

LETTER

Mean growth rate when rare is not a reliable metric for persistence of species

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Abstract

The coexistence of many species within ecological communities poses a long-standing theoretical puzzle. Modern coexistence theory (MCT) and related techniques explore this phenomenon by examining the chance of a species population growing from rarity in the presence of all other species. The mean growth rate when rare, $\mathbb{E}[r]$, is used in MCT as a metric that measures persistence properties (like invasibility or time to extinction) of a population. Here we critique this reliance on $\mathbb{E}[r]$ and show that it fails to capture the effect of temporal random abundance variations on persistence properties. The problem becomes particularly severe when an increase in the amplitude of stochastic temporal environmental variations leads to an increase in $\mathbb{E}[r]$, since at the same time it enhances random abundance fluctuations and the two effects are inherently intertwined. In this case, the chance of invasion and the mean extinction time of a population may even go down as $\mathbb{E}[r]$ increases.

Keywords

Coexistence, environmental stochasticity, invasibility, lottery model, mean growth rate, mean time to extinction, modern coexistence theory, persistence.

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INTRODUCTION

Understanding the factors and processes that shape the diversity of species in ecological communities is among the most important questions in ecology. The prevalence of highly diverse communities, in which many species interact with each other and with abiotic factors, has long been a source of wonder as it seems to violate the competitive exclusion principle (Hutchinson, 1961; Tilman, 1982) and/or May's negative relationship between complexity and diversity (May, 1972). Many possible mechanisms that may explain the maintenance of species diversity have been suggested (Chesson, 2000), but the identification of those which actually influence a given system is still a formidable task.

Modern coexistence theory (MCT) (Chesson, 1994, 2000, 2003; Barabás *et al.*, 2018; Chesson, 2018; Ellner *et al.*, 2019) is a widely used conceptual framework aimed at clarifying the conditions for species coexistence. Instead of fully considering the intricate network of dynamical interdependences between all the species populations in a community, MCT simplifies the coexistence problem tremendously by focussing on the invasibility of a single species population, i.e. on the chance of a single invading population (or a small group of invading populations) to establish, given the dynamics of all the other resident species and the external environment. Invasibility is related to persistence time: if a population tends to recover from low frequencies, then its time to extinction is taken to be large (Chesson, 1982). Two populations coexist if each of them invades the other, and analogously, the persistence of high-diversity assemblages is examined by looking at the chance of each of the species to invade the community (Ellner *et al.*, 2016). Importantly, MCT explicitly considers stochastic temporal environmental fluctuations, which have been found to be a key driver of community dynamics in natural

communities (Chisholm *et al.*, 2014; Kalyuzhny *et al.*, 2014, 2015; Fung *et al.*, 2016).

In MCT, invasibility is measured by a single metric, $\mathbb{E}[r]$, which is the mean growth rate of a population when rare – i.e. when its relative abundance (frequency) is so low that it does not affect the dynamics of all the other populations. Given a time series of (low) frequencies $\{x_t, x_{t+\Delta t}, x_{t+2\Delta t}, \dots\}$, this mean growth rate is defined as (Chesson, 2003)

$$\mathbb{E}[r] \equiv \frac{1}{\Delta t} \mathbb{E} \left[\ln \left(\frac{x_{t+\Delta t}}{x_t} \right) \right]. \quad (1)$$

Here we would like to critique the reliance of MCT (and related theories) on the metric $\mathbb{E}[r]$ as a quantitative measure for persistence. We shall argue that, while the **sign** of $\mathbb{E}[r]$ is indeed an important characteristic of persistence, the **magnitude** of $\mathbb{E}[r]$ does not relate directly to persistence, particularly in cases where the stabilising mechanism depends, fully or partially, on stochastic (temporal) environmental fluctuations. In these cases, once $\mathbb{E}[r] > 0$, a further increase in its value is not necessarily related to an increase in mean time to extinction or invasibility, and in some instances these quantities can even decrease when $\mathbb{E}[r]$ increases.

Accordingly, $\mathbb{E}[r]$ cannot be considered as a "general quantitative criterion for the persistence of a species" (Chesson, 1994) and its value cannot be used to "decompose and compare" (Ellner *et al.*, 2019) the mechanisms that determine persistence and their relative importance. In the presence of stochastic environmental fluctuations, a contribution to $\mathbb{E}[r]$ is not necessarily a contribution to persistence. Therefore, one cannot quantify the contribution of a certain mechanism to persistence by comparing the value of $\mathbb{E}[r]$ in the presence and in the absence of this mechanism, which was the method used in Ellner *et al.* (2016) and in Letten *et al.* (2018). Similarly, $\mathbb{E}[r]$ -based metrics cannot be used for comparing the

persistence properties of different communities, as done in Usinowicz *et al.* (2017).

The problem with the use of $\mathbb{E}[r]$ lies in its failure to reflect another important factor that affects persistence: the strength of random abundance variations, or technically, the "diffusion" along the log-abundance axis. As we shall show below, when this diffusion is strong it may increasingly reduce the effect of $\mathbb{E}[r]$, making its value less and less relevant. Thus, invasibility and other persistence measures are associated with the relative strength of $\mathbb{E}[r]$ with respect to the random abundance variations.

The problem is highlighted when one considers the ability of temporal environmental stochasticity to promote coexistence, an effect that has attracted a lot of interest in the last few decades (Chesson & Warner, 1981; Chesson, 1994, 2000; Usinowicz *et al.*, 2012; Ellner *et al.*, 2016, 2019). In this case, stochastic fluctuations in the environment produce stochastic fluctuations in the per capita reproductive success of a species, and thereby govern both $\mathbb{E}[r]$ and the strength of the random abundance variations. This means that an increase in the amplitude of the fluctuations increases both $\mathbb{E}[r]$ and the diffusion along the log-abundance axis, so that one cannot examine the two quantities separately.

