

## RESEARCH ARTICLE

# Invasions of ecological communities: Hints of impacts in the invader's growth rate

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## Abstract

1. Theory in ecology and evolution often relies on the analysis of invasion processes, and general approaches exist to understand the early stages of an invasion. However, predicting the long-term transformations of communities following an invasion remains a challenging endeavour.
2. We propose a general analytical method that uses both resident community and invader dynamical features to predict whether an invasion causes large long-term impacts on the invaded community.
3. This approach reveals a direction in which classic invasion analysis, based on initial invasion growth rate, can be extended. Indeed, we explain how *the density dependence* of invasion growth, if properly defined, synthetically encodes the long-term biotic transformations caused by an invasion, and therefore predicts its ultimate outcome. This approach further clarifies how the density dependence of the invasion growth rate is as much a property of the invading population as it is one of the invaded community.
4. Our theory applies to any stable community model, and directs us towards new questions that may enrich the toolset of invasion analysis, and suggests that indirect interactions and dynamical stability are key determinants of invasion outcomes.

## KEYWORDS

adaptive dynamics, alternative stable states, coexistence, ecological stability, extinctions, feedback loops, invasion fitness, press perturbation

## 1 | INTRODUCTION

Predicting the outcome of introducing a new species or phenotype in a resident community is key to answering fundamental as well as

applied ecological and evolutionary questions (Elton, 1958). Invasion analysis is invoked to understand evolutionary adaptation, epidemics, species coexistence and ecosystem assembly (Chesson, 2000; Law & Morton, 1996; O'Sullivan et al., 2019), while also playing an

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instrumental role in guiding management and conservation efforts in relation to invasive species (Galiana et al., 2014; Pimm, 1991; Williamson, 1999).

To analyse the initial stages of an invasion, powerful theoretical approaches exist, built on the notion of invasion fitness (from the invader's perspective) or invasibility (from the resident community's perspective; Geritz et al., 1998a; Grainger et al., 2019; Guo et al., 2015; Metz et al., 1995; Turelli, 1978). In essence, these approaches ask under which conditions the invader can grow and spread from a small initial population. The invasibility of a community involves both environmental conditions and direct interactions between the invader and resident species. These properties are the most studied aspects of the invasion process (Blackburn et al., 2011; Jiménez-Valverde et al., 2011; Sol et al., 2012), and determine whether the biotic and abiotic environments are favourable to the invader (Guo et al., 2015), and how this can be predicted in terms of environmental conditions and functional traits of the organisms (Eisenhauer et al., 2013; MacDougall et al., 2009). A large empirical literature also emphasizes the probabilistic nature of all stages leading up to the initial establishment and survival of an invader population (Blackburn et al., 2011), which has led to theoretical developments accounting for stochasticity (Pande et al., 2020b).

But if we know that an invader population can establish, can we predict the invasion's long-term consequences (Levine et al., 2003), such as whether it drives other species to extinction or even causes an ecosystem-wide regime shift (Gaertner et al., 2014; Kotta et al., 2018; Scheffer et al., 2001)? These long-term consequences are not only tied to characteristics of the invader and its immediate interaction partners (predators, prey, competitors, etc.), but also they can involve the whole web of interactions in the resident community (Hui & Richardson, 2019; Rossberg & Barabás, 2019; White et al., 2006). These consequences may thus be highly unpredictable (Catford et al., 2019), both because of their complexity and because few, if any, interaction networks are exhaustively known and accurately quantified (Frost et al., 2019). The question is, therefore, whether we can understand the essential features of invader and resident communities that control the qualitative nature and magnitude of long-term impacts, from benign effects to major extinction events.

We propose an extension of classic invasion analysis that sheds new light on the question of long-term invasion outcomes. Our premise is that one should not only consider the initial growth rate of the invading population, but also the way this growth rate changes as the invading population expands and modifies its biotic and abiotic environments. These feedbacks are generally acknowledged, but considered too complex to measure or predict. Yet, we show that it is possible to construct a synthetic indicator that plays a similar role to the invasion growth rate: it encapsulates a variety of factors (e.g. environmental characteristics and species interactions) into a single number that hints at, if not fully determines, the outcome of the invasion process.

