15, 65]. While of importance in understanding the underlying processes which lead to the gross deterministic behaviour, the importance of stochastic dynamics in biological systems cannot be understated [9].

Barring a few exceptions, majority of the literature focuses on a constant population size, neglecting potential ecological effects on the population dynamics. Further examinations on the interaction of evolutionary and population dynamics have recently gained more attention [11, 14–16, 52, 61, 74–76, 89]. Classical equations of ecology such as the co-evolutionary Lotka-Volterra dynamics have to be re-evaluated when finite populations are considered [33, 72]. Recent studies explicitly include evolutionary game dynamics into an ecological framework [8, 19, 32, 47, 59, 96]. In these models, one challenge is to re-interpret game interactions in terms of ecological dynamics so as to make sense in a fluctuating population size scenario. Recent work in this direction provides a mechanism by which such an amalgamation of techniques is possible [47]. Since the game interactions are between individuals with different traits, we

can interpret them as the interaction terms as in the competitive Lotka-Volterra type interactions [97]. Typically in evolutionary games when an individual interacts with another, it receives a payoff. In our eco-evolutionary setting, the payoffs translate inversely into competition outcomes. Thus, the more the payoff, the less likely is the interaction harmful for the actor.

Derivation of a stochastic formulation of a model begs further analysis. When drift dominates, i.e. in the limit of weak selection, the impact of the interactions on the fitness is minimal, approximations for the fixation probability are available [11, 14, 19, 52]. From a game theoretic perspective, all these studies are restricted to the highly abstract notion of two player games [87]. The mathematics of these games is the same as that of allele dynamics within a haploid population [18]. This framework has been extended to diploids [41, 77]. Multiplayer games would allow us to increase the ploidy level [39]. Therefore, multiplayer games are not just theoretically interesting [62], but have clear biological [13] as well as social interpretations. From multiple bacteria interacting together as in microbiomes [95], in quorum sensing [93] or during biofilm formation [22] to social dilemmas such as the classic tragedy of the commons [40], evolutionary games can be interpreted across scales of organization. For an extensive account for the applications of multiplayer games in biology we refer to Broom [10]. Of interest then, would be a complete eco-evolutionary analysis of fixation probability for multiplayer evolutionary games such that we can understand the effects of demographic changes on the combined eco-evolutionary trajectory.

Following this line of thought, we develop an ecological interpretation of a two trait multiplayer evolutionary game model. We calculate the fixation probability of a trait (strategy) in a competitive Lotka-Volterra model with higher order interactions (multiplayer game), where the population size fluctuates over time. The population size changes are not external shocks [27] but rather are a consequence of the mechanistic setup of the system. This individual based implementation of reactions also allows for a straight-forward interpretation of the fitness effects on the population level. The stochastic model so generated, generalizes previous results on fixation probability [19, 52]. It allows us to (partly) disentangle the impact of evolutionary and ecological forces on the fixation probability. We then apply our theory to a well studied example of a social dilemma, the so called threshold public goods game. This example allows us further insight into the structure of the expression of the fixation probability and we can thus extend the framework to general d-player interactions eco-evolutionary models.

II. FROM EVOLUTIONARY GAMES TO POPULATION DYNAMICS

While two player games form the crux of most of evolutionary game theory, multiplayer games are rather the norm in social as well as a number of biological situations. Usually the evolutionary dynamics is concerned with the change in frequencies of traits over time under the assumption of population densities being in an ecological equilibrium. This results in the ecological aspect of changing population densities often times being overlooked. We develop a multiplayer population dynamics model which is based upon ecological processes as in [47]. As an example we begin with a three player interaction.

A. Replicator dynamics

Consider a population consisting of two traits, A and B. The interactions between the individuals when they interact in groups of three are then denoted by,

$$\begin{array}{cc} & \begin{array}{ccc} AA & AB & BB \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a_2 & a_1 & a_0 \\ b_2 & b_1 & b_0 \end{pmatrix} \end{array} \tag{1}$$

The focal individual (row) with trait A interacts with two other individuals. If the other two individuals happen to be also A then the payoff to the focal individual is a_2. Typically in traditional evolutionary game theoretic terms the population size is considered to be infinitely large so that the number of A and B individuals can be represented by their frequencies $x_A = x$ and $x_B = 1 - x$. The fitness of the trait is then the product of the payoff and the frequency of the corresponding trait in the population, thus,

$$\pi_A = a_2 x^2 + 2a_1 x(1-x) + a_0(1-x)^2 \tag{2}$$
$$\pi_B = b_2 x^2 + 2b_1 x(1-x) + b_0(1-x)^2 \tag{3}$$

The evolutionary change in the frequencies of the types can then be captured by the standard replicator dynamics which is fully valid for multiplayer games [34, 45] given by,

$$\frac{dx}{dt} = x(1-x)(\pi_A(x) - \pi_B(x)). \tag{4}$$

We can recover the traditional outcomes of neutrality, dominance, bistability and coexistence for the three player game but furthermore the setup has the possibility to show two internal fixed points, one being stable and the other one unstable.

1. *Finite populations:*

Replicator dynamics is based on an assumption that the population size is infinitely large. This allows us to look at the gross qualitative dynamics of selection. Interactions however take place in finite population. The results so obtained when taking finite populations into account can force us to rethink the limits of the infinite populations size assumption [25, 28, 66, 88]. Various ways of handling finite

populations have been implemented and this applies also to multiplayer games [34, 54, 87].

A crucial concept in finite populations is that of selection intensity. We can control the effect of the game (interactions) on to the fitness of a trait by tuning the magnitude of the intensity of selection. Assuming a linear payoff to fitness mapping we have $f_a = 1 + \omega\pi_A$. If selection is weak, $\omega \ll 1$, then drift dominates and the average payoff has a minimal effect on the fitness. Thus the effective difference between the two types reduces. The mapping can be subsumed in the payoff matrix where each payoff entry say a_i is rescaled to $1 + \omega a_i$.

B. Population dynamics

As per [47] we rationalize that since the game contributes only to the competition between individuals, it can thus result in the death of the focal individual. The payoffs of a game usually translate positively towards the fitness of the focal individual, so an inverse relationship between the magnitude of the payoff and the probability of death. The microscopic interactions which lead to birth, competition and death of the types can be written down in the form of chemical reactions as in [30],

$$\begin{aligned}
A &\xrightarrow{\beta_A} A + A \\
B &\xrightarrow{\beta_B} B + B \\
A + (A + A) &\xrightarrow{\gamma_{a_2}} A + A \\
A + (A + B) &\xrightarrow{\gamma_{a_1}} A + B \\
A + (B + B) &\xrightarrow{\gamma_{a_0}} B + B \\
B + (A + A) &\xrightarrow{\gamma_{b_2}} A + A \\
B + (A + B) &\xrightarrow{\gamma_{b_1}} A + B \\
B + (B + B) &\xrightarrow{\gamma_{b_0}} B + B \\
A &\xrightarrow{\delta_A} 0 \\
B &\xrightarrow{\delta_B} 0,
\end{aligned} \tag{5}$$

where the reaction rates $\gamma_{k_i} = \binom{2}{i}/(M^2(1 + \omega k_i))$ with k_i the payoffs from the payoff matrix for the three player game. The reaction rates for the birth and death reactions are explicitly defined. The parameter M controls the abundance of the population size in equilibrium. The reactions are corrected according to their combinatorial possibilities as in [60]. Note, that this combinatorial correction is not the same as the standard mass-action kinetics from chemical reaction network theory [5, 30]. This different implementation is justified by the intuition of drawing the individuals participating in these reactions from the overall population instead of calculating the probability for particles to meet as argued in the context of biochemical reactions. This microscopic implementation of the model has the advantage of directly relating selective advantages to birth or death processes. This mechanistic way of thinking about evolutionary success has not been examined in the literature, see [21] for an essay about this. We believe that interpreting selection in a mechanistic way can give new insight into the concrete advantages of mutants and situations in which these mutants are beneficial.

We proceed by writing down the transition rates to go from a state $\mathbf{n} = (n_A, n_B)$ to another accessible state. These rates read as,

$$\begin{aligned}
T(n_A + 1, n_B|\mathbf{n}) &= \beta_A n_A, \\
T(n_A, n_B + 1|\mathbf{n}) &= \beta_B n_B, \\
T(n_A - 1, n_B|\mathbf{n}) &= \gamma_{a_2} n_A(n_A - 1)(n_A - 2) + 2\gamma_{a_1} n_A n_B(n_A - 1) \\
&\quad + \gamma_{a_0} n_A n_B(n_B - 1) + \delta_A n_A, \\
T(n_A, n_B - 1|\mathbf{n}) &= \gamma_{b_2} n_B(n_A - 1)(n_A - 2) + 2\gamma_{b_1} n_B n_B(n_A - 1) \\
&\quad + \gamma_{b_0} n_B n_B(n_B - 1) + \delta_B n_B.
\end{aligned}$$

Using these rates we can write down the stochastic master equation with the general form as

$$\frac{dP(\mathbf{n}, t)}{dt} = \sum_{\mathbf{n}' \neq \mathbf{n}} T(\mathbf{n}|\mathbf{n}')P(\mathbf{n}', t) - \sum_{\mathbf{n}' \neq \mathbf{n}} T(\mathbf{n}'|\mathbf{n})P(\mathbf{n}, t). \tag{6}$$

In the limit of a large population size we recover the mean field approximation or the population level model [60].

$$\begin{aligned}
\frac{d\langle n_A \rangle}{dt} = \beta_A n_A &- \frac{n_A(n_A - 1)(n_A - 2)}{M^2(1 + \omega a_2)} \\
&- \frac{2n_A n_B(n_A - 1)}{M^2(1 + \omega a_1)} - \frac{n_A n_B(n_B - 1)}{M^2(1 + \omega a_0)} - \delta_A n_A.
\end{aligned}$$

Rescaling population size by $x_A = n_A/M$ and time by $\tau = Mt$ we find

$$\begin{aligned}
\frac{dx_A}{dt} = x_A \Bigg[&\beta_A - \delta_A - \frac{1}{1 + \omega a_2}\left(x_A - \frac{1}{M}\right)\left(x_A - \frac{2}{M}\right) \\
&- \frac{2}{1 + \omega a_1} x_B \left(x_A - \frac{1}{M}\right) - \frac{1}{1 + \omega a_0} x_B \left(x_B - \frac{1}{M}\right)\Bigg].
\end{aligned} \tag{7}$$

Similarly for trait B we have

$$\begin{aligned}
\frac{dx_B}{dt} = x_B \Bigg[&\beta_B - \delta_B - \frac{1}{1 + \omega b_0}\left(x_B - \frac{1}{M}\right)\left(x_B - \frac{2}{M}\right) \\
&- \frac{2}{1 + \omega b_1} x_A \left(x_B - \frac{1}{M}\right) - \frac{1}{1 + \omega b_2} x_A \left(x_A - \frac{1}{M}\right)\Bigg].
\end{aligned} \tag{8}$$

The change in the number of the individual types is interesting in itself when considering co-evolutionary dynamics. This will relate to the interactions between different

species which in principle can have different carrying capacities (M_A,M_B, ...). The evolutionary process (change in the population composition) as well as the ecological dynamics (change in population density) can then be measured by transforming the above differential equations to the fraction of trait A individuals, $p = \frac{x_A}{x_A+x_B}$, and the total population size, $z = x_A + x_B$, thus given by,

$$\begin{aligned}\frac{dp}{dt} &= p(1-p)z\left(z+\frac{1}{M}\right)\left[\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_0}\right.\\ &+2p\left(\frac{1}{1+\omega b_1}-\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_1}+\frac{1}{1+\omega a_0}\right)\\ &+p^2\left(\frac{1}{1+\omega b_2}-\frac{2}{1+\omega b_1}+\frac{1}{1+\omega b_0}\right.\\ &\left.\left.-\frac{1}{1+\omega a_2}+\frac{2}{1+\omega a_1}-\frac{1}{1+\omega a_0}\right)\right],\end{aligned} \tag{9}$$

$$\begin{aligned}\frac{dz}{dt} &= z\left(\beta-\delta-z^2\left[\frac{1}{1+\omega b_0}\right.\right.\\ &+p\left(\frac{1}{1+\omega a_0}+\frac{2}{1+\omega b_1}-\frac{3}{1+\omega b_0}\right)\\ &+p^2\left(\frac{2}{1+\omega a_1}-\frac{2}{1+\omega a_0}+\frac{1}{1+\omega b_2}-\frac{4}{1+\omega b_1}+\frac{3}{1+\omega b_0}\right)\\ &+p^3\left(\frac{1}{1+\omega a_2}-\frac{2}{1+\omega a_1}+\frac{1}{1+\omega a_0}\right.\\ &\left.\left.\left.-\frac{1}{1+\omega b_2}+\frac{2}{1+\omega b_1}-\frac{1}{1+\omega b_0}\right)\right]\right).\end{aligned} \tag{10}$$

Since our ultimate goal is to approximate the fixation probability of type A individuals in the population, we now proceed by considering the stochastic counterpart of this eco-evolutionary model.

