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TECHNICAL COMMENT

Technical Comment on Pande *et al.* (2020): Why invasion analysis is important for understanding coexistence

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Abstract

Pande *et al.* (2020) point out that persistence time can decrease even as invader growth rates (IGRs) increase, which potentially undermines modern coexistence theory. However, because persistence time increases rapidly with system size only when IGR > 0, to understand how any real community persists, we should first identify the mechanisms producing positive IGR.

Keywords

Coexistence, invasion analysis, environmental variability, extinction, persistence.

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INTRODUCTION

Invasion analysis is central to coexistence theory (e.g. Chesson, 1994; Grainger *et al.*, 2019). Absent Allee effects and related complications (e.g. Barabás *et al.*, 2018, p. 292) we expect that two species coexist stably if each has a positive geometric mean population growth rate when rare (‘invasion growth rate’, IGR); similar invasion criteria imply coexistence in multi-species community models without demographic stochasticity (Schreiber, 2012; Benaïm and Schreiber, 2019; Hening *et al.*, 2020), meaning that all species maintain positive average long-term abundances.

Pande *et al.* (2020, hereafter PFCS) identified limits to IGRs as a quantitative measure of persistence, finding that $\bar{T}_{ext}$, the mean time to first extinction of a species, can sometimes decrease even as IGRs increase in finite population models. Communities with similar IGRs may differ substantially in $\bar{T}_{ext}$ and other persistence measures. They conclude that ‘one cannot quantify the contribution of a certain mechanism to persistence by comparing the value of [IGR] in the presence and in the absence of this mechanism’, directly challenging the current basis for both theoretical and empirical analyses of coexistence (e.g. Chesson, 1994, 2000; Angert *et al.*, 2009; Ellner *et al.*, 2016, 2019; Letten *et al.*, 2018; Hallett *et al.*, 2019).

We do not question any facts reported by PFCS, but we argue that they emphasised part of a larger picture, and therefore overstated implications for past and future research.

A two-species lottery model (Fig. 1a,b) illustrates why higher IGRs do not necessarily yield more robust persistence. IGR_1 (the IGR of the weaker competitor) increases with environmental variability, σ (the temporal standard deviation of log per capita fecundity). The weaker competitor quickly goes extinct when $IGR_1<0$ ($\sigma=0.2$) but not when $IGR_1>0$. But although IGR_1 is much larger at $\sigma=1.5$ than at $\sigma=0.6$, it is questionable whether persistence is stronger: excursions to low abundance are quickly reversed, but happen faster and more often. The same environmental fluctuations that boost IGR_1 through the storage effect increase the chance of extinction.

But Figs. 1a,b fail to show how persistence depends on scale (50 ha or whole forest?)[1]. Figs. 1c,d, inspired by Yahalom *et al.* (2019), display $\bar{T}_{ext}$ vs. the number of sites, N; curves are labelled in order of increasing IGR_1. $\bar{T}_{ext}$ increases slowly with N when $IGR_1<0$ and rapidly when $IGR_1>0$. When σ and δ (adult annual per capita mortality) both vary, the N dependence is more varied (Fig. 1D), but again, positive IGR_1 results in fast increase of $\bar{T}_{ext}$ with N. In these examples, $\bar{T}_{ext}$ increases with IGR_1 at large N, but this may not always occur; a mechanism increasing IGR_1 but decreasing mean population size can decrease $\bar{T}_{ext}$ (Schreiber *et al.*, 2018).

Persistence times diverge even more strongly with the sign of IGR_1 when demographic rather than environmental stochasticity is dominant (Fig. 2) and coexistence is fluctuation-independent. For all but the smallest systems, even mildly positive IGR_1 produces very long persistence. In general, when invasibility criteria apply, we expect logarithmic scaling of $\bar{T}_{ext}$ with N when $IGR_1<0$ and either power-law (Fig. 1c,d) or exponential scaling (Fig. 2a,b) when $IGR_1>0$, depending on whether extinctions are mainly driven by environmental or demographic stochasticity (see e.g. Assaf and Meerson (2017); Doering *et al.* (2005); Faure and Schreiber (2014); Yahalom and Shnerb (2019); Yahalom *et al.* (2019)).

IGR_1 thus emerges as a crucial persistence metric because it marks a transition between slow and rapid scaling of persistence time with system size, so that significantly positive values of IGR_1 lead to long persistence at all but small scales (e.g. Fig. 2c,d).