By combining invasion fitness and our measure of feedbacks, we draw a two-dimensional map of invasion scenarios, from which we can extrapolate both the eventual outcome for the invader, and its impact on the community of resident species. This extrapolation is exact for simple models, but it is also qualitatively successful for more complex interaction types, network structures, functional responses, or even when interactions between species are influenced by latent variables, such as unobserved species or resources. We first apply this idea to the case of two competing species, where it naturally connects with known results of coexistence theory and adaptive dynamics (Brännström et al., 2013; Champagnat et al., 2002; Dieckmann & Law, 1996; Geritz et al., 1998b; Meszéna, 2005; Meszéna et al., 2005; Metz et al., 1996; Roughgarden, 1983). We show, in particular, that when the total feedback on the invader is positive, signalling the existence of alternative stable states, the invasion is likely to cause an irreversible shift in community state. We then consider linear and nonlinear species-rich model communities to illustrate the general predictive power of our theory.

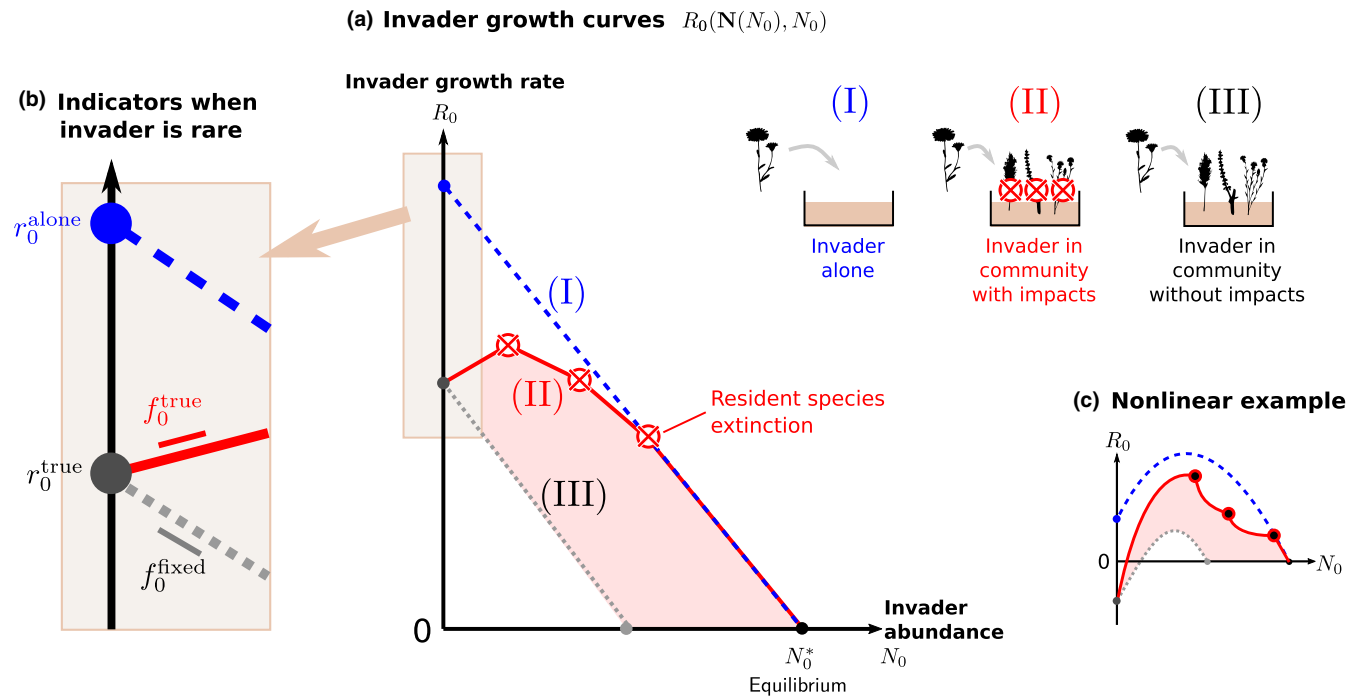
Overall, our work showcases the important information on biotic impacts that can be extracted from analysing the invader's dynamics, even without a detailed knowledge of the invaded community. We show that the invader's impact can be understood as a change of the community's biotic environment, and thus, our theory reveals a connection between a community's robustness against environmental perturbations (Barabás et al., 2014; Ives & Carpenter, 2007; Meszéna et al., 2006) and its vulnerability to invasions. Our approach suggests novel empirical intuitions, revealing feedbacks and stability as understudied, yet central, drivers of invasion dynamics.