1. *Stochastic eco-evolutionary dynamics:*

Most often stochastic models are derived from an individual based formulation as given in Eq. (5) and then approximated by a stochastic differential equation, the so called diffusion approximation, see e.g. [29, 91]. For our model we obtain (for a detailed derivation see part 1.1 in the supplementary information (SI))

$$\begin{aligned}dx_A(t) &= x_A\left(\beta_A-\delta_A-\frac{x_A^2}{1+\omega a_2}-\frac{2x_Ax_B}{1+\omega a_1}-\frac{x_B^2}{1+\omega a_0}\right)dt\\ &+\frac{1}{\sqrt{M}}\left((\beta_A+\delta_A)x_A\right.\\ &\left.+x_A\left(\frac{x_A^2}{1+\omega a_2}+\frac{2x_Ax_B}{1+\omega a_1}+\frac{x_B^2}{1+\omega a_0}\right)\right)^{1/2}dW_1(t),\\ dx_B(t) &= x_B\left(\beta_B-\delta_B-\frac{x_A^2}{1+\omega b_2}-\frac{2x_Ax_B}{1+\omega b_1}-\frac{x_B^2}{1+\omega b_0}\right)dt\\ &+\frac{1}{\sqrt{M}}\left((\beta_B+\delta_B)x_B\right.\\ &\left.+x_B\left(\frac{x_A^2}{1+\omega b_2}+\frac{2x_Ax_B}{1+\omega b_1}+\frac{x_B^2}{1+\omega b_0}\right)\right)^{1/2}dW_2(t),\end{aligned} \tag{11}$$

where W_i are independent Brownian motions.

Again, we can transform this to the relative frequency of A individuals denoted p and the total population size z. A visualization of this transformation along with stochastic simulations is shown in Figure 1.

III. FIXATION PROBABILITY

Under the assumption of weak selection, i.e. $\omega \ll 1$ we are able to approximate the probability of fixation $\varphi(p_0, z_0)$ of trait A. Note, that it only depends on the initial population size z_0 and the composition of the initial population characterized by p_0. The techniques used to derive an interpretable expression are first described in [11, 52] and refined for this specific setup in [19]. The interpretation relies on our ability to separate the evolutionary terms from the ecological variable z. In a two player system the condition for this separation to be valid conveniently coincides with a weak selection assumption, see [19]. However, in multiplayer games the separation of evolutionary and ecological scales becomes more complicated and harder to interpret. The conditions derived below are mainly on the location of the fixed points of the eco-evolutionary system. In the case of three players the equilibria are given by (Eq. (9) $= 0$)

$$\begin{aligned}p^*_{1,2} &= -\frac{\frac{1}{1+\omega b_1}-\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_1}+\frac{1}{1+\omega a_0}}{\frac{1}{1+\omega b_2}-\frac{2}{1+\omega b_1}+\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_2}+\frac{2}{1+\omega a_1}-\frac{1}{1+\omega a_0}}\\ &\pm\left(\left(\frac{\frac{1}{1+\omega b_1}-\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_1}+\frac{1}{1+\omega a_0}}{\frac{1}{1+\omega b_2}-\frac{2}{1+\omega b_1}+\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_2}+\frac{2}{1+\omega a_1}-\frac{1}{1+\omega a_0}}\right)^2\right.\\ &\left.+\frac{\frac{1}{1+\omega a_0}-\frac{1}{1+\omega b_0}}{\frac{1}{1+\omega b_2}-\frac{2}{1+\omega b_1}+\frac{1}{1+\omega b_0}-\frac{1}{1+\omega a_2}+\frac{2}{1+\omega a_1}-\frac{1}{1+\omega a_0}}\right)^{1/2}\end{aligned} \tag{12}$$

and the conditions necessary for the approximation read

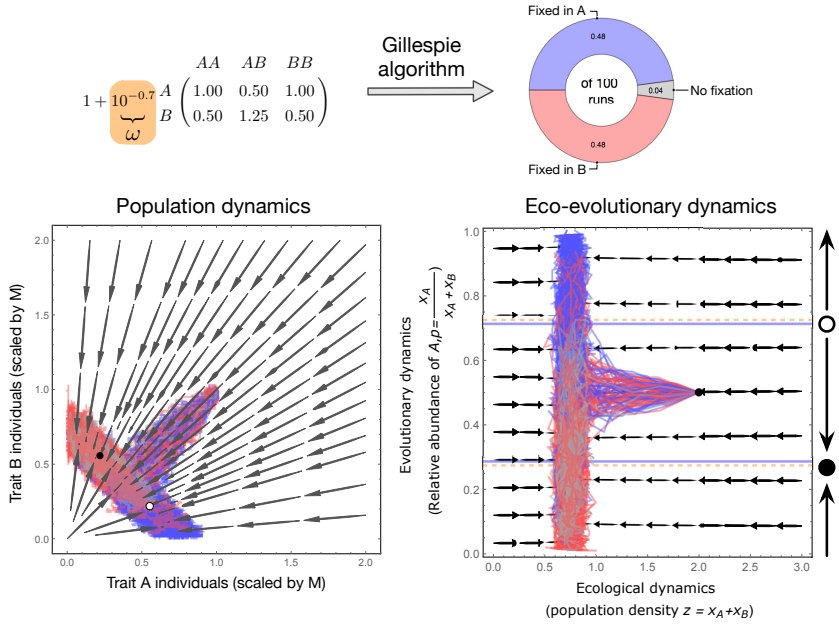

FIG. 1. **From an evolutionary game to population dynamics.** The interaction between two types A and B is represented by the payoff matrix as shown in the top left of the figure. We include weak selection via a linear payoff to fitness mapping such that the effective matrix is $1+\omega\times$ matrix. Then we compute the population dynamics of this interaction matrix for weak selection $\omega = 10^{-0.7}$. Weak selection as implemented here only makes sure that the average payoffs are close to each other. Weak selection as per population dynamics would mean that the payoff entries are close to each other. Thus as the dynamics comes close to neutrality the number of runs fixed in either type A or B is almost equal. From an eco-evolutionary point of view (bottom right), the population density rapidly converges to the ecological equilibrium and then the almost neutral dynamics proceeds in the evolutionary dimension of the fraction of type A individuals. The fixed points in the evolutionary dimension are denoted by the solid horizontal lines (given by Eq. (12)) which reduce to the dashed lines in case of weak selection as per Eq. (14).

(i) $\omega \ll 1$ (weak selection),

(ii) $p_1^* + p_2^* = 1$ and

(iii) $p_1^* p_2^* = \frac{1}{5}$.

The latter two conditions basically ensure that selection when looked at over the whole frequency space is negligible, i.e. the integral of the replicator dynamics over the frequency space is zero or at least close to it. Or more formally, conditions (ii) and (iii) yield

$$\int_0^1 \frac{dx}{dt} dx = \int_0^1 x(1-x)(\pi_A(x) - \pi_B(x))dx \approx 0, \quad (13)$$

where the equality is explained by equation (4). Note, that this is an extension of the two-player case where the ecological condition reduced to p^* being close to $1/2$, [19]. Appyling conditions (i)-(iii) we find a function $\psi(z)$ independent of p thus separating the effects of the initial population size and the initial frequency of type A individuals, cf. part 1.2 of SI for a detailed derivation. Furthermore, under condition (i) the fixed points simplify to

$$p^*_{1,2} \approx -\frac{b_0 - b_1 + a_1 - a_0}{2b_1 - b_2 - b_0 + a_2 - 2a_1 + a_0} \pm \left(\left(\frac{b_0 - b_1 + a_1 - a_0}{2b_1 - b_2 - b_0 + a_2 - 2a_1 + a_0} \right)^2 + \frac{b_0 - a_0}{2b_1 - b_2 - b_0 + a_2 - 2a_1 + a_0} \right)^{1/2}. \quad (14)$$

Finally, under assumptions (i)-(iii) we find the following expression for the fixation probability when dropping the subscript for the initial population size and fraction of type A individuals (details are stated in the SI part 1.2):

$$\varphi(p,z) \approx p + \omega p(1-p)(p-p_1^*)(p-p_2^*) \times (2b_1 - b_2 - b_0 + a_2 - 2a_1 + a_0)\,\psi(z), \quad (15)$$

where $\psi(z)$ satisfies

$$0 = z\left(z+\frac{1}{M}\right) + z\left(\beta-\delta-z^2\right)\psi'(z) - \frac{6}{zM}\left(\beta+\delta+z^2\right)\psi(z) + \frac{z}{2M}\left(\beta+\delta+2z^2\right)\psi''(z). \tag{16}$$

The approximation $\varphi(p,z)$ (Eq. (15)) shows a nice fit with simulation results obtained from Gillespie runs with parameters in the vicinity of the assumptions (i)-(iii), see Fig. 2.

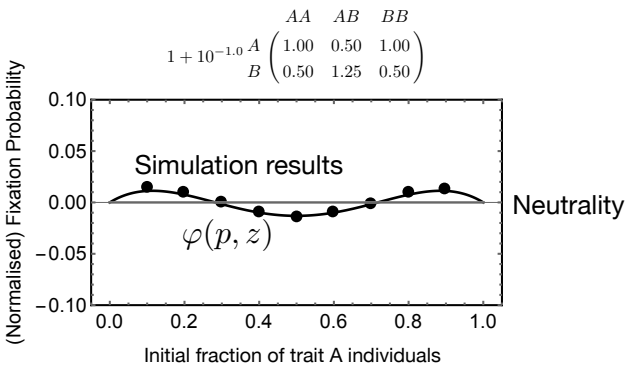

FIG. 2. **Fixation probability for a three player game under weak selection.** For a selection intensity of $\omega = 10^{-1.0}$ the three player game shows qualitatively three different regimes. When the initial frequency of type A individuals is low or high, the fixation probability is larger than neutral. For intermediate initial fraction of type A individuals the fixation probability is lower than neutral. The simulations were averaged over 10^5 runs where each was run until type A fixed or went extinct. Total initial population size was 200 with $M = 100, \beta = 0.6, \delta = 0.1$ which leads to $\psi \approx 5.85$. For the numerically calculation of ψ we refer to part 1.4 of SI.