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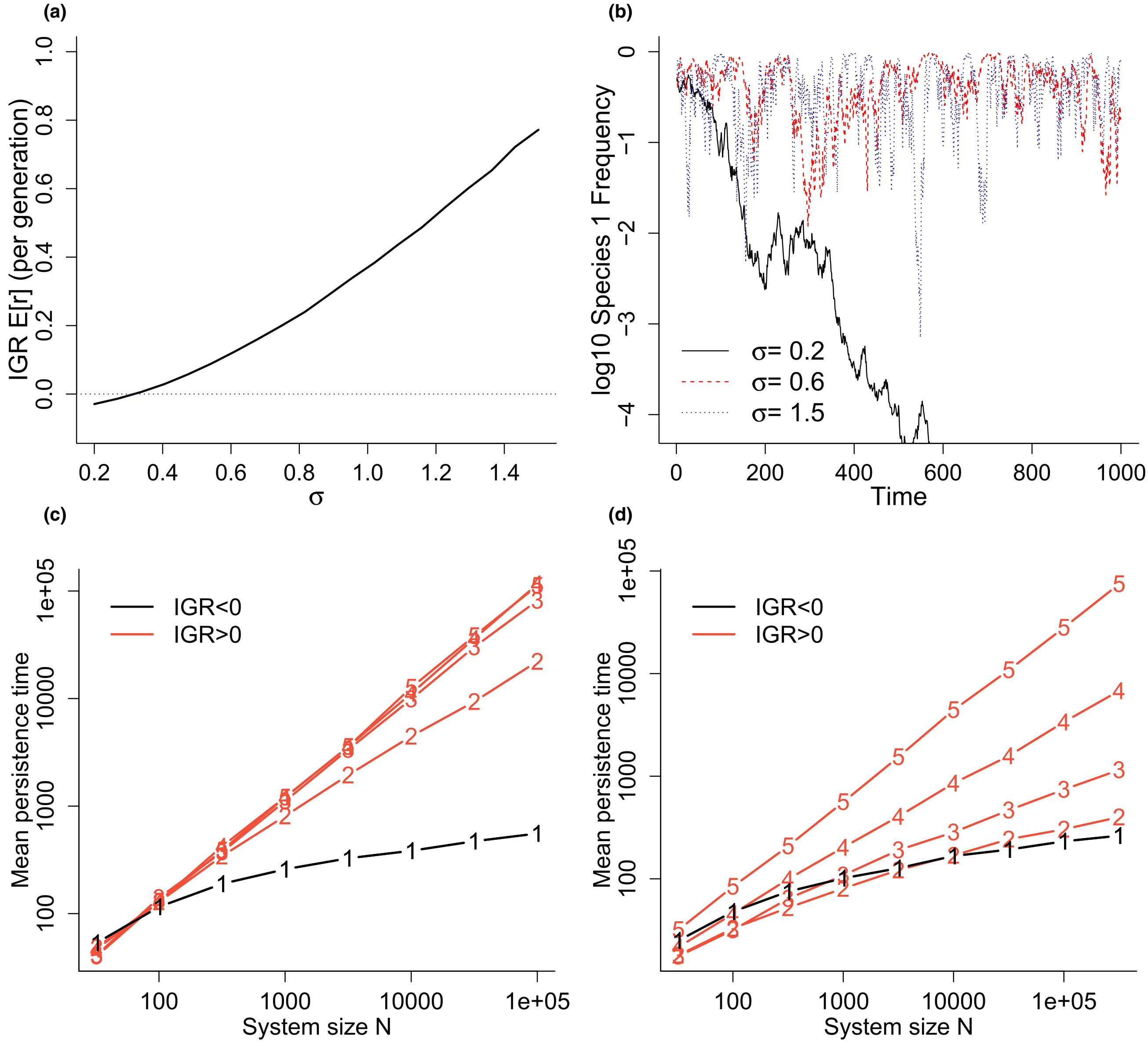

Figure 1 Simulation results for an asymmetric lottery model with lognormal temporal variation in per capita fecundity, $\log B_j(t) \sim \text{Normal}\left(\mu_j,\sigma^2\right), \mu_1=0.45, \mu_2=0.5$. (a) IGR_1 (the smaller of the two IGRs) with $\delta=0.5$. (b) Simulations of the continuous-state model (in infinite-N limit, where N is the total number of sites) with different σ values, $\delta=0.5$. (c) Average time to first species loss in 500 simulations of the finite-N model with different σ values, $\delta=0.5$. Simulations started with $n_1(0)=n_2(0)=N/2$. In each time step, random coin-tosses determined whether each adult dies (probability δ) or lives, and whether each site vacated by mortality is occupied by species 1 (probability $B_1(t)n_1(t)/(B_1(t)n_1(t)+B_2(t)n_2(t))$) or by species 2. σ values on curves 1–5 are (0.2, 0.6, 1, 1.5, 2), respectively, and IGR_1 values are $(-0.015, 0.06, 0.18, 0.39, 0.62)$. (d) As in C), varying both σ and δ. Curves 1–5 have $IGR_1=(-0.039,0.044,0.207,0.407,0.614)$ resulting from $\sigma=(0.4,0.8,1.2,1.6,2.0)$ and $\delta=(0.95,0.85,0.75,0.65,0.55)$. Figure made by scripts Figure 1.R and finiteLotteryTbarScaling{1,2}.R