## 2 | AN EXTENSION OF INVASION ANALYSIS

As usual in invasion analysis (Barabás et al., 2018; Geritz et al., 1998a; Lewis et al., 2016; Turelli, 1978; Williamson, 1999), we start from a stable resident community comprised of  $S$  resident species, to which we add a small invading population. Stochasticity can be a determinant factor of invasion success in the early stages of establishment so that the invasion growth rate is not necessarily a good quantitative metric of success (Pande et al., 2020b). Here, we consider whether invasion is deterministically possible (Pande et al., 2020a), and more importantly, what will be its impact if successful, assuming that in that case, the invader population will be large enough that demographic stochasticity can be neglected (Blackburn et al., 2015).

We will take two complementary perspectives. First the one of the invader, and then that of the invaded community. The first allows us to derive essential characteristics of the invasion dynamics, such as whether the invader is expected to coexist with resident species or whether it will cause abrupt shifts in abundance and composition. From the second perspective, we relate these





**FIGURE 1** Observing invasion outcomes and impacts through the invader's density-dependent growth curves. (a) Three theoretical curves of invader growth rate  $R_0$  versus invader abundance  $N_0$  can be drawn, depending on whether (I) resident species are absent ( $R_0^{\text{alone}}$  in the main text), (II) residents are allowed to settle at a new equilibrium impacted by the invader  $N(N_0)$  and some may go extinct ( $R_0^{\text{true}}$ ), or (III) residents are maintained at their pre-invasion abundances ( $R_0^{\text{fixed}}$ ). The latter two curves would be observed empirically if resident species dynamics were, respectively, (II) much faster or (III) much slower than the invader's. The red shaded area provides an indication of how much the invasion dynamics impact resident species abundances. The piecewise linear growth curves shown here arise in a Lotka–Volterra model (15). (b) By a linear expansion of the growth curves for rare invaders  $N_0 \approx 0$ , we define initial growth rates  $r_0$  and slopes  $f_0$ , the latter representing density dependence, that is, feedbacks on invader growth occurring through resident species and the invader itself. (c) A more general dynamical model may exhibit nonlinear growth curves, such as an Allee effect for the invader alone. Yet, our overall argument and results from linear approximations are still expected to apply

characteristics to species interactions and resident community stability, and explain how, from both the invasion fitness and feedbacks, we can approximate long-term impacts on resident species (e.g. relative change in species abundance or extinctions). We illustrate the predictive power of our approach on examples that range from a simple two-species system to random multispecies Lotka–Volterra communities, and structured food webs with nonlinear functional responses.

## 2.1 | Probing the community's response through its feedback on the invader

We start from the perspective of the invading population. Our central argument, illustrated in Figure 1, is that transformations in the resident community are partially reflected in the growth rate of the invader itself. We suppose that the invading population, whose abundance we denote  $N_0$ , follows some potentially complex, yet deterministic, dynamics of the form

$$\frac{1}{N_0} \frac{dN_0}{dt} = R_0(\mathbf{E}), \quad (1)$$

where  $\mathbf{E}$  is a vector of latent dynamical variables representing the full abiotic and biotic environments of the invader. We hereafter use the shorthand<sup>1</sup>

$$R_0(\mathbf{E}) = R_0(\mathbf{N}, N_0), \quad (4)$$

displaying only the dependence in  $N_0$  and in the abundances  $\mathbf{N} = (N_i)_{i=1, \dots, S}$  of resident species on which we intend to measure the impacts of the invasion. Let us further assume that resident species are at a stationary state  $\mathbf{N}_{/0}^*$  (the abundances without the invader species  $i = 0$ ) prior to the invasion of species 0.