Throughout this paper, we consider the reliability of $\mathbb{E}[r]$ in different scenarios, mainly those in which stochastic environmental fluctuations promote coexistence. We begin with the Chesson–Warner lottery model (Chesson & Warner, 1981; Chesson, 1994, 2000) and examine it first for an infinite population and then for a finite population (i.e. with demographic stochasticity). We also study related models, like the forest dynamics model of Usinowicz *et al.* (2012, 2017), and comment on related metrics, like $\Delta I_{b,i}$ used in Ellner *et al.* (2016). In all these cases, we show that $\mathbb{E}[r]$ cannot be used as a single indicator for persistence properties.

METHODS

The two main characteristics of stochastic temporal environmental fluctuations are their typical amplitude σ and typical duration (correlation time) δ (Lande *et al.*, 2003). If the relative fitness of a focal species is related to the mean number of offspring (or seeds or larvae) per individual, then this relative fitness is taken to be $W_t = e^{s_t}$, where s_t is a stochastic process with variance σ^2 and correlation time δ .

We examine two measures of persistence: one is the chance of invasion from rarity, a standard metric used in MCT and many other theories (Grainger *et al.*, 2019), and the other is the time to extinction of an already established population, another standard metric whose importance has been highlighted in recent studies (Adler & Drake, 2008; Carmel *et al.*, 2017; Jeltsch *et al.*, 2019). The chance of invasion is the probability of a rare population to reach a given density before going extinct. This property depends only on the probabilities of transition between different states of the system, and is independent of the overall rate of events: for a given stochastic process, if all rates are doubled or halved, the chance of invasion remains the same. On the other hand, the time to extinction of an established population depends on both the transition probabilities and on their rates: when all rates are doubled, the time to extinction is halved.

To assess the use of $\mathbb{E}[r]$, we perform numerical experiments and examine the chance of invasion from rarity and the time to extinction of an established population when σ and δ vary across experiments. For $\mathbb{E}[r]$ to be used as a metric for a persistence property, it should satisfy the following requirements with respect to that property:

- (1) The persistence property in question (for example, invasibility or coexistence time) increases monotonically with $\mathbb{E}[r]$.
- (2) The persistence property is the same for different combinations of δ and σ^2 , when these combinations yield the same $\mathbb{E}[r]$.

In our numerical experiments, we simulate two models: the classic lottery model of Chesson & Warner (1981) and the forest tree community model of Usinowicz *et al.* (2012, 2017). MCT is focussed on the chance of invasion of a single species when rare, in the presence of all other resident species. Here we limit ourselves to the simplest case, that of two species for each model.

In the original form of the lottery model, the frequency of the focal species x satisfies

$$x_{t+\delta} = (1 - \delta)x_t + \delta \frac{W_t x_t}{W_t x_t + 1 - x_t} \quad (2)$$

over a single time-step (without loss of generality, we use yearly time-steps). Here, t is time measured in units of the generation time, δ is the fraction of the individuals in the community dying in each year and W_t is the relative fitness of the focal species with respect to its rival species at time t (reflecting, for example, the mean number of seeds produced by a single individual of the focal species per one seed produced by the rival species). Under these dynamics the lifetime of adults is distributed geometrically with mean $1/\delta$ years, so $1/\delta$ is the generation time in years. If W_t is picked at random in each year, then δ is the correlation time of the environment as measured in units of the generation time. The tree community model, which takes into account life-history stages (seeds and adult trees), is presented in detail in Supplement 5.

As we shall see, $\mathbb{E}[r]$ does not satisfy either of the two requirements described above, for either of the two persistence properties examined. In the presence of stochastic environmental fluctuations, the magnitude of $\mathbb{E}[r]$ tends to increase with σ and to decrease with δ , but the actual persistence properties may respond differently. Even when the response is in the 'correct' direction, requirement 2 above is not fulfilled.

When the amplitude of random abundance variations is small, one can implement the diffusion approximation (Karlín & Taylor, 1981; Lande *et al.*, 2003). The theory of stochasticity-induced stabilisation is considered within the diffusion approximation framework in Dean & Shnerb (2019). Here (in Supplements 1 and 2) we reproduce some of these results and use them to obtain some insight into the failure of $\mathbb{E}[r]$, to suggest alternative metrics and to compare (when possible) our numerical results with analytical predictions. In particular, when the diffusion approximation is applicable (i.e. for small σ), the association mentioned in the Introduction above becomes a direct relationship: both the chance of invasion and the mean time to extinction are determined by $\mathbb{E}[r]/g$, where g is the strength of the abundance variations.

Most of the parameter space surveyed in our numerical experiments lies outside the region in which the diffusion approximation holds. Nevertheless, the insights gained using the diffusion approximation (i.e. in the small- σ regime) provide a qualitative understanding of the general relationships between $\mathbb{E}[r]$, abundance variations and persistence.

RESULTS

The lottery model: Extinction time, invisibility and $\mathbb{E}[r]$ in a two-species community

Persistence is related to the chance of invasion (the probability that a rare population will grow and reach some threshold abundance or frequency) and to the time to extinction of an established population. Both these quantities have to do with the dynamics of a population close to its extinction state (in other words, in an "extinction zone"). In reality, any population is a collection of n discrete individuals, and the frequency $x = n/N$ reflects the fraction of a given population in an entire community of N individuals. In this case, the extinction zone is naturally defined as the state with one individual, or only a few individuals. For theories that do not take into account the discreteness of individuals (i.e. theories without demographic stochasticity), the definition of the extinction zone is arbitrary, say $0 \leq x \leq \epsilon$ where ϵ is some small number, but to make sense in practical situations one should posit this ϵ to be of order $1/N$.