A. Deviating from the assumptions

In the following we examine the impact of deviating from the conditions under which the theory holds. Therefore, as a "benchmark" model we choose the matrix

$$\begin{array}{c} \\ A \\ B \end{array}\begin{array}{c} \begin{array}{ccc} AA & AB & BB \end{array} \\ \begin{pmatrix} 1.00 & 0.50 & 1.00 \\ 0.50 & 1.25 & 0.50 \end{pmatrix} \end{array}. \tag{17}$$

The internal equilibria, according to equation (14), corresponding to this matrix are given by $p^*_{1,2} = \{0.7236, 0.2764\}$. For this combination of equilibrium values, we have $p^*_1 + p^*_2 = 1.0$ and $p^*_1 p^*_2 = 0.2$ which holds for $\omega \ll 1$ thus satisfying the required conditions.

Our aim is to calculate the fixation probability of type A when the population size is fluctuating. The theory developed is applicable under weak selection which results in a separation of the parameter p and z and leads to the technical conditions (i)-(iii) above. Our setting allows for two possible ways to deviate from the idea of weak selection. We can assume larger values of ω corresponding to a overall larger impact of the evolutionary fitness differences on the model. Thus, by increasing ω the fixation probability is less and less captured by our theoretical expectation, see x-axis of Fig. 3. Alternatively, weak selection is achieved when the payoff values of the matrix satisfy conditions (ii) and (iii) from above. Varying the values in the payoff matrix changes the intensity of selection but more importantly also alters the location of the fixed points (Eq. (12)). In this case the theory is able to capture qualitatively the direction of deviation from neutrality (Fig. 3 y-axis). We call these two deviations either evolutionary or ecological weak selection even though it is not possible to strictly disentangle the effects as they are intertwined via the calculation of the fixed points.

1. *Evolutionary weak selection - varying ω:*

Typically in evolutionary games, changing the intensity of selection does not affect the stability of the fixed points in the infinite population size limit. This only holds approximately in our considered eco-evolutionary model. Due to varying the influence of the underlying game on the competition parameters we slightly change the location of the fixed points in the system. Calculating fitness as $1+\omega(matrix)$, weak selection can be imposed when $\omega \ll 1$. In this case we get the theoretical optimum value for $p^*_1 p^*_2$ (Fig. 4 horizontal axis). Increasing the values of ω leads to a deviation of $p^*_1 p^*_2 = 0.2$ and thus the approximations become worse (Fig. 3). However, Figure 4 shows that we can recover this formally strict separation of p and z by slightly altering the payoff matrix such that even for higher values of ω the predicted fixation probability fits well to the observed values obtained by simulations (for the set of results for value 1 on the y-axis in Fig. 4).

2. *Ecological weak selection - varying the payoffs:*

When we alter the payoffs, we change the location of the equilibria drastically which can be seen as changing the ecological output of the model, i.e. the carrying capacities of the two strains. For instance, in the monomorphic states these are given by $(\beta+\delta)(1+\omega a_2)M$ and $(\beta+\delta)(1+\omega b_0)M$ for type A and B, respectively. By fixing ω this indeed only affects the ecological dynamics since the impact itself from the evolutionary process it determined by ω and thus constant. Hence, to implement weak selection as per closeness to the ecological conditions, i.e. assumptions (ii) and (iii) from above, we change the payoff entries such that $p^*_1 + p^*_2 = 1$ whereas $p^*_1 p^*_2 \neq 0.2$ (Fig. 4 vertical axis).

Overall, as can be seen in Figure 4, increasing ω has a larger impact on the goodness of our predictions than varying the payoff values. This is also intuitive since ω is

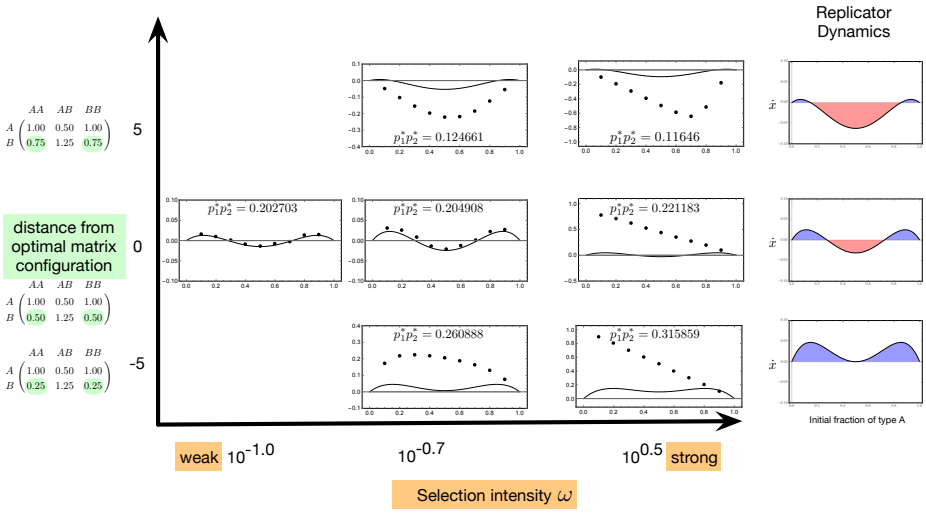

FIG. 3. **Weak selection(s).** Typically in evolutionary games, scaling the payoffs (by the selection intensity) does not change the deterministic dynamics. Thus across the x-axis the replicator dynamics Eq. (4) can be visualized, see right column. A positive value (blue) determines that type A is favored over type B and vice versa for negative values (red). In a stochastic setting in general and especially in a model with fluctuating population size however, the intensity of selection plays a major role (x-axis). For weaker selection, the magnitudes of the positive and negative values are extremely small, tending towards neutrality. Taking population dynamics into account, another way of introducing weak selection is when the payoff entries are close to our "benchmark" model (y-axis). If we increase the difference between the payoffs, we change the dynamics of the game and the fixed points of the (ecological) system, thus also affecting the regions where the theory is applicable ($p_1^* p_2^* = 0.2$).

the parameter determining the strength of all the selection effects. When large enough, the concrete payoffs can play a role and thus have an impact on the system. Hence, one should rather think of a nested selection characterization (first evolutionary impact, then ecological variance) rather than two distinct variables acting on two different scales.

IV. POPULATION DYNAMICS OF COLLECTIVE ACTION

We now extend the analytical calculations to a particular example of multiplayer game. The evolutionary dynamics of collective action is an extremely well studied topic in the social sciences [68, 69]. How social structures overcome the tragedy of the common is a recurring theme in this field [40, 82]. The tragedy of the commons is a case where the defectors benefit at a cost to the cooperators. However the tragedy is relaxed if a part of the benefit can be recovered by the acting cooperator. This negative frequency dependence is the essence of the snowdrift game [20]. It has been proposed that the snowdrift game might better reflect human social dilemmas than the otherwise famous Prisoners Dilemma [51]. Also biological observations like phenotypic heterogeneity, a well established phenomena in microbes, can be a result of snowdrift like, negative frequency dynamics [44].

A. (Multiplayer) Snowdrift game

The metaphor (for d players) states that if d drivers meet at an intersection where a snowdrift has occurred, if everyone helps out in clearing it then all can go home (benefit $b > c$) while paying a cost of c/d. If only k of the drivers decide to shovel then they get $b - c/k$ while the defectors enjoy the warmth of the car and get home, obtaining b. We are interested in further realistic cases where a certain threshold number of cooperators are necessary to get the job done [84]. Thus imagine that it is not a snowdrift but a large tree has fallen across the road, then a certain number of individuals are necessary to pick up the heavy trunk. Hence if θ is the threshold number of cooperators necessary to generate the benefit, then for $k < \theta$ the efforts of the cooperators go waste resulting in $0 - c/\theta$ (assuming that each cooperator does the best it can). The defectors also get nothing 0. Once the number of cooperators is equal to or above the threshold, then the trunk is moved from the road, and everyone can go home. The cooperators having paid the cost get $b - c/k$ while the defectors get b. If the number of other cooperators is $\theta - 1$ then it is profitable to be a cooperator, fill the quorum, and reap the benefit $b - c/\theta$ as opposed to defect and end up with nothing. This concept of threshold public goods games is applicable not just in humans but in other species as well [4, 7]. For big game hunting or territory defence a certain number of individuals are necessary. If the number of cooperators is not met then the quarry cannot be captured [85]. In microbes quorum sensing, or simply density dependent effects, play a

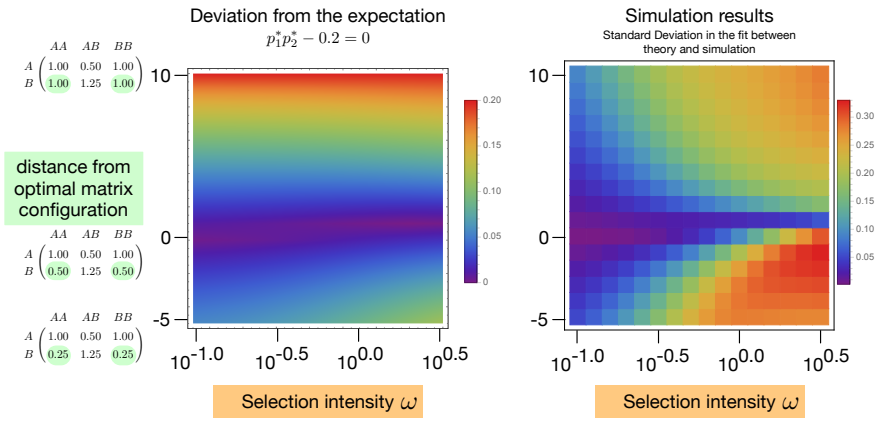

FIG. 4. **Disentangling weak selection.** As we change the payoff entries in steps of $0.05 \times y$ we are changing the fixed points such that $p_1^* + p_2^* = 1$ still holds but the condition of $p_1^* p_2^* = 0.2$ is not necessarily met (y-axis). In contrast we can modify ω which keeps the fixed points of the replicator dynamics constant while changing the impact of the game and thus the interactions strength between the strategies (x-axis). While in evolutionary games ω has been termed as the evolutionary selection intensity, we can interpret the distance as the ecological selection intensity, since it directly affects the carrying capacity of the two types. As we change these two selection intensities, the expected theoretical performance is illustrated in the left panel as the magnitude by which the condition $p_1^* p_2^* = 0.2$ is violated. Gillespie simulations, starting at different initial fraction of A individuals $(0.1, 0.2, \ldots, 0.9)$ were performed and the fixation probabilities were calculated over 10^5 realizations. The total initial population size was set to 200 with $M = 100, \beta = 0.6, \delta = 0.1$ resulting in $\psi \approx 5.85$. We calculate the mean standard deviation between the simulation results and the expectation from Eq. (15). The right panel is a histogram of such deviations from the expectation for different ω and different matrix configurations. We see that the deviation is the least where the violation of $p_1^* p_2^* = 0.2$ is the least. The discrepancy that we see for high ω and but negative y-axis values can be attributed to ecological shifts of the equilibria, namely the carrying capacities. In the region of the discrepancy, the theory estimates the fixation probability still in the shape of the replicator dynamics, which is a gross underestimate (for example $\omega = 10^{0.5}$ and distance $= 0$ in Fig. 3.) As the distance decreases further, the replicator dynamics and the fixation probability both, increase above neutrality, reducing the standard deviation from the simulation results ($\omega = 10^{0.5}$ and distance $= -5$) . No such discrepancy exists for positive y values since the simulations are progressively overestimated while maintaining the qualitative picture ($\omega = 10^{0.5}$ and distance $= 5$) .

critical role in the so called social behaviour evolution [56]. As follows from the concept of multiplayer games, a necessary condition for observing n fixed points in the interior of the replicator simplex [34, 43] is the n changes in the sign of the payoff difference.