<sup>1</sup>The instantaneous growth rate (1) could be affected or even fully mediated by various latent variables, such as pH (Ratzke & Gore, 2018), metabolite concentration (Goldford et al., 2018), abundances of auxiliary species and resources (see Section S4 and Figure S2 in the Appendix) or even phenotypic modifications in the populations such as adaptive foraging (Valdovinos & Marsland III, 2021; Valdovinos et al., 2013), and whose time-scale of change could be comparable to population dynamics. To deal with this potential complexity, we fix invader and resident abundances and let all latent variables relax to steady values. Those values, if the dynamics are deterministic, will be uniquely determined by the invader and resident species abundances:

$$\lim_{t \rightarrow \infty} \mathbf{E}(t) = \mathbf{E}^*(\mathbf{N}, N_0). \quad (2)$$

Thus, our shorthand denotes

$$R_0(\mathbf{N}, N_0) = R_0(\mathbf{E}^*(\mathbf{N}, N_0)). \quad (3)$$

It is a common practice in population biology to plot population growth rate against abundance, and use this density-dependent growth curve to analyse both short- and long-term dynamics (Arim et al., 2006; Sibly et al., 2005). At first glance, this is not possible in our case due to the fact that  $R_0$  depends on many other variables  $\mathbf{N}$ . Yet, if we assume that population dynamics always reach steady states, there is a way to define an effective one-dimensional growth curve, and study it in the classic way. To deduce an estimation of invasion impact, we will consider three different growth curves, all drawn in Figure 1, and corresponding to different scenarios.

The first scenario corresponds to the actual invasion. To draw the associated growth curve, we assume that, for each possible value  $N_0$ , we maintain the invader population density fixed until the community settles to a new steady state. Because initial conditions are fixed, and the dynamics are deterministic, there will be a unique equilibrium vector  $\mathbf{N}^*(N_0)$ , where some resident species may have gone extinct. Therefore, we can define a growth rate function  $R_0^{\text{true}}$  (solid red line in Figure 1) that *only* depends on  $N_0$ , in the following way:

$$R_0^{\text{true}}(N_0) = R_0(\mathbf{N}^*(N_0), N_0), \quad (5)$$

We generally expect this curve to decrease at larger values of  $N_0$ , indicating effective self-limitation: the expanding invader population transforms the environment in a way that makes it less favourable to its growth. The invasion ends at the first value  $N_0$  where  $R_0^{\text{true}}$  vanishes after having been positive, that is, where the curve crosses the horizontal axis from above.

In a second scenario, we assume instead that resident species abundances are kept fixed at their initial values prior to the invasion,  $\mathbf{N}_{/0}$ . Again, we can define a growth curve that depends only on  $N_0$  (dotted grey line in Figure 1).

$$R_0^{\text{fixed}}(N_0) = R_0(\mathbf{N}_{/0}, N_0). \quad (6)$$

Our central insight is that any transformation in the environment that feeds back onto the invader will lead to a difference between the two growth curves  $R_0^{\text{true}}$  and  $R_0^{\text{fixed}}$ . Thus, if we had the possibility of accessing these curves, the gap between them (red shaded area in Figure 1) would provide a hint of whether resident species densities change in response to the invasion.

Given this qualitative indicator of whether resident species are impacted, how can we turn it into a quantitative metric of whether the impact is mild or severe? We propose that the deviation between  $R_0^{\text{true}}$  and  $R_0^{\text{fixed}}$  must be expressed in relative terms, using a third curve: the growth curve observed if there had been no resident species at all (dashed blue line in Figure 1).

$$R_0^{\text{alone}}(N_0) = R_0(0, N_0). \quad (7)$$

If, for instance, the invader eventually drives all resident species extinct as  $N_0$  increases, then the true growth curve  $R_0^{\text{true}}$  will depart from the impact-less curve  $R_0^{\text{fixed}}$ , and will eventually converge to the

curve drawn in the absence of resident species  $R_0^{\text{alone}}$  (Figure 1a). In general, the invader need not cause extinctions, and resident populations could even increase through predation or facilitation. In that case,  $R_0^{\text{true}}$  will move away from  $R_0^{\text{alone}}$ . In any case, the difference between  $R_0^{\text{fixed}}$  and  $R_0^{\text{alone}}$  gives us a reference measure for the difference between the unperturbed environment and the bare one, to which we can compare the measured effect of the invader.

Thus, using all three growth curves, for a given invader abundance  $N_0$ , we get a dimensionless measure of the invasion impacts as:

$$\left| \frac{R_0^{\text{true}}(N_0) - R_0^{\text{fixed}}(N_0)}{R_0^{\text{alone}}(N_0) - R_0^{\text{fixed}}(N_0)} \right| \quad (8)$$

Absolute values are there to ensure that we quantify absolute impact. This quantifies, in relative terms, how different the environment has become, from the perspective of the invading species, compared to what it would have been if the invader had no impact on the resident community. The ultimate impact is found by evaluating this expression at the final invader abundance  $N_0^*$ , where  $R_0^{\text{true}}$  vanishes.