What are the relationships between the metric $\mathbb{E}[r]$ and persistence? To examine this, let us look at the most famous example of stochasticity-induced stabilisation, the two-species Chesson–Warner lottery model (Chesson & Warner, 1981). When the dynamics are given by eqn (2) and the focal species is rare ($x_t \ll 1$, $1 - x_t \approx 1$),

$$\mathbb{E}[r] = \frac{\mathbb{E}[\ln(x_{t+\delta}/x_t)]}{\delta} = \frac{\mathbb{E}[\ln(1 - \delta + \delta W_t)]}{\delta}. \quad (3)$$

Clearly, the value of $\mathbb{E}[r]$ is determined by δ and by the statistical properties of W_t . In what follows, we consider the symmetric case, where the mean (over time) fitness of both species is the same and hence $\mathbb{E}[\ln W_t] = 0$. In this case, we manipulate the amplitude of log-fitness variations $\sigma^2 = \text{var}(\ln W_t)$. The asymmetric case $\mathbb{E}[\ln W_t] \neq 0$ is considered briefly below (see Fig. 3).

Fig. 1 shows how the invisibility and the time to absorption (mean time to fixation or extinction of the focal species, i.e. the mean time to extinction of either species), as measured in numerical simulations of the lottery process (2), are related to $\mathbb{E}[r]$. Evidently, neither of the reliability conditions (presented in the Methods section above) is satisfied. Different combinations of δ and σ^2 yield different persistence properties even if they correspond to the same $\mathbb{E}[r]$. Moreover, not only does invisibility not grow monotonically with $\mathbb{E}[r]$, but the time to absorption can even *decrease monotonically* with $\mathbb{E}[r]$ when σ is manipulated.

Insights from the diffusion approximation

While the trends in Fig. 1 speak for themselves, one may understand them better by looking at the case where $\sigma^2 \ll 1$,

i.e. when the diffusion approximation holds (Karlin & Taylor, 1981). This case is analysed in detail in Dean & Shnerb (2019), and in Supplement 1 we reproduce some of this analysis. In this parameter regime the mean growth rate as defined in eqn (3) is

$$\mathbb{E}[r] = \frac{\sigma^2}{2}(1 - \delta), \quad (4)$$

and the strength of stochastic fluctuations along the log-abundance axis, g , is equal to the following:

$$g = \frac{\sigma^2 \delta}{2}. \quad (5)$$

In Supplement 1 [see derivation of eqn (S10)], we show that in the diffusive regime the chance of invasion ϵ_+ is given by the following:

$$\epsilon_+ = \frac{1 - e^{-\frac{\mathbb{E}[r]}{g} \ln(\frac{x_0}{\epsilon})}}{1 - e^{-\frac{\mathbb{E}[r]}{g} \ln(\frac{x_1}{\epsilon})}}, \quad (6)$$

where x_0 is the starting frequency, ϵ is the frequency at which extinction is defined, and x_1 is the frequency at which invasion is defined to have occurred. Therefore, the chance of invasion is determined by the *ratio* $\mathbb{E}[r]/g$, not by $\mathbb{E}[r]$ alone. The validity of eqn (6) in the small- σ regime is demonstrated in Fig. 1(a). Since $\mathbb{E}[r]/g = (1 - \delta)/\delta$, in this weak-stochasticity regime the chance of invasion is independent of σ . In contrast, $\mathbb{E}[r]$ grows like σ^2 , so its value may change without any corresponding change in ϵ_+ .

The rate of extinction events is proportional to the chance to find the system in the extinction zone (Chesson, 1982). When a stochastic system like (2) admits a coexistence state, it relaxes in the long run to an equilibrium state $P_{\text{eq}}(x)$ and forgets its initial condition. In Supplement 1, we show that when $\sigma^2 \ll 1$ the chance to find the system in the extinction zone after relaxation is

$$P_{\text{eq}}(x \leq \epsilon) \sim \epsilon^{\frac{\mathbb{E}[r]}{g}}. \quad (7)$$

Again, the crucial quantity is the ratio $\mathbb{E}[r]/g$, not $\mathbb{E}[r]$ itself, and when σ is small this chance is independent of σ .

The decrease in the time to absorption as σ increases, demonstrated in Fig. 1(b), is related to the overall rate of events which determines the relaxation times. The dynamics defined in eqn (2) halt when $\sigma = 0$, so the time to equilibration diverges like $1/\sigma^2$ as $\sigma \rightarrow 0$.

The sign of $\mathbb{E}[r]$ is indeed an important qualitative feature of the system. As long as $\mathbb{E}[r]$ is positive, the chance of invasion ϵ_+ is finite even when one invader is introduced in an infinite community (see Supplement 3), and the mean time to extinction of an established population grows with the size of the community N and diverges if this size goes to infinity. On the other hand, if $\mathbb{E}[r]$ is negative, a single invader cannot establish in an infinite community. This follows from eqn (6): if ϵ is taken to be $1/N$, the term $e^{-\frac{\mathbb{E}[r]}{g} \ln(\frac{x_1}{\epsilon})}$ in eqn (6) vanishes if $\mathbb{E}[r]$ is positive and diverges if $\mathbb{E}[r]$ is negative. Moreover, as explained in Dean & Shnerb (2019), the divergence of $P_{\text{eq}}(x)$ in the extinction zone when $\mathbb{E}[r] < 0$ [see eqn (S7)] implies that the mean time to extinction becomes independent of the community size.