Because extended persistence is only possible when $IGR_1>0$, understanding how a real community persists must begin by identifying the mechanisms contributing to positivity of IGR_1. While PFCS acknowledged that the sign of IGR_1 can be used as an indicator of persistence, they criticise papers doing exactly that. Ellner *et al.* (2019) asked: ‘If we observe that two warbler species forage in different parts of the tree, is this crucial for coexistence, or irrelevant because neither species is resource-limited?’’ *Contra* the ‘cease and desist’ advice from PFCS (quoted above), the way to start answering that question is by comparing IGRs for each species in the presence and absence of each mechanism, as we and others have done (e.g. Angert *et al.*, 2009; Usinowicz *et al.*, 2012; Letten *et al.*, 2018; Hallett *et al.*, 2019). Analysis of IGRs can be supplemented when necessary with other persistence metrics (Jeltsch *et al.*, 2019); a challenge for future research will be to understand when and how the positive relationship between IGR_1 and $\bar{T}_{ext}$ breaks down.

In principle, any persistence metric, including $\bar{T}_{ext}$, can be partitioned into contributions from different mechanisms, as

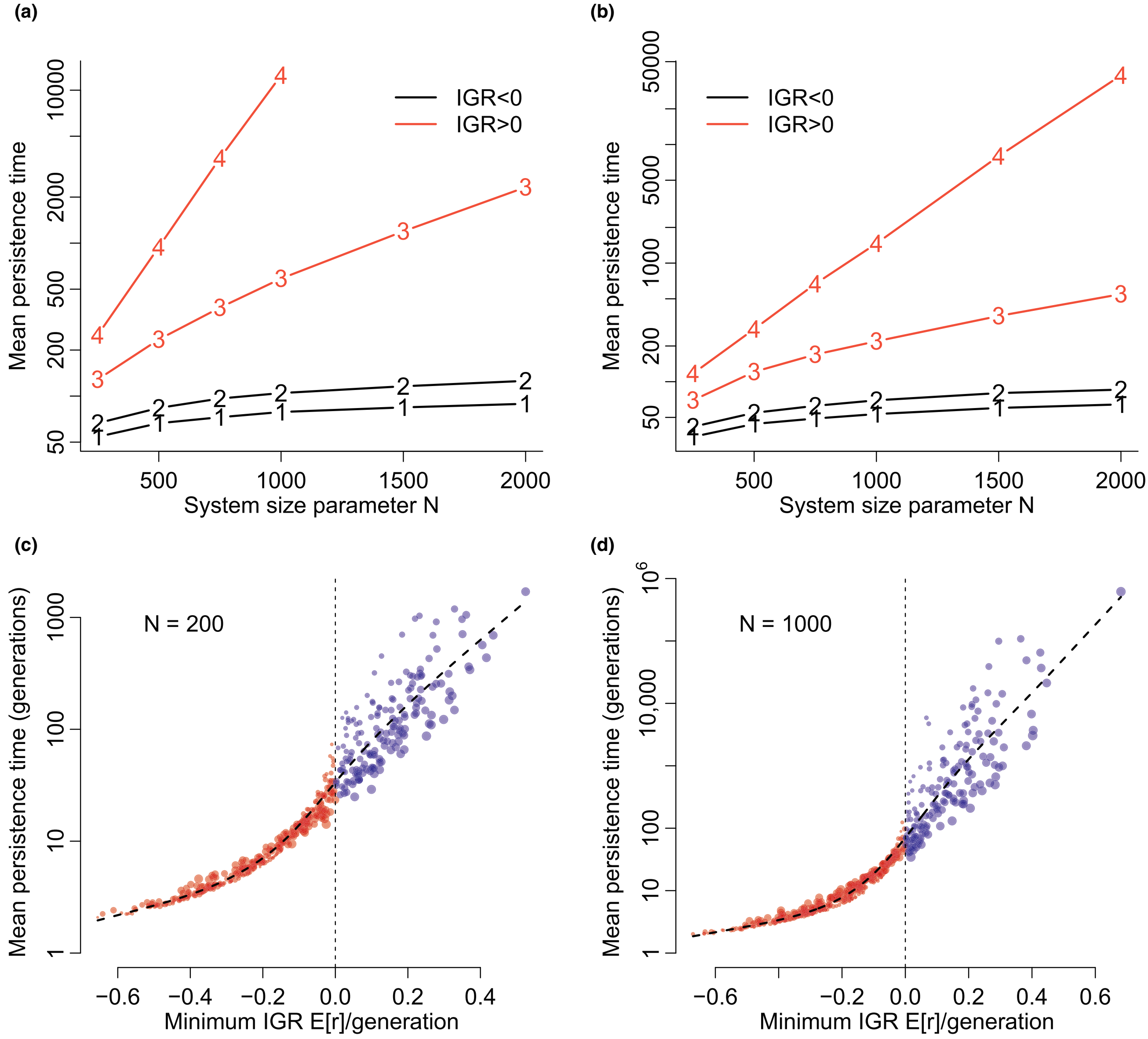

Figure 2 (a,b) Simulation results for the Watkinson annual plant competition model with demographic and environmental stochasticity. For populations $n_i(t)$ in year t, $i=1,2$, expected populations in year t+1 are $\bar{n}_i(t+1)=\lambda_i(t)n_i(t)/(1+a_{i,1}n_1(t)+a_{i,2}n_2(t))$ and actual populations are Poisson with means $\bar{n}_i(t+1)$. We set $a_{1,1}=a_{2,2}=1/N$ and $a_{1,2}=a_{2,1}=\rho a_{1,1}$, and $\lambda_i(t)$ were Uniform $[0.9\bar{\lambda}_i, 1.1\bar{\lambda}_i]$ independent over time: mild environmental stochasticity that does not maintain coexistence or cause extinction. Absent stochasticity each species alone has stable equilibrium $N(\bar{\lambda}_i-1)$, so N is a measure of system size, and both coexist stably if $\rho<(\bar{\lambda}_i-1)/(\bar{\lambda}_j-1)<1/\rho$ for $i=1,j=2$ and vice-versa. Simulations started with $n_1=n_2=N/2$. (a) Average time to first species loss in 1000 simulations with small fecundity differences ($\bar{\lambda}_1=1.4,\bar{\lambda}_2=1.5$) and $\rho=(1.2,1.1,0.9,0.8)$ times the maximum ρ allowing coexistence. IGRs for species 1 (the weaker competitor) are weakly dependent