We will provide a linear approximation for this quantity and show that this intuitive characterization of invasion impacts can be formally linked to measurable changes of abundances in the community.

There are two caveats. First, we can only measure those changes in the community that feedback on the invader, so we cannot see impacts on resident species that have no direct or indirect effect on  $R_0$ . Second, we generally do not expect to be able to fully access these three density-dependent growth curves, in either theory or experiment. This limitation motivates our next step: finding approximate indicators that can be deduced from small perturbations of the resident community.

## 2.2 | Linearization near invader rarity

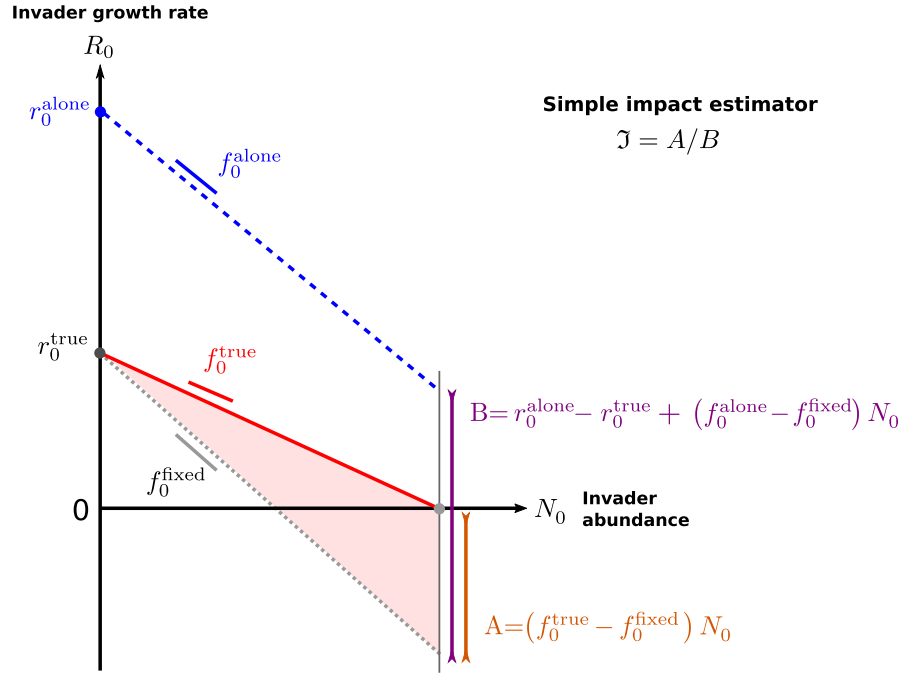
Invasion analysis classically focuses on the early stages of an invasion, when the invader population is small (Metz et al., 1995). Here, we will also consider a small invader population, and analyse the growth curves  $R_0^{\text{true}}$ ,  $R_0^{\text{fixed}}$  and  $R_0^{\text{alone}}$  near  $N_0 = 0$ . However, we do not only consider short-term effects: the curve  $R_0^{\text{true}}$  incorporates the long-term response of the community, measuring it would require keeping the invader population small until residents reach a new equilibrium. Our analysis provides simple indicators that can be extrapolated to predict long-term invasion dynamics beyond the limit of small populations. We later discuss the theoretical interpretation and empirical accessibility of these indicators.

Evaluated at  $N_0 = 0$ , the two curves  $R_0^{\text{true}}$  and  $R_0^{\text{fixed}}$  coincide at the initial growth rate of the invading population, called invasion fitness, or Invasion Growth Rate (Ellner et al., 2020). We denote it as

$$r_0^{\text{true}} = R_0^{\text{true}}(0) = R_0(\mathbf{N}_{/0}, 0). \quad (9)$$

We also denote the initial growth rate of the invading population in the absence of resident species as:

**FIGURE 2** Geometric argument for the linear approximation (14) of our heuristic impact metric (8). The value chosen for  $N_0$  is the one where the linear approximation of  $R_0^{\text{true}}$  vanishes, a simple way to guess what the ultimate invader abundance will be. We can trust this guess only for strongly negative feedbacks (thus leading to a low  $N_0$ ). Note that in Equation (14), we neglect the second term in (B), only retaining first order terms in  $N_0$



$$r_0^{\text{alone}} = R_0^{\text{alone}}(0) = R_0(0, 0), \quad (10)$$

representing the invasion fitness in the bare environment.