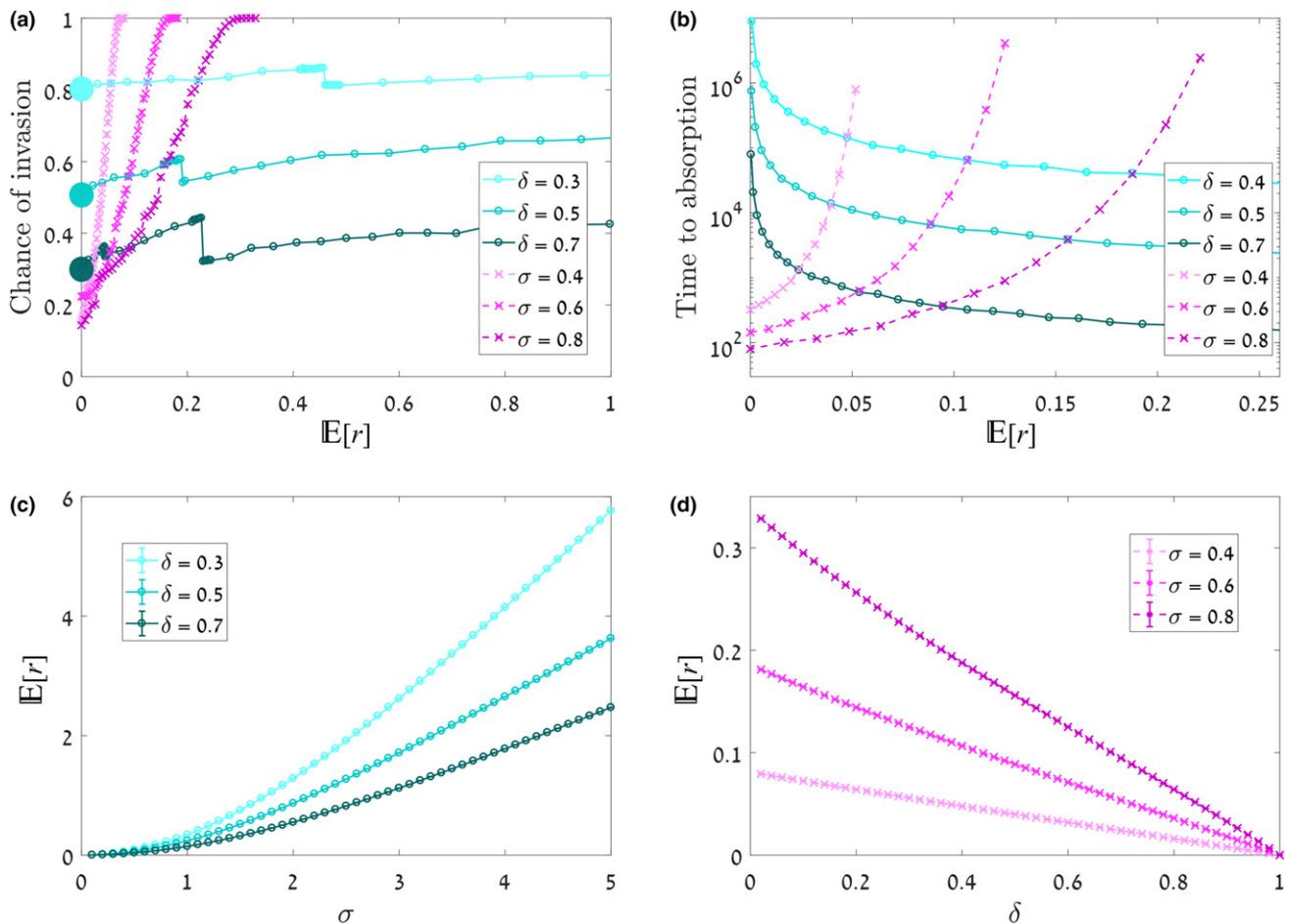


Figure 1 Persistence properties and $\mathbb{E}[r]$ for the symmetric two-species lottery model without demographic stochasticity, eqn (2). The upper panels show the chance of invasion [panel (a)] and mean time to absorption [panel (b)] for different values of $\mathbb{E}[r]$. The lower panels, (c) and (d), show the dependence of $\mathbb{E}[r]$ on the parameters σ and δ (amplitude and temporal correlation of stochastic environmental fluctuations, respectively). Circles (connected by full lines) represent the case where δ is held fixed and σ is varied, while crosses (connected by dashed lines) correspond to the reverse case. Clearly, different combinations of σ and δ that correspond to the same value of $\mathbb{E}[r]$ have completely different persistence properties. Moreover, when $\mathbb{E}[r]$ increases via an increase in σ , the chance of invasion is non-monotonic and the time to absorption decreases. Some features of these graphs are explained qualitatively, and even predicted quantitatively, by the diffusion approximation-based theory reviewed in Supplement 1. For example, the chance of invasion when $\sigma \rightarrow 0$ fits perfectly the predictions of eqn (6), marked by large filled circles for different values of δ in panel (a). The jumps in the invasion curves are not numerical artefacts but may be traced to the chance of extinction in a single step or a few steps, see Supplement 1.2. To find the chance of invasion, the process given by eqn (2) was incremented from the initial condition $x = 2\epsilon$, where $\epsilon = 0.001$, with invasion being defined as reaching the state $x = 0.1$ before $x = \epsilon$. To obtain the time to absorption, the same process was iterated from $x = 0.5$ until either $x < \epsilon$ or $1 - x < \epsilon$. For both kinds of experiments, the fluctuations in the relative fitness of the focal species were assumed to be dichotomous (in eqn (2), $W_i = e^{\pm\sigma}$), and all results were averaged over 1000 simulation runs for each set of parameters.

The effect of demographic stochasticity

The lottery model (2) assumes that the frequency x may take any value. In practice, a community is made of an integer number N of individuals and x (which now equals n/N , where n is the number of individuals of the focal species) can change only in units of $1/N$. The endogenous random birth-death process associated with this discreteness is known as demographic stochasticity (or ecological drift), and provides an extra source of abundance fluctuations, even if the environment is kept fixed (Lande *et al.*, 2003).