Excluding finite populations precludes the possibility of ecologically relevant events such as extinctions. Population dynamics in social dilemmas have been considered before via deterministic dynamics [32, 42]. In a stochastic system as ours, the fixed points p_i^* for a multiplayer game in the eco-evolutionary space $(p-z)$ can be calculated in a similar way as in the three player game from above, see also Eq. (A.7) in the SI. In general for any $d-$player game the fixation probability can then be approximated by (details in part 1.3 of SI)

$$\varphi(p,z) \approx p + \omega p(1-p)(-1)^{d-1} \times \left(\sum_{i=0}^{d-1} (-1)^i \binom{d-1}{i} (a_i - b_i) \right) \left(\prod_{i=1}^{d-1} (p - p_i^*) \right) \psi(z) \tag{18}$$

where $\psi(z)$ satisfies the following equation:

$$\begin{aligned} 0 = {} & z^{d-2} \left(z + \frac{1}{M} \right) + z \left(\beta - \delta - z^{d-1} \right) \psi'(z) \\ & + \frac{1}{2zM} \left(\beta + \delta + z^{d-1} \right) \chi(p, p_1^*, ..., p_{d-1}^*) \psi(z) \\ & + \frac{z}{2M} \left(\beta + \delta + 2z^{d-1} \right) \psi''(z). \end{aligned}$$

The term $\chi(p, p_1^*, ..., p_{d-1}^*)$, explicitly given in Eq.(A.8) in the SI, needs to be independent of p for the theory to apply. However, to investigate the concrete conditions for it to be so is beyond the scope of this study. We note that Eq. (18) reduces to the already obtained fixation probabilities in the cases $d = 2$, see [19, Theorem 1], and $d = 3$, see Eq. (15).

While the main features of the fixation probability are the same as in the cases with less players (intersections with the neutral fixation probability at internal equilibria, qualitative agreement with the replicator dynamics, i.e. $\varphi(p,z) - p > 0$ when $\frac{dx}{dt}\big|_{x=p} > 0$ and vice versa - note however that the fixed points are not exactly the same), there is also a notable exception. Doing the general approximation it becomes apparent that not only the internal (and meaningful) fixed points determine the evolutionary success but so do the other (potentially imaginary) solutions of the corresponding

deterministic model.

Given all these uncertainties, as well as the fixed points not satisfying the required conditions perfectly, the general formula in equation (18) describes the qualitative behaviour of the fixation probability of the system, reflecting the replicator dynamics Fig. 5.

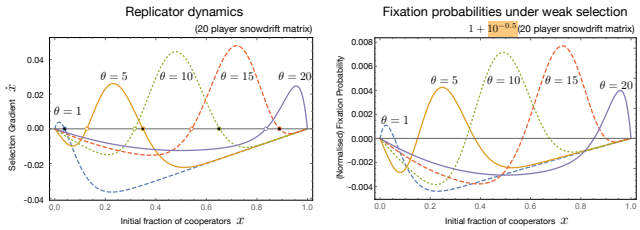

FIG. 5. **Eco-evolutionary fixation probabilities in a snowdrift game.** The graph (on the left) shows the evolutionary dynamics as per the replicator equation for a 20 player game with different number of threshold snowdrift game scenarios ($\theta = 1, 5, 10, 15$ and 20) and benefit $b = 1.5$ and a cost of $c = 1$. No benefit is generated if the number of cooperators is less than θ. If the number of cooperators is $\theta - 1$ then it is preferable to switch to the cooperate trait. For each case we calculate the corresponding fixation probability using Eq. (18) (right panel) for $M = 100, \beta = 0.6, \delta = 0.1$, initial total population size of 200, weak selection $\omega = 10^{-0.5}$ and $\psi \approx 0.53$. Comparing the structure of the fixation probability we see that it follows the gradient of selection qualitatively. Thus the replicator dynamics is a good approximation of the fixation probability in populations with a fluctuating size under weak selection.

To precisely determine if the approximation is valid we employed the Gillespie algorithm to simulate the stochastic population dynamics. As above, we consider a snowdrift game with $d = 20$ players. To construct a stochastic version of this we need to consider 44 reactions (4 made up of birth and death processes for the two types and the rest as competition terms coming from the payoff matrix). As already observed in [84], varying the threshold number of necessary cooperators (θ) we change the location of the fixed points in the replicator dynamics, see Fig. 5. Alternatively we fix the threshold $\theta = 10$, and starting with equal number of cooperators and defectors, we calculate the fixation probability while varying ω, Fig. 6.

For weak selection the dynamics is essentially neutral with the trajectories randomly fixing in either $allC$ or $allD$. However as selection increases, the distance between the two fixed points starts to matter. For example, for $\omega = 10^{0.1}$ the fixed points within the relevant space are $p^*_{1,2} = \{0.405328, 0.708458\}$. Thus it is closer for the trajectories to go from p^*_1 to the stable fixed point p^*_2 which is closer to $allC$ than to $allD$. Interestingly, drift may be an explanation for the results with strong selection dynamics in this multiplayer case. Take for instance the last data point, the case $\omega = 10^{0.5}$, where the fixed points are approximately $p^*_{1,2} = \{0.509443, 0.732788\}$. Then considering that for our initial population we have $p = 0.5$ we can argue that in approximately one half of the cases the population drops below that value, ending up in fixation of the resident. This is an underestimation since under strong selection starting below p^*_1 all trajectories should end up in $p = 0$. However, due to the fluctuating population size the population is decreasing at first and due to random drift p might be larger than p^*_1 when hitting the ecological equilibrium such that in these cases p tends quickly to p^*_2 which in our approximation corresponds to the other half of the cases. Once, the population is close to this value due to random drift the population eventually drops under p^*_1 (thus the resident reaches fixation) or the mutant strain becomes fixed in the population. This heuristic reasoning is captured by hitting probabilities of a Brownian motion or a random walk. Thus, we have:

$$\varphi(0.5, z) = 1 - \underbrace{0.5}_{\text{immediate fixation of the resident}} - \underbrace{0.5 \times \frac{1 - 0.73}{1 - 0.51}}_{\text{fixation of the resident after reaching } p^*_2} \approx 0.225.$$

This value is approximately the observed frequency of trajectories where the mutant reaches fixation for large ω in Figure 6. The difference emerges from our assumption that half of the trajectories immediately end up in $p = 0$. To further validate this reasoning we have performed additional simulations starting from the coexistence state. The above reasoning indeed gives a very accurate approximation of the fixation probability in case of strong selection, see part 1.5 of SI.

V. DISCUSSION AND CONCLUSION

Experimental evolution, which has boomed since the seminal results of [53] relies on serial transfers. The population is subjected to repeated bouts of population size bottlenecks. The approximation of extinction of a beneficial trait in this situation has been studied in [92]. However, an eco-evolutionary approach, where stochastic fluctuations in population size are included and the carrying capacity is chosen to be very low ($M \sim 100$), is a viable alternative.

Previous studies, beautifully combining theoretical and experimental approaches in microbes have shown that how often populations undergo bottleneck events as well as their actual size can determine the eco-evolutionary trajectory [16, 17, 61]. Bottleneck events are not just important for the evolution of fixation of traits in a microbial system itself but can act as a mechanism of transition from one level of organization to the next. For example, the periodic single cell bottleneck event ($M \sim 10$) was a necessary condition for the evolution of multicellularity [38].

In co-evolutionary systems too, populations are repeatedly subjected to changes in population sizes. While typical host-parasite systems undergo periodic cycles, the population sizes are actively regulated by the antagonist. Early on, it was shown how the population size of the azuki bean weevil was affected by its parasitoid wasp [90]. However the

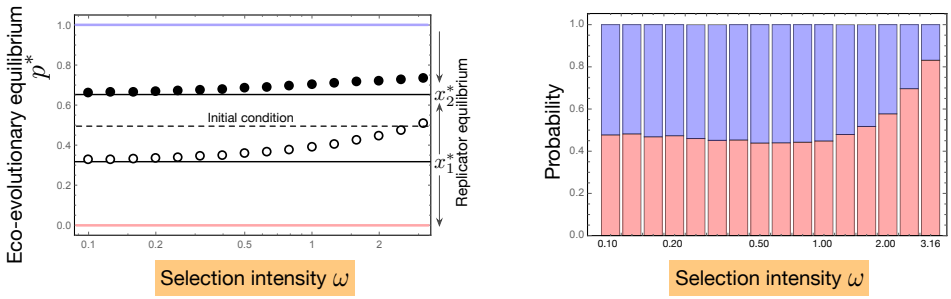

FIG. 6. **Snowdrift under selection.** The snowdrift as discussed in the main text can have two internal equilibria depending on the value of θ. For $\theta = 10$ we have two internal equilibria $(x^*_{1,2})$. In a scenario with changing population sizes, the intensity of selection drives the population to fixation in all C (blue, $p^* = 1$) or all D (red, $p^* = 0$). For weak selection the effect of the selection gradient is minimal and drift plays a dominant role and hence the fixation probabilities are close to neutral. As selection increases, the stable fixed point (filled circle) , close to all C, attracts and holds most of the trajectories. Whenever drift is possible it takes the population to the closest monomorphic state, i.e. of all C. However for extremely strong selection the stable point is strongly attracting and the only escape is again explained by random drift. Either the population fixes in the all C state or it overcomes the unstable point (empty circle) and then selection driving the population to all D. To grasp the exact intensity of selection where the switch takes place, we have performed 10^5 Gillespie simulations for $M = 100$ and a 20 player snowdrift game with an initial population of 200, $b = 1.5$, $c = 1$, $\beta = 0.6$, $\delta = 0.1$, $\psi \approx 0.53$ and $1 + \omega(matrix)$ mapping for different intensities of selection. The bar charts show the probability of a trajectory fixing in either all C (blue) or all D (red). All simulations were executed until one of the types fixed. The selection intensity ranges as $\omega = 10^{-1.0}, \ldots, 10^{0.5}$.

drastic population size change can affect other important evolutionary properties such as genetics diversity as well as the effect of evolutionary selection on the traits [46, 70, 76].

Extending on [19] we have derived the fixation probability in a stochastic Lotka-Volterra-model including higher order dynamics. These higher order interactions can be interpreted in terms of multiplayer games from evolutionary game theory. The model explicitly deals with finite and especially fluctuating population sizes which are important in the context of co-evolution [33, 73, 83, 97]. While constant or infinite population size is captured by birth-death processes and the replicator equation we apply stochastic diffusion theory to tackle the fluctuating size complication.

Going from two player to three player interactions might seem like a minor extension but this work shows that as often in many systems, two body interacts are a special case. From linkage issues when moving from diseases with single locus determinants to complex traits to change in dimensionality in predatory prey dynamics [79, 80]. Extending the conditions required for the theory from two player games [19] to three players we see a general outline of the assumption. While two player games required the internal fixed point to be at $p^* = 0.5$, the conditions for higher order games clarify that in fact the requirement is that of the fitness of the strategies over the complete frequency space need to be balanced. For instance, conditions (ii) and (iii), i.e. $p_1^* + p_2^* = 1$ and $p_1^* p_2^* = 0.2$, ensure that the selective advantage in the evolutionary dynamics of the replicator equation vanishes when considered on the whole frequency space. To be more precise:

$$\int_0^1 \frac{dx}{dt}\, dx = \int_0^1 x(1-x)(\pi_A(x) - \pi_B(x)) = 0,$$

see also equation (13). This is an interesting interplay between the ecological parameter of the model. The linkage between the deterministic equilibria of Lotka-Volterra dynamics and the trait frequency dynamics comes about when the pure birth-death processes are neglected. Furthermore, as we have seen in Figures 3 and 4 the intertwined nature of ecological and evolutionary effects in our model cannot be entirely separated. Even for strong selection the fit of our prediction is still surprisingly good as long as the eco-evolutionary equilibria satisfy the conditions affecting the ecological scale. Deviating from the ecological conditions has a strong effect on our predictions. The reason being that by increasing selection intensity ω the dynamics do not converge to a stable ecological trajectory. Equilibria are displaced from the optimal values in the z space. Hence, changing the evolutionary selection intensity has an effect on the ecological equilibrium as well.