If  $r_0^{\text{true}} < 0$ , the species cannot grow if rare. By construction, invasion fitness describes short-term dynamics immediately after the species' introduction. It does not account for any feedbacks caused by the invading population itself, since the invader is too rare to have an appreciable influence on the residents. Invasion fitness measures how initially favourable the resident community is to the invader species, both in terms of abiotic and biotic conditions, and common approaches of invasion analysis mainly focus on this quantity (Geritz et al., 1998b; Lewis et al., 2016; Metz et al., 1995; Turelli, 1978; Williamson, 1999).

To provide an indicator of long-term effects, we expand the growth curves beyond their initial value by computing their initial slope, that is, their derivatives at the steady state prior to the invasion. The initial slope of the growth curve including impacts on resident species

$$f_0^{\text{true}} = \frac{dR_0^{\text{true}}}{dN_0}, \quad (11)$$

is a simple measure of the effective feedbacks that the invader experiences from its environment, including itself and other species. By contrast,

$$f_0^{\text{fixed}} = \frac{dR_0^{\text{fixed}}}{dN_0}, \quad (12)$$

represents the feedback of the invader on itself: the density dependence of its growth if it did not impact the resident community, or did not experience any feedbacks from it.<sup>2</sup>

<sup>2</sup>This density dependence represents intraspecific feedbacks in an environmental context that may still have been affected by the presence of resident community. Thus, it is not necessarily equal to the feedback  $f_0^{\text{alone}} = dR_0^{\text{alone}}/dN_0$  observed if the invader was alone.

Let us note that if  $f_0^{\text{true}}$  is strongly negative, we expect the growth curve  $R_0^{\text{true}}$  to rapidly decrease to zero, meaning that the invader will typically attain equilibrium at a small population

$$R_0^{\text{true}}(N_0) = 0 \Leftrightarrow N_0 \approx -r_0^{\text{true}}/f_0^{\text{true}}, \quad (13)$$

In that linear approximation, we can see from simple geometric arguments (Figure 2) that our indicator of impact on the community defined above in (8) becomes, at first order<sup>3</sup> in  $N_0$

$$\mathfrak{I} = \left| \frac{(f_0^{\text{true}} - f_0^{\text{fixed}}) N_0}{r_0^{\text{alone}} - r_0^{\text{fixed}}} \right|, \quad (14)$$

We will show that this expression can be recovered by explicitly analysing how species abundances in the resident community are impacted by the invasion.

## 2.3 | Invasion scenarios

The reasoning in the previous section suggests using the difference between  $f_0^{\text{true}}$  and  $f_0^{\text{fixed}}$  as a simple indicator of how the invader is transforming its environment as its abundance increases. For instance,  $f_0^{\text{true}} < f_0^{\text{fixed}}$  means that impacts on resident species induce a negative feedback on the invader (e.g. a predator depleting its prey and therefore hindering its own growth), and conversely if

<sup>3</sup>The complete expression being

$$\mathfrak{I} = \left| \frac{(f_0^{\text{true}} - f_0^{\text{fixed}}) N_0}{r_0^{\text{alone}} - r_0^{\text{fixed}} + (f_0^{\text{alone}} - f_0^{\text{fixed}}) N_0} \right|,$$

which corresponds to (14) at first order in  $N_0$ , unless the difference in initial growth rates is also of the order of  $N_0$ , a highly untypical behaviour, since these growth rates do not depend, a priori, on  $N_0$ .