on N, but are approximately $(-0.05,-0.03,0.03,0.06)$ on curves 1–4. (b) as in A) with $\bar{\lambda}_1=1.4,\bar{\lambda}_2=2.5$. IGRs for species 1 are approximately $(-0.06,-0.03,0.03,0.06)$ on curves 1–4. (c,d) Simulation estimates of mean extinction time for the finite-population lottery model (as in Fig. 1c,d) with 500 randomly chosen parameter sets: means and standard deviations of log per capita fecundity were Uniform [0,1], and δ was Uniform [0.2,0.5]. Mean persistence times were estimated by the Aldous algorithm (Schreiber et al. 2018) with simulation lengths 10^5 and 10^6 for N = 200 and 1000, respectively, 25 replicates for each parameter set. Circle size is proportional to fecundity variability. The dashed line is a nonparametric regression of log persistence time in generations on IGR_1 per generation (using gam in **mgcv**). Figure made by WatkinsonSimulateTbarScaling.R and Lottery-random-sampling.R

in invasion analysis (Ellner *et al.*, 2019). However, at present, that is easier said than done. Differences between long persistence times (between two communities, or with/without a mechanism) are hard to estimate by simulation (but may be ecologically irrelevant, if both exceed the time scale of environmental change). Estimating $\bar{T}_{ext}$ requires much more information, for example while mean per capita fecundity suffices for IGR_1, extinction risk depends on the entire probability distribution of offspring numbers. It is also not evident if or how the canonical fluctuation-dependent mechanisms

(Chesson, 1994, 2000) extend to other persistence metrics. We need new theory to relate other persistence metrics to underlying ecological mechanisms.

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AUTHORSHIP

All authors discussed all aspects of the research and contributed to writing and revising the paper. SPE and SJS wrote simulation scripts.

OPEN RESEARCH BADGES

This article has earned an Open Materials badge for making publicly available the components of the research methodology needed to reproduce the reported procedure and analysis. All materials are available at https://doi.org/10.6084/m9.figshare.12515422

DATA AVAILABILITY STATEMENT

No original data appear in this paper. Computer scripts supporting all results are archived at figshare, https://doi.org/10.6084/m9.figshare.12515422.

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