Besides providing a generalization of the fixation probability for multiplayer games, we apply our analysis in context of social evolution. In particular to the situations captured by the snowdrift game. For a game with a large number of players there can be multiple internal equilibria [43]. Such social dilemmas, particularly the threshold version of social dilemmas, resonate with the concept of quorum sensing in microbes.

Increasingly used as models of social evolution, the fixation of traits in microbes is then of crucial importance. Clearly in microbes, assuming that they play a two player game, i.e. the interactions are linear is an assumption which can be easily violated as in general biological systems [81]. However for multiplayer games, we show that it is not possible to undertake a quantitative analysis of the fixation probability since (we hypothesize that) $d - 1$ different conditions would need to be met for a d player game. Knowing

the replicator dynamics can already allow us to estimate the qualitative structure of the fixation probability (Fig. 5) when including Lotka-Volterra type of ecological interactions. Excluding Lotka-Volterra dynamics, it would not be surprising if we recover the replicator-like behaviour for weak selection. The dynamics of the fixation probability for fixed population sizes would then be expected to follow the shape of the deterministic dynamics as well.

This is however not a general rule as other studies of infinite populations show distinctly opposite qualitative behavior when compared to the deterministic dynamics. A well known example of this phenomena is the one-third rule where a deterministically unfavorable trait can have a larger than neutral fixation probability [67].

In conclusion, we have brought together the concept of weak selection from population genetics, multiplayer games from evolutionary game theory and populations dynamics from theoretical ecology. By this synthesis of fields we have added new insight on the dynamics of fixation under demographic fluctuations by extending the previously studied competitive Lotka-Volterra model now including higher order interactions between traits. We find that by increasing the complexity of the model, the separation of ecological and evolutionary processes becomes more and more difficult. The emergence of such complexity in the intertwined nature of eco-evolutionary dynamics is a natural outcome of biological processes derived from mechanistic first principles [21].

ACKNOWLEDGEMENTS

The authors thank Christoph Hauert for helpful discussion. Funding from the Max Planck Society is greatly appreciated.

[1] Ackermann, M., B. Stecher, N. E. Freed, P. Songhet, W.-D. Hardt, and M. Doebeli, 2008 Self-destructive cooperation mediated by phenotypic noise. Nature **454**: 987–990.

[2] Altrock, P. M. and A. Traulsen, 2009a Deterministic evolutionary game dynamics in finite populations. Physical Review E **80**: 011909.

[3] Altrock, P. M. and A. Traulsen, 2009b Fixation times in evolutionary games under weak selection. New Journal of Physics **11**: 013012.

[4] Alvard, M. S. and D. A. Nolin, 2002 Rousseau's whale hunt? coordination among big-game hunters. Current Anthropolpgy **43**: 533–559.

[5] Anderson, D. and T. G. Kurtz, 2015 *Stochastic Analysis of Biochemical Systems*. Springer.

[6] Antal, T. and I. Scheuring, 2006 Fixation of strategies for an evolutionary game in finite populations. Bulletin of Mathematical Biology **68**: 1923–1944.

[7] Apicella, C. L., F. W. Marlowe, J. H. Fowler, and N. A. Christakis, 2012 Social networks and cooperation in hunter-gatherers. Nature **481**: 497–501.

[8] Ashcroft, P., C. Smith, M. Garrod, and T. Galla, 2017 Effects of population growth on the success of invading mutants. Journal of Theoretical Biology **420**: 232–240.

[9] Black, A. J. and A. J. McKane, 2012 Stochastic formulation of ecological models and their applications. Trends in Ecology and Evolution **27**: 337–345.

[10] Broom, M., 2003 The use of multiplayer game theory in the modeling of biological populations. Comments on Theoretical Biology **8**: 103–123.

[11] Champagnat, N. and A. Lambert, 2007 Evolution of discrete populations and the canonical diffusion of adaptive dynamics. The Annals of Applied Probability **17**: 102–155.

[12] Chuang, J. S., O. Rivoire, and S. S. Leibler, 2010 Cooperation and Hamilton's rule in a simple synthetic microbial system. Molecular systems biology **6**: 398.

[13] Connor, R. C., 2010 Cooperation beyond the dyad: on simple models and a complex society. Philosophical Transactions of the Royal Society B **365**: 2687–2697.

[14] Constable, G. and A. McKane, 2015 Models of genetic drift as limiting forms of the lotka-volterra competition model. Physical Review Letters **114**: 038101.

[15] Constable, G. W. A., T. Rogers, A. J. McKane, and C. E. Tarnita, 2016 Demographic noise can reverse the direction of deterministic selection. Proceedings of the National Academy of Sciences **113**: E4745–E4754.

[16] Cremer, J., A. Melbinger, and E. Frey, 2011 Evolutionary and population dynamics: a coupled approach. Physical Review E **84**: 051921.

[17] Cremer, J., A. Melbinger, and E. Frey, 2012 Growth dynamics and the evolution of cooperation in microbial populations. Scientific Reports **2**.

[18] Crow, J. F. and M. Kimura, 1970 *An Introduction to Population Genetics Theory*. Harper and Row, New York.

[19] Czuppon, P. and A. Traulsen, 2017 Fixation probabilities in populations under demographic fluctuations. arXiv.org p. arXiv:1708.09665.

[20] Doebeli, M., C. Hauert, and T. Killingback, 2004 The evolutionary origin of cooperators and defectors. Science **306**: 859–62.

[21] Doebeli, M., Y. Ispolatov, and B. Simon, 2017 Towards a mechanistic foundation of evolutionary theory. eLife **6**: e23804.

[22] Drescher, K., C. D. Nadell, H. A. Stone, N. S. Wingreen, and B. L. Bassler, 2014 Solutions to the Public Goods Dilemma in Bacterial Biofilms. Current Biology **24**: 50–55.

[23] Ewens, W. J., 1967 The probability of survival of a new mutant in a fluctuating enviroment. Heredity **22**: 438–443.

[24] Fisher, R. A., 1922 On the dominance ratio. Proceedings of the Royal Society of Edinburgh **42**: 321–341.

[25] Fogel, G., P. Andrews, and D. Fogel, 1998 On the instability of evolutionary stable strategies in small populations. Ecological Modelling **109**: 283–294.

[26] Frickel, J., M. Sieber, and L. Becks, 2016 Eco-evolutionary dynamics in a coevolving host–virus system. Ecology Letters **19**: 450–459.

[27] Fudenberg, D. and C. Harris, 1992 Evolutionary dynamics with aggregate shocks. Journal of Economic Theory **57**: 420–441.

[28] García, J. and A. Traulsen, 2012 The structure of mutations and the evolution of cooperation. PLoS One **7**: e35287.

[29] Gardiner, C. W., 2004 *Handbook of Stochastic Methods*. Springer, NY, third edition.

[30] Gillespie, D., 1976 A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. Journal of Computational Physics **22**: 403–434.

[31] Goel, N. and N. Richter-Dyn, 1974 *Stochastic Models in Biology*. Academic Press, New York.

[32] Gokhale, C. S. and C. Hauert, 2016 Eco-evolutionary dynamics of social dilemmas. Theoretical Population Biology **111**: 28–42.

[33] Gokhale, C. S., A. Papkou, A. Traulsen, and H. Schulenburg, 2013 Lotka-Volterra dynamics kills the Red Queen: population size fluctuations and associated stochasticity dramatically change host-parasite coevolution. BMC Evolutionary Biology **13**: 254.

[34] Gokhale, C. S. and A. Traulsen, 2010 Evolutionary games in the multiverse. Proceedings of the National Academy of Sciences USA **107**: 5500–5504.

[35] Gore, J., H. Youk, and A. van Oudenaarden, 2009 Snowdrift game dynamics and facultative cheating in yeast. Nature **459**: 253–256.

[36] Haafke, J., M. Abou Chakra, and L. Becks, 2016 Eco-evolutionary feedback promotes red queen dynamics and selects for sex in predator populations. Evolution **70**: 641–652.

[37] Haldane, J. B. S., 1927 A mathematical theory of natural and artificial selection. v. selection and mutation. Proceedings of the Cambridge Philosophical Society **23**: 838–844.

[38] Hammerschmidt, K., C. J. Rose, B. Kerr, and P. B. Rainey, 2014 Life cycles, fitness decoupling and the evolution of multicellularity. Nature **515**: 75–79.

[39] Han, T. A., A. Traulsen, and C. S. Gokhale, 2012 On equilibrium properties of evolutionary multi-player games with random payoff matrices. Theoretical Population Biology **81**: 264–72.

[40] Hardin, G., 1968 The tragedy of the commons. Science **162**: 1243–1248.

[41] Hashimoto, K. and K. Aihara, 2009 Fixation probabilities in evolutionary game dynamics with a two-strategy game in finite diploid populations. Journal of Theoretical Biology **258**.

[42] Hauert, C., M. Holmes, and M. Doebeli, 2006a Evolutionary games and population dynamics: maintenance of cooperation in public goods games. Proceedings of the Royal Society B **273**: 2565–2570.

[43] Hauert, C., F. Michor, M. A. Nowak, and M. Doebeli, 2006b Synergy and discounting of cooperation in social dilemmas. Journal of Theoretical Biology **239**: 195–202.

[44] Healey, D., K. Axelrod, and J. Gore, 2016 Negative frequency-dependent interactions can underlie phenotypic heterogeneity in a clonal microbial population. Molecular systems biology **12**.

[45] Hofbauer, J. and K. Sigmund, 1998 *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, UK.

[46] Hoffman, J. I., F. Simpson, P. David, J. M. Rijks, T. Kuiken, M. A. S. Thorne, R. C. Lacy, and K. K. Dasmahapatra, 2014 High-throughput sequencing reveals inbreeding depression in a natural population. Proceedings of the National Academy of Sciences of the United States of America **111**: 3775–3780.

[47] Huang, W., C. Hauert, and A. Traulsen, 2015 Stochastic game dynamics under demographic fluctuations. Proceedings of the National Academy of Sciences of the United States of America **112**: 9064–9069.

[48] Kimura, M., 1962 On the probability of fixation of mutant genes in a population. Genetics **47**: 713–719.

[49] Kimura, M. and T. Ohta, 1974 Probability of gene fixation in an expanding finite population. Proceedings of the National Academy of Sciences USA **71**: 3377–3379.

[50] Koth, M. and K. Sigmund, 1987 Gradients for the evolution of bimatrix games. Journal of Mathematical Biology **25**: 623–635.

[51] Kummerli, R., C. Colliard, N. Fiechter, B. Petitpierre, F. Russier, and L. Keller, 2007 Human cooperation in social dilemmas: comparing the snowdrift game with the prisoner's dilemma. Proceedings of the Royal Society B **274**: 2965–2970.

[52] Lambert, A., 2006 Probability of fixation under weak selection: a branching process unifying approach. Theoretical population biology **69**: 419–441.

[53] Lenski, R. E., M. R. Rose, S. C. Simpson, and S. C. Tadler, 1991 Long-term experimental evolution in escherichia coli. I. adaptation and divergence during 2,000 generations. The American Naturalist **138**: 1315–1341.

[54] Lessard, S., 2011 On the robustness of the extension of the one-third law of evolution to the multi-player game. Dynamic Games and Applications **1**: 408–418.

[55] Lewontin, R. C., 1961 Evolution and the theory of games. Journal of Theoretical Biology **1**: 382–403.

[56] Lyon, P., 2007 From quorum to cooperation: lessons from bacterial sociality for evolutionary theory. Studies in History and Philosophy of Biological and Biomedical Sciences **38**: 820–833.

[57] Maynard Smith, J., 1986 Evolutionary game theory. Physica D: Nonlinear Phenomena **22**: 43–49.

[58] Maynard Smith, J. and G. R. Price, 1973 The logic of animal conflict. Nature **246**: 15–18.