In the absence of demographic stochasticity, the lottery model (2) has two drawbacks: it does not have a naturally defined state of extinction (the frequency never reaches zero,

so one has to impose a cutoff at $x = \epsilon$ as explained above), and its dynamics halt (extinction time diverges) when $\sigma = 0$. To consider a more realistic scenario, we would like to examine the effectiveness of $\mathbb{E}[r]$ as a measure of persistence when the lottery dynamics admit demographic stochasticity. When individuals are discrete the setup of an invasion experiment becomes natural: the extinction state is $n = 0$, and we measure the chance of a species with an initial population of a single individual to reach a finite fraction $x_1 = n_1/N$ before extinction. The detailed definition of the model and the simulation procedure are given in Supplement 2.

A few typical results are depicted in Fig. 2. Clearly, the addition of demographic stochasticity does not fundamentally improve the usefulness of $\mathbb{E}[r]$ as an indicator of persistence.

Again, the chance of invasion and the time to absorption are not unique functions of $\mathbb{E}[r]$, and an increase in $\mathbb{E}[r]$ may correspond to a decrease in these quantities, although the range of parameters for which this behaviour is observed is narrower than in the absence of demographic stochasticity.

So far we have discussed only communities with symmetric competition (i.e. with both species having the same mean fitness, or $s_0 \equiv \mathbb{E}[\ln W_i] = 0$). We have verified that for non-zero values of s_0 it is still true that the persistence may be a non-monotonic function of $\mathbb{E}[r]$ (Fig. 3).

Diffusion approximation insights

To obtain further insight, one may again use the diffusion approximation, as explained in Supplement 2. Demographic stochasticity provides an additional source of random abundance variations: in every time-step of the lottery dynamics, δN individuals are killed, so if $\sigma = 0$, the amplitude of abundance variations per time-step is $\sqrt{\delta N}$. Accordingly, the variance of frequency fluctuations per time-step (of length δ generations) is δ/N , and the variance per unit time is $1/N$. In Supplement 2, this extra term is included in the corresponding Fokker–Planck equation.

When $\sigma = 0$ (neutral dynamics), the only source of abundance variations is these demographic fluctuations. In this neutral limit, they dictate the absorption time (which is of course independent of δ) and the chance of invasion [which is very small, $1/(Nx_1)$]. As a result, the mean times to absorption that were obtained from numerical experiments with fixed δ and varying σ (Fig. 2(b), circles joined by full lines) meet at the point $\sigma = \mathbb{E}[r] = 0$, and the chance of invasion (Fig. 2(a), circles joined by full lines) approaches zero in this limit.

Even if σ is larger than zero, the strength of the random abundance variations is bounded from below by $1/N$ (see

eqn (S16) of Supplement 2). Accordingly, at very small values of σ (and g), eqn (S16) suggests that the chance of invasion increases with δ (and decreases with $\mathbb{E}[r]$), as demonstrated in the inset of Fig. 2(a). On the other hand, for larger values of σ our numerical experiments suggest that the chance of invasion decreases with δ (i.e. increases with $\mathbb{E}[r]$). More work is needed to better characterise the relationship between the chance of invasion and $\mathbb{E}[r]$ in general scenarios (when the diffusion approximation does not hold, or when the system admits long-term memory as in the case of Usinowicz *et al.* (2012, 2017) discussed below). However, the existence of even a small region where the chance of invasion runs counter to $\mathbb{E}[r]$ demonstrates the fallacy in relying on the latter as a measure of the former.

With regard to the time to absorption (i.e. the time to extinction of either of the two species), an increase in σ has two opposite effects. On the one hand, it leads to an increase in the abundance variations, thus impeding coexistence and shortening absorption times. On the other hand, it increases the relative importance of stabilising mechanisms with respect to demographic stochasticity (ecological drift). As seen in Fig. 2(b), the net effect on the absorption time depends on the value of δ – with increasing σ (and $\mathbb{E}[r]$), the absorption time increases when δ is low and decreases when δ is high.

Despite the ubiquity of demographic fluctuations, many studies focus on models without demographic stochasticity (like eqn (2) above). This may be justified if the invading population, of size $n \ll N$, is still large enough such that the effect of demographic stochasticity is negligible. But if the abundance of the invader population is taken to be small [this is the standard procedure in population genetics, when one considers the chance of a single mutant to establish (Ewens, 2012; Chelo *et al.*, 2013), and it is also relevant to the establishment