[59] McAvoy, A., N. Fraiman, C. Hauert, J. Wakeley, and M. A. Nowak, 2017 Public goods games in populations with fluctuating size. arXiv.org p. arXiv:1709.03630.

[60] McKane, A. J. and T. J. Newman, 2004 Stochastic models in population biology and their deterministic analogs. Physical Review E **70**: 19.

[61] Melbinger, A., J. Cremer, and E. Frey, 2010 Evolutionary game theory in growing populations. Physical Review Letters **105**: 178101.

[62] Nash, J., 1951 Non-cooperative games. Annals of Mathematics **54**: 286–299.

[63] Nielsen, R. and M. Slatkin, 2013 *An Introduction to Population Genetics: Theory and Applications*. Oxford University Press, first edition.

[64] Nowak, M. A., 2006 *Evolutionary dynamics*. Harvard University Press, Cambridge MA.

[65] Nowak, M. A., A. Sasaki, C. Taylor, and D. Fudenberg, 2004 Emergence of cooperation and evolutionary stability in finite populations. Nature **428**: 646–650.

[66] Nowak, M. A. and K. Sigmund, 2004 Evolutionary dynamics of biological games. Science **303**: 793–799.

[67] Ohtsuki, H., P. Bordalo, and M. A. Nowak, 2007 The one-third law of evolutionary dynamics. Journal of Theoretical Biology **249**: 289–295.

[68] Ostrom, E., 1990 *Governing the commons: The evolution of institutions for collective action*. Cambridge Univ. Press.

[69] Ostrom, E., J. Burger, C. B. Field, R. B. Norgaard, and D. Policansky, 1999 Revisiting the commons: Local lessons, global challenges. Science **284**: 278–282.

[70] Otto, S. P. and M. C. Whitlock, 1997 The probability of

fixation in populations of changing size. Genetics **146**: 723–733.

[71] Pacheco, J. M., F. C. Santos, and D. Dingli, 2014 The ecology of cancer from an evolutionary game theory perspective. Interface Focus **4**: 20140019–20140019.

[72] Papkou, A., C. S. Gokhale, A. Traulsen, and H. Schulenburg, 2016 Host-parasite coevolution: why changing population size matters. Zoology **119**: 330–338.

[73] Parker, M. and A. Kamenev, 2009 Extinction in the lotka-volterra model. Phys. Rev. E **80**: 021129.

[74] Parsons, T. L. and C. Quince, 2007a Fixation in haploid populations exhibiting density dependence i: the non-neutral case. Theoretical population biology **72**: 121–135.

[75] Parsons, T. L. and C. Quince, 2007b Fixation in haploid populations exhibiting density dependence ii: The quasi-neutral case. Theoretical population biology **72**: 468–479.

[76] Parsons, T. L., C. Quince, and J. B. Plotkin, 2010 Some consequences of demographic stochasticity in population genetics. Genetics **185**: 1345–1354.

[77] Rowe, G. W., 1988 To each genotype a separate strategy - a dynamic game theory model of a general diploid system. Journal of Theoretical Biology **134**: 89–101.

[78] Sanchez, A. and J. Gore, 2013 Feedback between Population and Evolutionary Dynamics Determines the Fate of Social Microbial Populations. PLoS Biology **11**: e1001547.

[79] Schenk, H., A. Traulsen, and C. S. Gokhale, 2017 Chaotic provinces in the kingdom of the red queen. Journal of Theoretical Biology **in press**.

[80] Schork, N. J., M. Boehnke, J. D. Terwilliger, and J. Ott, 1993 Two-trait-locus linkage analysis: a powerful strategy for mapping complex genetic traits. American journal of human genetics **53**: 1127–1136.

[81] Shirakihara, K. and S. Tanaka, 1978 Two fish species competition model with nonlinear interactions and equilibrium catches. Researches on Population Ecology **20**: 123–140.

[82] Skyrms, B., 2003 *The Stag-Hunt Game and the Evolution of Social Structure*. Cambridge University Press, Cambridge.

[83] Song, Y., C. S. Gokhale, A. Papkou, H. Schulenburg, and A. Traulsen, 2015 Host-parasite coevolution in populations of constant and variable size. BMC Evolutionary Biology **15**: 212.

[84] Souza, M. O., J. M. Pacheco, and F. C. Santos, 2009 Evolution of cooperation under n-person snowdrift games. Journal of Theoretical Biology **260**: 581–588.

[85] Stander, P. E., 1992 Cooperative hunting in lions: the role of the individual. Behavioral Ecology and Sociobiology **29**: 445–454.

[86] Traulsen, A., J. C. Claussen, and C. Hauert, 2006a Coevolutionary dynamics in large, but finite populations. Physical Review E **74**: 011901.

[87] Traulsen, A. and C. Hauert, 2009 Stochastic evolutionary game dynamics. In *Reviews of Nonlinear Dynamics and Complexity*, edited by H. G. Schuster, volume II, pp. 25–61, Wiley-VCH, Weinheim.

[88] Traulsen, A., J. M. Pacheco, and L. A. Imhof, 2006b Stochasticity and evolutionary stability. Physical Review E **74**: 021905.

[89] Uecker, H. and J. Hermisson, 2011 On the Fixation Process of a Beneficial Mutation in a Variable Environment. Genetics **188**: 915–930.

[90] Utida, S., 1957 Cyclic fluctuations of population density intrinsic to the host-parasite system. Ecology **38**: 442–449.

[91] van Kampen, N. G., 1997 *Stochastic Processes in Physics and Chemistry*. Elsevier, Amsterdam, second edition.

[92] Wahl, L. M. and P. J. Gerrish, 2001 The probability that beneficial mutations are lost in populations with periodic bottlenecks. Evolution **55**: 2606–2610.

[93] Whiteley, M., D. S.P., and G. E.P., 2017 Progress in and promise of bacterial quorum sensing research. Nature **551**: 313–320.

[94] Wright, S., 1931 Evolution in Mendelian populations. Genetics **16**: 97–159.

[95] Wu, A. and D. Ross, 2016 Evolutionary Game between Commensal and Pathogenic Microbes in Intestinal Microbiota. Games **7**: 26–10.

[96] Yang, Q., T. Rogers, and J. H. Dawes, 2017 Demographic noise slows down cycles of dominance. Journal of Theoretical Biology **432**: 157 – 168.

[97] Zeeman, M. L., 1995 Extinction in competitive Lotka-Volterra systems. Proceedings of the American Mathematical Society **123**: 87–96.

Supplementary Information: Disentangling eco-evolutionary effects on trait fixation

Peter Czuppon[1] & Chaitanya S. Gokhale[1]

[1]Max Planck Institute for Evolutionary Biology,

August-Thienemann-Straße 2, 24306 Plön, Germany,

1 Appendix

1.1 Deriving the diffusion approximation

Here we derive the stochastic differential equations of the eco-evolutionary system in the main text. Therefore, let us first write down the infinitesimal change of the stochastic system given by the reactions listed in Eqs. (5). This is basically the infinitesimal generator G of the Markov process, i.e. for a twice differentiable function f we find (just considering the reactions affecting type A)

$$\begin{aligned}(Gf)(n_A(t)) &= \lim_{h\to 0}\frac{\mathbf{E}[f(n_A(t+h))]-f(n_A(t))}{h}\\ &= \beta n_A(f(n_A(t)+1)-f(n_A(t))+n_A(t)\left(\delta+\gamma_{a_2}(n_A(t)-1)(n_A(t)-2)\right.\\ &\qquad \left.+\gamma_{a_1}(n_A(t)-1)n_B(t)+\gamma_{a_0}n_B(t)(n_B(t)-1)\right)(f(n_A(t)-1)-f(n_A(t)).\end{aligned}$$

Setting $x_A(t)=\frac{n_A(t)}{M}$, expanding in terms of $\frac{1}{M}$ and neglecting terms of order higher than M^{-1} we obtain

$$\begin{aligned}(Gf)(x_A) &= M\beta x_A\left(f\left(x_A+\frac{1}{M}\right)-f(x_A)\right)\\ &\quad + Mx_A\left[\delta+\gamma_{a_2}M^2\left(x_A-\frac{1}{M}\right)\left(x_A-\frac{2}{M}\right)\right.\\ &\quad \left.+\gamma_{a_1}M^2\left(x_A-\frac{1}{M}\right)x_B+\gamma_{a_0}M^2x_B\left(x_B-\frac{1}{M}\right)\right]\left(f\left(x_A-\frac{1}{M}\right)-f(x_A)\right)\\ &\approx x_A\left(\beta-\delta-\frac{1}{1+\omega a_2}x_A^2-\frac{2}{1+\omega a_1}x_Ax_B-\frac{1}{1+\omega a_0}x_B^2\right)\frac{\partial f}{\partial x}\\ &\quad +\frac{1}{2M}x_A\left(\beta+\delta+\frac{1}{1+\omega a_2}x_A^2+\frac{2}{1+\omega a_1}x_Ax_B+\frac{1}{1+\omega a_0}x_B^2\right)\frac{\partial^2 f}{\partial x^2}.\end{aligned}$$

We can do the analogous calculation for the variable n_B. Lastly, we note that this infinitesimal generator corresponds to a stochastic differential equation precisely given in equation (11) in the main text (cf. (Kallenberg, 2002, Chapter 21)).

For completeness we write down the infinitesimal generator corresponding to the two-dimensional stochastic differential equation:

$$\begin{aligned}(Gf)(x_A, x_B) = x_A &\left(\beta_A - \delta_A - \frac{x_A^2}{1+\omega a_2} - \frac{2x_A x_B}{1+\omega a_1} - \frac{x_B^2}{1+\omega a_0}\right)\frac{\partial f}{\partial x_A} \\ &+ x_B \left(\beta_B - \delta_B - \frac{x_A^2}{1+\omega b_2} - \frac{2x_A x_B}{1+\omega b_1} - \frac{x_B^2}{1+\omega b_0}\right)\frac{\partial f}{\partial x_B} \\ &+ \frac{x_A}{2M}\left(\beta_A + \delta_A + \frac{x_A^2}{1+\omega a_2} + \frac{2x_A x_B}{1+\omega a_1} + \frac{x_B^2}{1+\omega a_0}\right)\frac{\partial^2 f}{\partial x_A^2} \\ &+ \frac{x_B}{2M}\left(\beta_B + \delta_B + \frac{x_A^2}{1+\omega b_2} + \frac{2x_A x_B}{1+\omega b_1} + \frac{x_B^2}{1+\omega b_0}\right)\frac{\partial^2 f}{\partial x_B^2}.\end{aligned} \tag{A.1}$$

1.2 Approximating the fixation probability

In order to get an approximation for the fixation probability of type A individuals we first transform the system to the parameter space $p = \frac{x_A}{x_A+x_B}$, fraction of type A particles, and $z = x_A + x_B$, the population size. Additionally, setting $\beta_A = \beta_B = \beta$ and $\delta_A = \delta_B = \delta$ the transformed generator is then given by

$$\begin{aligned}(\tilde{G}f)(p,z) = x_A &\left(\beta - \delta - \frac{x_A^2}{1+\omega a_2} - \frac{2x_A x_B}{1+\omega a_1} - \frac{x_B^2}{1+\omega a_0}\right)\left(\frac{1-p}{z}\frac{\partial f}{\partial p} + \frac{\partial f}{\partial z}\right) \\ &+ x_B \left(\beta - \delta - \frac{x_A^2}{1+\omega b_2} - \frac{2x_A x_B}{1+\omega b_1} - \frac{x_B^2}{1+\omega b_0}\right)\left(-\frac{p}{z}\frac{\partial f}{\partial p} + \frac{\partial f}{\partial z}\right) \\ &+ \frac{1}{2M}x_A\left(\beta + \delta + \frac{x_A^2}{1+\omega a_2} + \frac{2x_A x_B}{1+\omega a_1} + \frac{x_B^2}{1+\omega a_0}\right) \\ &\qquad \times \left(-\frac{2(1-p)}{z^2}\frac{\partial f}{\partial p} + \frac{(1-p)^2}{z^2}\frac{\partial^2 f}{\partial p^2} + \frac{2(1-p)}{z}\frac{\partial^2 f}{\partial p \partial z} + \frac{\partial^2 f}{\partial z^2}\right) \\ &+ \frac{1}{2M}x_B\left(\beta + \delta + \frac{x_A^2}{1+\omega b_2} + \frac{2x_A x_B}{1+\omega b_1} + \frac{x_B^2}{1+\omega b_0}\right) \\ &\qquad \times \left(\frac{2p}{z^2}\frac{\partial f}{\partial p} + \frac{p^2}{z^2}\frac{\partial^2 f}{\partial p^2} - \frac{2p}{z}\frac{\partial^2 f}{\partial p \partial z} + \frac{\partial^2 f}{\partial z^2}\right) \\ = p(1-p) &\left(\beta - \delta - \frac{p^2 z^2}{1+\omega a_2} - \frac{2p(1-p)z^2}{1+\omega a_1} - \frac{(1-p)^2 z^2}{1+\omega a_0}\ 0\right. \\ &\qquad \left. -\beta + \delta + \frac{p^2 z^2}{1+\omega b_2} + \frac{2p(1-p)z^2}{1+\omega b_1} + \frac{(1-p)^2 z^2}{1+\omega b_0}\right)\frac{\partial f}{\partial p} \\ &+ \frac{p(1-p)}{Mz}\left(\beta + \delta + \frac{p^2 z^2}{1+\omega b_2} + \frac{2p(1-p)z^2}{1+\omega b_1} + \frac{(1-p)^2 z^2}{1+\omega b_0}\right.\end{aligned}$$

$$
\begin{aligned}
&\qquad -\beta-\delta-\frac{p^2z^2}{1+\omega a_2}-\frac{2p(1-p)z^2}{1+\omega a_1}-\frac{(1-p)^2z^2}{1+\omega a_0}\Bigg)\frac{\partial f}{\partial p}\\
&+z\Bigg(p(\beta-\delta)-\frac{p^3z^2}{1+\omega a_2}-\frac{2p^2(1-p)z^2}{1+\omega a_1}-\frac{p(1-p)^2z^2}{1+\omega a_0}\\
&\qquad +(1-p)(\beta-\delta)-\frac{(1-p)p^2z^2}{1+\omega b_2}-\frac{2p(1-p)^2z^2}{1+\omega b_1}-\frac{(1-p)^3z^2}{1+\omega b_0}\Bigg)\frac{\partial f}{\partial z}\\
&+\Bigg[\frac{(1-p)^2p}{2zM}\Bigg(\beta+\delta+\frac{p^2z^2}{1+\omega a_2}+\frac{2p(1-p)z^2}{1+\omega a_1}+\frac{(1-p)^2z^2}{1+\omega a_0}\Bigg)\\
&\qquad +\frac{p^2(1-p)}{2zM}\Bigg(\beta+\delta+\frac{p^2z^2}{1+\omega b_2}+\frac{2p(1-p)z^2}{1+\omega b_1}+\frac{(1-p)^2z^2}{1+\omega b_0}\Bigg)\Bigg]\frac{\partial^2 f}{\partial p^2}\\
&+\frac{p(1-p)}{M}\Bigg(\beta+\delta+\frac{p^2z^2}{1+\omega a_2}+\frac{2p(1-p)z^2}{1+\omega a_1}+\frac{(1-p)^2z^2}{1+\omega a_0}\\
&\qquad -\beta-\delta-\frac{p^2z^2}{1+\omega b_2}-\frac{2p(1-p)z^2}{1+\omega b_1}-\frac{(1-p)^2z^2}{1+\omega b_0}\Bigg)\frac{\partial^2 f}{\partial p\partial z}\\
&+\frac{z}{2M}\Bigg[p\Bigg(\beta+\delta+\frac{p^2z^2}{1+\omega a_2}+\frac{2p(1-p)z^2}{1+\omega a_1}+\frac{(1-p)^2z^2}{1+\omega a_0}\Bigg)\\
&\qquad + +(1-p)\Bigg(\beta+\delta+\frac{p^2z^2}{1+\omega b_2}+\frac{2p(1-p)z^2}{1+\omega b_1}+\frac{(1-p)^2z^2}{1+\omega b_0}\Bigg)\Bigg]\frac{\partial^2 f}{\partial z^2}\\
&=p(1-p)z\Bigg(z+\frac{1}{M}\Bigg)\Bigg(\frac{p^2}{1+\omega b_2}+\frac{2p(1-p)}{1+\omega b_1}+\frac{(1-p)^2}{1+\omega b_0}\\
&\qquad -\frac{p^2}{1+\omega a_2}-\frac{2p(1-p)}{1+\omega a_1}-\frac{(1-p)^2}{1+\omega a_0}\Bigg)\frac{\partial f}{\partial p}\\
&+z\Bigg(\beta-\delta-z^2\Bigg(\frac{p^3}{1+\omega a_2}+\frac{2p^2(1-p)}{1+\omega a_1}+\frac{p(1-p)^2}{1+\omega a_0}\\
&\qquad +\frac{(1-p)p^2}{1+\omega b_2}+\frac{2(1-p)^2p}{1+\omega b_1}+\frac{(1-p)^3}{1+\omega b_0}\Bigg)\Bigg)\frac{\partial f}{\partial z}\\
&+\frac{p(1-p)}{2zM}\Bigg(\beta+\delta+z^2\Bigg(\frac{p^2(1-p)}{1+\omega a_2}+\frac{2p(1-p)^2}{1+\omega a_1}+\frac{(1-p)^3}{1+\omega a_0}\\
&\qquad +\frac{p^3}{1+\omega b_2}+\frac{2(1-p)p^2}{1+\omega b_1}+\frac{(1-p)^2p}{1+\omega b_0}\Bigg)\Bigg)\frac{\partial^2 f}{\partial p^2}\\
&+\frac{p(1-p)z^2}{M}\Bigg(\frac{p^2}{1+\omega a_2}+\frac{2p(1-p)}{1+\omega a_1}+\frac{(1-p)^2}{1+\omega a_0}\\
&\qquad -\frac{p^2}{1+\omega b_2}-\frac{2p(1-p)}{1+\omega b_1}-\frac{(1-p)^2}{1+\omega b_0}\Bigg)\frac{\partial^2 f}{\partial p\partial z}\\
&+\frac{z}{2M}\Bigg[\beta+\delta+z^2\Bigg(\frac{p^3}{1+\omega a_2}+\frac{2p^2(1-p)}{1+\omega a_1}+\frac{p(1-p)^2}{1+\omega a_0}\\
&\qquad +\frac{p^2(1-p)}{1+\omega b_2}+\frac{2p(1-p)^2}{1+\omega b_1}+\frac{(1-p)^3}{1+\omega b_0}\Bigg)\Bigg]\frac{\partial^2 f}{\partial z^2}.
\end{aligned}
$$

Next, we assume $\omega \ll 1$, i.e. the payoffs only have a small impact on the overall evolution of the model. This also allows us to simplify the generator:

$$
\begin{aligned}
(\tilde{G}f)(p,z) \approx\; & p(1-p)z\left(z+\frac{1}{M}\right)\omega\left[a_0-b_0+2p\left(b_0-b_1+a_1-a_0\right)\right. \\
& \left.+p^2\left(2b_1-b_2-b_0+a_2-2a_1+a_0\right)\right]\frac{\partial f}{\partial p} \\
& + z\left(\beta-\delta-z^2\left[1-\omega b_0+\omega p\left(3b_0-2b_1-a_0\right)\right.\right. \\
& \left.\left.+\omega p^2\left(2a_0-2a_1+4b_1-b_2-3b_0\right)+\omega p^3\left(2a_1-a_2-a_0+b_2-2b_1+b_0\right)\right]\right)\frac{\partial f}{\partial z} \\
& + \frac{p(1-p)}{2zM}\left(\beta+\delta+z^2+\omega z^2\left[-a_0+p\left(3a_0-2a_1-b_0\right)\right.\right. \\
& \left.\left.+p^2\left(4a_1-a_2-3a_0+2b_0-2b_1\right)+p^3\left(a_2-2a_1+a_0-b_2+2b_1-b_0\right)\right]\right)\frac{\partial^2 f}{\partial p^2} \\
& + \frac{p(1-p)z^2}{M}\omega\left[b_0-a_0+2p\left(b_0-b_1+a_1-a_0\right)\right. \\
& \left.+p^2\left(2b_1-b_2-b_0+a_2-2a_1+a_0\right)\right]\frac{\partial^2 f}{\partial p\partial z} \\
& + \frac{z}{2M}\left(\beta+\delta+z^2+\omega z^2\left[-a_0+p\left(3a_0-2a_1-b_0\right)\right.\right. \\
& \left.\left.+p^2\left(4a_1-a_2-3a_0+2b_0-2b_1\right)+p^3\left(a_2-2a_1+a_0-b_2+2b_1-b_0\right)\right]\right)\frac{\partial^2 f}{\partial z^2}.
\end{aligned}
$$

Using the same techniques as developed in (Lambert, 2006) and refined for this setting in (Czuppon and Traulsen, 2017, Appendix B, C, D) we find the following approximation for the fixation probability:

$$
\varphi(p,z) \approx p+\omega p(1-p)(p-p_1^*)(p-p_2^*)\left(2b_1-b_2-b_0+a_2-2a_1+a_0\right)\psi(z), \tag{A.2}
$$

where the internal equilibria $p_{1,2}^*$ are given by

$$
\begin{aligned}
p_{1,2}^* = & -\frac{b_0-b_1+a_1-a_0}{2b_1-b_2-b_0+a_2-2a_1+a_0} \\
& \pm\sqrt{\left(\frac{b_0-b_1+a_1-a_0}{2b_1-b_2-b_0+a_2-2a_1+a_0}\right)^2+\frac{b_0-a_0}{2b_1-b_2-b_0+a_2-2a_1+a_0}},
\end{aligned} \tag{A.3}
$$

For the fixed points one solves the deterministic term of the frequency variation of the approximated infinitesimal generator, i.e. $\frac{\partial f}{\partial p}=0$.

To see that the formula for the fixation probability holds we plug in φ into $\tilde{G}$. Setting $\tilde{G}\varphi=0$ and simplifying we end up with an equation for $\psi(z)$:

$$
\begin{aligned}
0 = z\left(z+\frac{1}{M}\right)+z\left(\beta-\delta-z^2\right)\psi'(z)+\frac{1}{2zM}\left(\beta+\delta+z^2\right)\chi(p,p_1^*,p_2^*)\psi(z) \\
+\frac{z}{2M}\left(\beta+\delta+z^2\right)\psi''(z),
\end{aligned} \tag{A.4}
$$

where

$$\chi(p, p_1^*, p_2^*) = \frac{-2(p_1^* + p_2^* + p_1^* p_2^*) + 6p(1 + p_1^* + p_2^*) - 12p^2}{(p - p_1^*)(p - p_2^*)}.$$

Since for the method to work it is important that ψ depends only on the total population size z and not also on the frequency of mutants p we need $\chi =$ constant. Resolving this yields:

$$\begin{aligned}
\chi(p, p_1^*, p_2^*) &= \frac{-2(p_1^* + p_2^* + p_1^* p_2^*) + 6p(1 + p_1^* + p_2^*) - 12p^2}{(p - p_1^*)(p - p_2^*)} \\
&= \frac{-12p^2 + 12p(p_1^* + p_2^*) - 12p_1^* p_2^* - 2(p_1^* + p_2^* - 5p_1^* p_2^*) + 6p(1 - p_1^* - p_2^*)}{(p - p_1^*)(p - p_2^*)} \\
&= \frac{-12(p - p_1^*)(p - p_2^*) - 2(p_1^* + p_2^* - 5p_1^* p_2^*) + 6p(1 - p_1^* - p_2^*)}{(p - p_1^*)(p - p_2^*)} \\
&= -12 + \frac{-2(p_1^* + p_2^* - 5p_1^* p_2^*) + 6p(1 - p_1^* - p_2^*)}{(p - p_1^*)(p - p_2^*)}
\end{aligned}$$

For the second term to vanish we condition the fixed points to satisfy:

$$p_1^* + p_2^* = 1 \qquad \text{and} \qquad p_1^* p_2^* = \frac{1}{5},$$

which in the end gives $\chi(p, p_1^*, p_2^*) = -12$. This gives equation (16) in the main text.