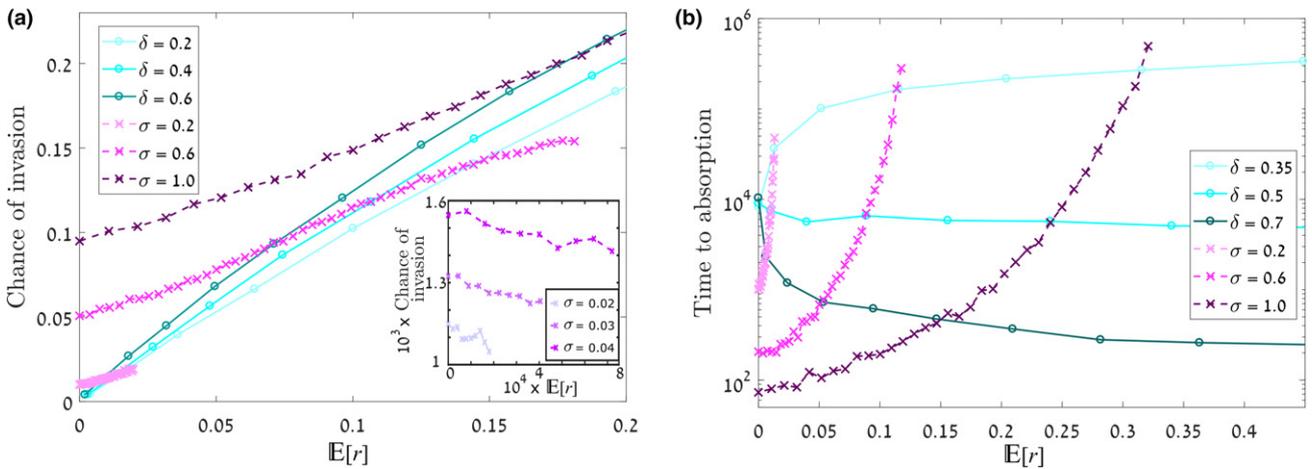


Figure 2 The chance of invasion [panel (a)] and the mean time to absorption [panel (b)] vs. $\mathbb{E}[r]$ as obtained from simulations of the lottery model with demographic stochasticity and $N = 10000$, for different values of σ and δ like in Fig. 1. The inset in panel (a) shows the chance of invasion for small values of σ as δ varies. In both panels, circles connected with full lines denote the case when δ is held fixed and σ is varied, while crosses connected with dashed lines denote the reverse case. The details of the simulation procedure are explained in Supplement 2. In invasion experiments, the simulation is initiated at $n = 1$ and the chance to reach $0.1 N$ before extinction is plotted vs. $\mathbb{E}[r]$, the results averaged over 1000 simulation runs for each parameter set. For the time to absorption (extinction or fixation) experiments, the results are averaged for each parameter set over 100 different realisations starting from $n = N/2$, where now extinction and fixation are defined as the states $n = 0$ and $n = N$, respectively. As in the model without demographic stochasticity, different combinations of σ and δ yield different persistence properties even if they correspond to the same $\mathbb{E}[r]$, and an increase in $\mathbb{E}[r]$ does not necessarily imply a higher chance of invasion or longer absorption times. Moreover, while for most of the parameter space invasion becomes more likely as $\mathbb{E}[r]$ increases, for small enough values of σ the chance of invasion decreases with $\mathbb{E}[r]$ [inset, panel (a)].

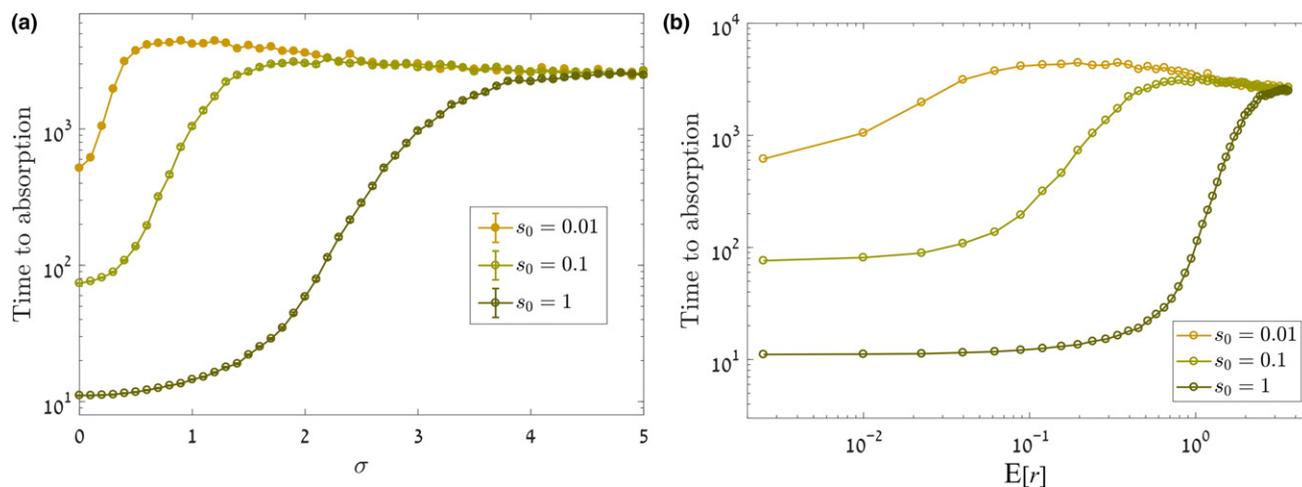


Figure 3 The time to absorption (extinction or fixation) for an asymmetric two-species lottery model with demographic stochasticity, with $N = 10000$ and $\delta = 0.5$, plotted against (a) the parameter σ (amplitude of environmental fluctuations), and (b) the metric $\mathbb{E}[r]$. The asymmetry in the model arises from the fitness advantage of the focal species over the other species, with the mean fitness advantage given by $s_0 \equiv \mathbb{E}[\ln W_i] \neq 0$. As for the symmetric model in Fig. 2, the starting population of the focal species (and also of the competing species) is $n = N/2$, and extinction and fixation are defined to be the states $n = 0$ and $n = N$, respectively. The time to absorption, as in the symmetric case, can rise or fall with $\mathbb{E}[r]$ and σ .

of a single immigrant or a small group of immigrants (Adler *et al.*, 2006)], demographic stochasticity affects invaders even in the large- N limit. As a result, our $n = 1$ invasion curves converge to an N -independent limit when $N \rightarrow \infty$ (as was checked numerically, results not shown), but this limit does not coincide with the curves of Fig. 1 which were obtained from eqn (2) without demographic stochasticity. For more discussion of this observation, see Supplement 3.

Related metrics for persistence

One of the main goals of MCT is to untangle the relative contribution of certain mechanisms to coexistence. To that aim, Ellner *et al.* (2016) considered the role of the storage effect, i.e. the effect of the covariance between the environment and the competition strength (EC covariance), by comparing the value of $\mathbb{E}[r]$ in two numerical experiments, one with and one without EC covariance. This work is reviewed in Supplement 4. First, Ellner *et al.* simulated the dynamics of a two-species lottery model with correlations between the fitnesses of the two species (without demographic stochasticity), corresponding to the case with EC covariance, and calculated the value of $\mathbb{E}[r]$ in this case. Second, they removed the EC covariance and found the mean growth rate when rare in this case, denoted now by $\mathbb{E}[r^\#]$. These authors have suggested the metric (see Supplement 4 for technical details)

$$\Delta I_{b,i} = \mathbb{E}[r] - \mathbb{E}[r^\#] \quad (8)$$

as a quantitative measure of the contribution of EC covariance to the persistence of a focal species, labelled with the subscript i (and with the subscript b standing for ‘between-species’).