1.3 Extension to d players

We now extend the formalism to the general setting with $d-$players and two strategies. The payoff matrix is then given by

$$\begin{pmatrix} a_{d-1} & \cdots & a_0 \\ b_{d-1} & \cdots & b_0 \end{pmatrix}.$$

The death rates due to competition need to change accordingly, i.e. a death of a type A particle occurring due to the interaction with $k-1$ type A and $d-k$ type B individuals is given by

$$\gamma_{a_{k-1}} = \binom{d-1}{k} \frac{x_A^{k-1} x_B^{d-k}}{M^{d-1}(1 + \omega a_{k-1}}).$$

Note, that instead of scaling these interactions between individuals with $1/M^2$ we now need the scaling $1/M^{d-1}$ in order to obtain a reasonable diffusion limit. Doing the same steps as in

the three player case we end up with the following stochastic differential equations:

$$
\begin{aligned}
dx_A(t) &= x_A\left(\beta_A - \delta_A - \sum_{i=0}^{d-1}\binom{d-1}{i}\frac{x_A^i x_B^{d-1-i}}{1+\omega a_i}\right)dt \\
&\quad + \frac{1}{\sqrt{M}}\sqrt{(\beta_A+\delta_A)x_A + x_A\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{x_A^i x_B^{d-1-i}}{1+\omega a_i}}dW^1(t), \\
dx_B(t) &= x_B\left(\beta_B - \delta_B - \sum_{i=0}^{d-1}\binom{d-1}{i}\frac{x_A^i x_B^{d-1-i}}{1+\omega b_i}\right)dt \\
&\quad + \frac{1}{\sqrt{M}}\sqrt{(\beta_B+\delta_B)x_B + x_B\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{x_A^i x_B^{d-1-i}}{1+\omega b_i}}dW^2(t).
\end{aligned}
\tag{A.5}
$$

The transformed generator, i.e. in terms of p and z, can again be derived analogously to the three player scenario and yields:

$$
\begin{aligned}
(\tilde{G}f)(p,z) &= p(1-p)z^{d-2}\left(z+\frac{1}{M}\right) \\
&\quad \times\left[\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i} - \sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i}\right]\frac{\partial f}{\partial p} \\
&\quad + z\Bigg(\beta - \delta - z^{d-1} \\
&\quad \times\left[p\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i} + (1-p)\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i}\right]\Bigg)\frac{\partial f}{\partial z} \\
&\quad + \frac{p(1-p)}{2zM}\Bigg(\beta + \delta + z^{d-1} \\
&\quad \times\left[(1-p)\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i} + p\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i}\right]\Bigg)\frac{\partial^2 f}{\partial p^2} \\
&\quad + \frac{p(1-p)z^{d-1}}{M}\left[\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i} - \sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i}\right]\frac{\partial^2 f}{\partial p\partial z} \\
&\quad + \frac{z}{2M}\Bigg(\beta + \delta + z^{d-1} \\
&\quad \times\left[p\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i} + (1-p)\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i}\right]\Bigg)\frac{\partial^2 f}{\partial z^2}
\end{aligned}
$$

The solution to $\tilde{G}\varphi = 0$ for $\omega \ll 1$ can be approximated by

$$\varphi(p,z) \approx p + \omega(-1)^{d-1}\left(\sum_{i=0}^{d-1}(-1)^i\binom{d-1}{i}(a_i - b_i)\right)p(1-p)\prod_{i=1}^{d-1}(p-p_i^*)\psi(z), \quad \text{(A.6)}$$

where p_i^* are the roots of

$$\sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega b_i} - \sum_{i=0}^{d-1}\binom{d-1}{i}\frac{p^i(1-p)^{d-1-i}}{1+\omega a_i} = 0. \quad \text{(A.7)}$$

This can be seen by again plugging in the resulting approximation of φ into $\tilde{G}$. Along the way one needs to see that $\sum_{i=0}^{d-1}(-1)^i\binom{d-1}{i} = 0$ which can be seen by induction. Then the remaining equation that ψ needs to satisfy reads

$$\begin{aligned} 0 = z^{d-2}\left(z + \frac{1}{M}\right) + z\left(\beta - \delta - z^{d-1}\right)\psi'(z) \\ + \frac{1}{2zM}\left(\beta + \delta + z^{d-1}\right)\chi(p, p_1^*, ..., p_{d-1}^*)\psi(z) + \frac{z}{2M}\left(\beta + \delta + z^{d-1}\right)\psi''(z), \end{aligned} \quad \text{(A.8)}$$

where

$$\begin{aligned} \chi(p, p_1^*, ..., p_{d-1}^*) = \frac{1}{\prod_{i=1}^{d-1}(p-p_i^*)}\Bigg(2(1-2p)\sum_{i=1}^{d-1}\prod_{j\neq i}(p-p_i^*) \\ + p(1-p)\sum_{i=1}^{d-1}\sum_{j\neq i}\prod_{k\neq i,j}(p-p_k^*) - 2\prod_{i=1}^{d-1}(p-p_i^*)\Bigg). \end{aligned} \quad \text{(A.9)}$$

Technically, for χ to be independent of p this formula gives conditions on the location of the fixed points p_i^* such that the above approximation of the fixation probability, i.e. the separation of the p and z coordinates, is valid. However the general form of this condition is beyond the scope of our analysis.

1.4 Numerical evaluation of ψ

In order to calculate values of ψ we numerically evaluate, dependent on the number of players, equation (16) (main text) or (A.8), respectively. For this we use the predefined function "`solve_bvp`" from the `scipy.integrate` library in Python, Jones *et al.* (2001–). Therefore we need to input boundary values for the algorithm to work with. In particular we evaluate ψ in the interval $[0.0001, 10]$ with boundary values $\psi(0.0001) = 0.0001$ and $\psi(10) = \ln(10)$. The concrete choice of the boundary values is not very relevant since the method is quite robust. For instance, we tested for different values of $\psi(0.0001) \in [0.00000001, 0.1]$ and all solutions gave the same values for $z = 2$. The same applies for the boundary value $\psi(10)$. For a more thorough analysis of ψ we refer to (Czuppon and Traulsen, 2017, Appendices E,F).

1.5 Fixation probability under strong selection

We give an approximation of the fixation probability in the d-trait eco-evolutionary model in case of the snowdrift game dynamics, for details see the main text. We perform the same simulations which led to Figure 6 in the main text, i.e. we vary the selection intensity ω and analyze the fixation behavior of the cooperative trait. The dynamics allow for two internal fixed points $p_1^* < p_2^*$ where p_1^* is locally unstable and p_2^* is locally stable.
As opposed to the main text we start the simulations in the close vicinity of the fixed point p_2^*. Weak selection then predicts fixation probabilities close to the initial frequency of cooperative individuals, i.e. $\varphi_{\text{weak}} \approx p_2^*$. As we see in Figure A.1 this is a good approximation for the simulation outcome until some intermediate value.
For very strong selection we argue that the system is dominated by the replicator dynamics. Hence, trajectories stay in p_2^* for a long time and randomly fluctuate around this stable equilibrium. The escape probability of the attracting domain is then given by standard stochastic diffusion theory, i.e.

$$\varphi_{\text{strong}} = \frac{1 - p_2^*}{1 - p_1^*}. \tag{A.10}$$

For the strongest considered selection intensity this exactly fits the simulation result (rightmost value in the right subfigure of Figure A.1) validating our heuristic reasoning in the main text.
This has an interesting implication since it basically means that both weak and strong selection can be explained by random drift. Still there is a difference since in the weak selection limit the replicator dynamics is close to neutral, i.e. the stability of the fixed points just has a minor impact on the dynamical behavior. Hence, the fixation process can be described by a Brownian motion over the whole frequency space resulting in a fixation probability close to the initial frequency. However, for strong selection the deterministic dynamics define the trajectories of the individual based model. Thus, in this case the escape behavior out of the attractor region of the stable fixed point is described by a Brownian motion yielding the approximation obtained in equation (A.10).

References

Czuppon, P. and A. Traulsen, 2017 Fixation probabilities in populations under demographic fluctuations. arXiv.org p. arXiv:1708.09665.

Jones, E., T. Oliphant, P. Peterson, *et al.*, 2001– SciPy: Open source scientific tools for Python.

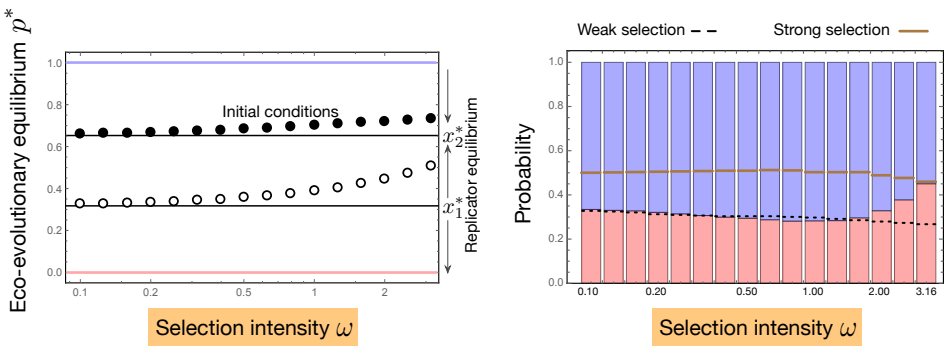

Figure A.1: **Comparison between weak and strong selection.** Re-evaluating the findings from Figure 6 (where the initial condition was set to $p_0 = 0.5$) we now consider $p_0 = p_2^*$ (filled circle). The deterministic behavior of the system is visualized in the left panel. By varying the selection intensity ω we also alter the location of the deterministic fixed points. For weak selection the effect of the selection gradient is minimal and drift plays a dominant role and hence the fixation probabilities are close to neutral (dashed lines in the right panel). As selection increases, the stable fixed point, close to all C, attracts and holds most of the trajectories. This is why we describe the escape behavior of the attractor region by a Brownian motion, leading to equation (A.10). These values are shown as solid lines in the right panel. They are indeed approaching the simulation results for stronger selection intensities. In these cases the trajectories either hit the monomorphic C state or overcome the unstable equilibrium p_1^* (empty circle) and end in the monomorphic D state. We have performed 10^5 Gillespie simulations for $M = 100$ and a 20 player snowdrift game with an initial population of 200, $b = 1.5$, $c = 1$, $\beta = 0.6$, $\delta = 0.1$, $\psi \approx 0.53$ and $1 + \omega(matrix)$ mapping for different intensities of selection. The bar charts show the probability of a trajectory fixing in either all C (blue) or all D (red). All simulations were executed until one of the types fixed. The selection intensity ranges as $\omega = 10^{-1.0}, \ldots, 10^{0.5}$.

Kallenberg, O., 2002 *Foundations of modern probability*. Springer, Verlag.

Lambert, A., 2006 Probability of fixation under weak selection: a branching process unifying approach. Theoretical population biology **69**: 419–441.