Given the results presented above, it is clear that this $\mathbb{E}[r]$ -based metric $\Delta I_{b,i}$ does not reflect correctly the contribution of EC covariance to persistence. An increase in the contribution of EC covariance to the mean growth rate when rare

does not simply translate to an increase in the actual persistence of a population. To decompose the effect of different mechanisms on persistence, one would like to develop a similar procedure in order to assess, for example, the contribution of EC covariance to a metric that is more directly related to persistence, such as $\mathbb{E}[r]/g$ in the regime where σ^2 is small enough.

Usinowicz *et al.* (2012, 2017) have examined the stabilising effect of stochastic environmental fluctuations by ‘neutralising’ all other aspects of the community dynamics. To do so, they studied the dynamics of a tree community in which the mean growth, death and competition terms of all the tree species are exactly equal and the different species differ only in their (empirically calibrated) yearly fluctuations in seed, seedling or sapling production. The persistence observed in a numerical experiment must be attributed to environmental fluctuations, since there is no other stabilising factor. The aim of Usinowicz *et al.* (2017) was to compare the effect of environmental fluctuations between different forests along the latitudinal gradient, so [unlike Ellner *et al.* (2016)] they did not try to disentangle the effect of different stabilising factors. The metric they used is $A_{ij}A_{ji}$ (reviewed in Supplement 5). This metric is defined for a focal species i in competition with another species j , and is related to the *inverse* of the mean growth rate when the focal species is rare. Thus, when the value of $A_{ij}A_{ji}$ **decreases**, the absorption time and invasibility are supposed to increase.

To examine the use of this metric, we implemented the same forest dynamics model suggested in Usinowicz *et al.* (2012, 2017). We simulated a two-species model, where stochastic fluctuations in the reproductive success are specified by the observed time-series of recruitment rates, $R_i(t)$, for two species of trees (*Spondias mombin* and *Spondias radlkoferi*) over 14 years, as reported in Usinowicz *et al.* (2012). We incorporated this dataset in a model with finite community size, $N = 10000$. As explained in Supplement 5, we used a

parameter κ to manipulate the amplitude of the environmental fluctuations (with κ analogous, but not identical, to σ above), such that $\kappa = 1$ gives environmental fluctuations that are the same as those reported in Usinowicz *et al.* (2012), whereas $\kappa = 0$ is the case with no environmental fluctuations. As κ varies, the amplitude of the environmental fluctuations changes, but all the other statistical properties of the environment (e.g. correlations) are left intact.

In Fig. 4, both $A_{ij}A_{ji}$ and the metrics that more directly measure persistence – namely, the chance of invasion and the mean absorption time – are plotted against κ . Again, there are no trivial relationships between the quantities. In particular, while $A_{ij}A_{ji}$ decreases monotonically with κ (indicating greater persistence), the mean absorption time may decrease. The chance of invasion does grow when $A_{ij}A_{ji}$ decreases, at least in the regime of parameters we have checked.

DISCUSSION

Throughout this paper, we have examined the utility of the mean growth rate of a species population when rare, $\mathbb{E}[r]$, as an indicator of the invasibility and the extinction time of the population in a community context. We suggest that the use of the sign of $\mathbb{E}[r]$ to identify a qualitative shift in persistence is correct, but this does not imply that the value of $\mathbb{E}[r]$ provides quantitative information about persistence. When the sign of $\mathbb{E}[r]$ is positive, the chance to find the population in the extinction zone goes to zero when the width of this zone goes to zero (Schreiber *et al.*, 2011; Schreiber, 2012). If the extinction zone is defined as the region $0 \leq x \leq 1/N$, it becomes narrower and narrower when the size of the community N increases. As a result, the mean time to extinction diverges with N for an established population. On the other hand, when $\mathbb{E}[r]$ is negative the chance to find the population in the extinction zone is finite even when the width of the extinction zone goes to zero, as the dynamics tend to take the population closer and closer to the limit of vanishingly small frequencies. In this case one expects an N -independent

extinction time, as discussed in detail in Dean & Shnerb (2019). This distinction between positive and negative $\mathbb{E}[r]$ was demonstrated explicitly in many studies of stochastic-logistic (and logistic-like) systems (Lande *et al.*, 2003; Spanio *et al.*, 2017; Wada *et al.*, 2018; Yahalom & Shnerb, 2019).

So the sign of $\mathbb{E}[r]$ provides a fair binary classification scheme, and the ability to decompose $\mathbb{E}[r]$ and decide what mechanisms or what combinations of mechanisms are required to make $\mathbb{E}[r]$ positive is a sound feature of MCT. However, the assumption that higher values of $\mathbb{E}[r]$ imply greater persistence (as measured by, for example, the chance of a population visiting the extinction zone or invading a community), on which the practical strategy of "decompose and compare" is based, is very problematic.

As a simple example one may think about stochastic-logistic systems. In these systems the intrinsic growth rate of the focal species, $r(t)$, fluctuates in time, such that its mean is $\mathbb{E}[r]$, its variance is σ^2 and the typical correlation time of the environment is δ . The mean time to extinction when N is large and $\mathbb{E}[r] > 0$ scales like $N^{\mathbb{E}[r]/g}$, where, as above, $g = \sigma^2\delta/2$ measures the strength of the stochastic abundance fluctuations. Accordingly, two systems with the same $\mathbb{E}[r]$ may have different persistence properties if the value of g is different.

For stochastic-logistic dynamics, it is still true that an increase in $\mathbb{E}[r]$ leads to an increase in the persistence *if* g is kept fixed. In such systems, the value of $\mathbb{E}[r]$ may be used for comparison between different cases with the same g (the larger the value of $\mathbb{E}[r]$, the more stable the coexistence state) or as a measure of structural stability (i.e. how far the system is from the transition at $\mathbb{E}[r] = 0$).

For dynamics wherein stochastic environmental fluctuations produce a stabilising mechanism that promotes coexistence, the situation is more intricate. Parameters like δ and σ control both the amplitude of the stochastic abundance variations g and (through the stochasticity-induced stabilising mechanism, like the storage effect) the value of $\mathbb{E}[r]$. As the same environmental factors govern the mean growth rate and the amplitude of the abundance fluctuations, one cannot consider these

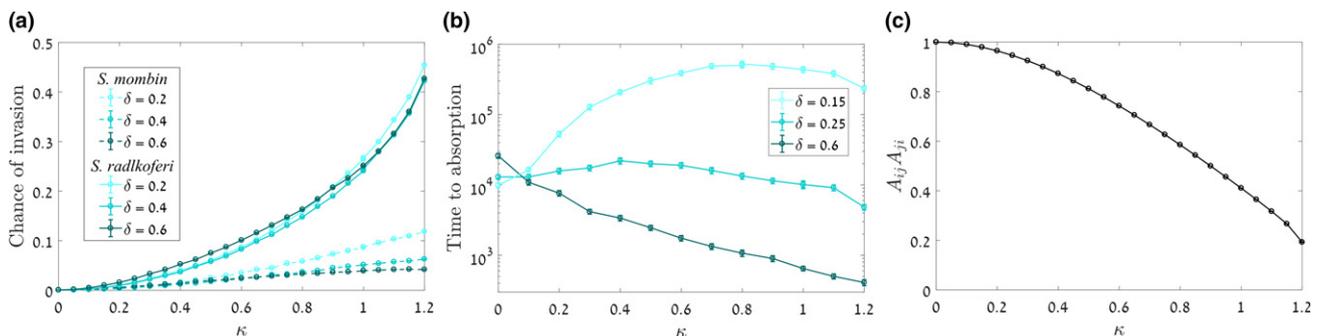


Figure 4 The chance of invasion [panel (a), dashed lines for *Spondias mombin*, full lines for *Spondias radlkoferi*] and the mean time to absorption [panel (b)] are plotted against the amplitude of stochastic environmental fluctuations κ for the forest dynamics model of Usinowicz *et al.* (2012, 2017) for various values of δ (temporal correlation of environmental fluctuations). The case $\kappa = 1$ corresponds to the environmental stochasticity in Usinowicz *et al.* (2012) and we explore the parameter space for lower and higher stochasticity in the environment. The details of the model (which includes demographic stochasticity) and the simulation procedure are given in Supplement 5. Note that for $\kappa \geq 1.171$ some of the modified recruitment rates [eqn (S25)] become negative, so we restrict the plots to smaller κ -values. The dependence of the $A_{ij}A_{ji}$ metric used in Usinowicz *et al.* (2012, 2017) on κ is shown in panel (c). The metric $A_{ij}A_{ji}$ decreases with increasing κ [panel (c)], and thus greater κ should indicate greater persistence properties. Instead, the mean time to absorption sometimes increases and sometimes decreases with κ . In this case, the chance of invasion indeed increases when $A_{ij}A_{ji}$ decreases.

quantities independently anymore. As shown throughout this paper, this implies that $\mathbb{E}[r]$ is not a reliable metric for persistence.

In this study, we considered only two-species communities in order to clearly highlight the problems with using $\mathbb{E}[r]$ to measure persistence. MCT relies on the examination of the chance of invasion for each species given the background community. As long as the invading population is rare, it is reasonable to believe that the effect of all resident species may be incorporated into an ‘effective’ rival species, so our criticism extends *a priori* to models with more than two species. For the time to absorption, the situation in the presence of many species is more complicated and more work is needed; see Supplement 3 for further details.

The ineffectiveness of $\mathbb{E}[r]$ in quantifying persistence in multi-species communities is further supported by some recently published simulation results [Figs. 5 and 6 of Danino *et al.* (2016)], which show the species richness in high-diversity communities as a function of σ^2 . The model considered in Danino *et al.* (2016) supports stochasticity-induced stabilisation, so the mean growth rate when rare (for each population) increases with the amplitude of environmental variations σ . However, the species richness decreases with σ if the correlation time δ is long.

Is there any alternative indicator to $\mathbb{E}[r]$? As we have seen, when the diffusion approximation holds, the parameter $\mathbb{E}[r]/g$ governs the chance of invasion and the mean time to extinction. A recent work (Yahalom & Shnerb, 2019) suggests that when the dynamics of a population (when rare) are logistic or logistic-like, the persistence properties are determined by a parameter q that satisfies the equation

$$e^{-\delta\mathbb{E}[r]q} \cosh(\delta\sigma q) = 1. \quad (9)$$

The value of q converges to $\mathbb{E}[r]/g$ when the diffusion approximation holds, and the time to extinction scales like N^q even when the diffusion approximation does not hold.

For the moment, we believe that the simplest way to achieve the goals of MCT – to assess the persistence of species in a way that allows a quantitative comparison between different systems (e.g. forests) and a quantitative assessment of the relative contributions of different stabilising mechanisms (e.g. EC covariance vs. relative nonlinearity) – is by simulation of an appropriately calibrated model. These simulations can be used to estimate metrics that more directly measure persistence, such as the mean time to absorption, the chance of invasion of a species in a community, and species turnover rates.

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AUTHORSHIP

N.M.S. and J.P. led analyses and wrote the first draft; R.A.C. and T.F. contributed to analyses and to revising the text.

DATA AVAILABILITY STATEMENT

No new data were used.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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