TABLE 1 Notations used throughout the manuscript with Lotka–Volterra models as a special case

Definition	Notation	General expression	Lotka–Volterra models
Invader density	$N_0$		
Resident species	$i, j \in \{1, \dots, S\}$		
Initial resident state	$\mathbf{N}_{/0}^* = (N_{i/0}^*)$		
Community at fixed $N_0$	$\mathbf{N}^*(N_0) = (N_i^*(N_0))$		
Effective growth rate	$R_0(\mathbf{N}^*, N_0)$	$R_0(\mathbf{E}^*(\mathbf{N}^*, N_0))$ E: latent variables	$r_0 + A_{00}N_0 + \sum_i A_{0i}N_i^*$
Invasion fitness if alone	$r_0^{\text{alone}}$	$R_0(0, 0)$	$r_0$
Invasion fitness	$r_0^{\text{true}}$	$R_0(N_{/0}^*, 0)$	$r_0 + \sum_i A_{0i}N_{i/0}^*$
Initial total feedbacks	$f_0^{\text{true}}$	$\frac{dR_0}{dN_0}$	
Initial intraspecific feedbacks	$f_0^{\text{fixed}}$	$\frac{\partial R_0}{\partial N_0}$	$A_{00} \leq 0$
Initial community feedbacks	$f_0^{\text{true}} - f_0^{\text{fixed}}$	$\sum_{i,j} \frac{\partial R_0}{\partial N_i} \frac{\partial N_{i/0}^*}{\partial R_j} \frac{\partial R_j}{\partial N_0}$	$\sum_{i,j} A_{0i} \left( -A_{/0}^{-1} \right)_{ij} A_{j0}$
Indicator of impact	$\mathfrak{I} = \left  \frac{f_0^{\text{true}} - f_0^{\text{fixed}}}{r_0^{\text{true}} - r_0^{\text{alone}}} N_0 \right $	$N_0 = 0, \left  \frac{r_0^{\text{true}}}{f_0^{\text{true}}} \right  \text{ or } \left  \frac{r_0^{\text{alone}}}{f_0^{\text{fixed}}} \right $	

$f_0^{\text{true}} > f_0^{\text{fixed}}$  (e.g. a species weakening its competitors and therefore enhancing its own growth).

In fact, by mapping out the magnitudes of  $r_0^{\text{true}}$  and  $f_0^{\text{true}}$ , we identify five different invasion scenarios. These are described and summarized in Box 1, and justified more formally in Appendix S1. The five scenarios are as follows: No Invasion (NI), Enhanced Regulatory feedbacks (ER), Reduced Regulatory feedbacks (RR), Positive Feedbacks (PF) and Allee Effect (AE). The first three scenarios correspond to negative total feedbacks. The last two correspond to cases where total feedbacks  $f_0^{\text{true}}$  are positive. There the invading population cannot remain small, even if its invasion fitness is arbitrarily low.<sup>4</sup> In the last scenario (AE), we can predict the occurrence of alternative states of the invader–resident system. In this case, if  $f_0^{\text{true}}$  is positive while  $f_0^{\text{fixed}}$  is negative, the occurrence of alternative stable states is an emergent property of community dynamics.

## 2.4 | Relating indicators to species interactions and community stability

So far, we have defined the growth curves and derived indicators abstractly, without connecting them explicitly to properties of the invader and the resident community, including species abundance and interactions. Let us now assume that the growth rates of resident species are likewise described by differentiable functions of species abundances  $R_i(\mathbf{N}, N_0)$ .

As for the invader, these growth rate functions do not necessarily represent instantaneous population growth rates  $\left( \frac{1}{N_i} \frac{dN_i}{dt} \right)$ , but can be mediated by other factors. To be more concrete, we also introduce the particular example of the Lotka–Volterra model, which

provides useful interpretations for the quantities that we manipulate, where

$$R_i(\mathbf{N}, N_0) = r_i^{\text{alone}} + \sum_{j=0}^S A_{ij}N_j. \quad (15)$$

See Table 1 for the full set of notations.

The total feedback experienced by the invader when rare can be decomposed into two terms

$$f_0^{\text{true}} = \frac{dR_0^{\text{true}}}{dN_0} = \frac{\partial R_0}{\partial N_0} + \sum_{i=1}^S \frac{\partial R_0}{\partial N_i} \frac{dN_i^*}{dN_0}, \quad (16)$$

where the first term,  $\partial R_0 / \partial N_0$  is the partial derivative with respect to  $N_0$ , that is, the direct intraspecific feedbacks, or response of  $R_0$  to a change of  $N_0$  if all other species abundances were held constant. Therefore, it is also by definition the initial slope of the function  $R_0^{\text{fixed}}$ ,

$$f_0^{\text{fixed}} = \frac{dR_0^{\text{fixed}}}{dN_0} = \frac{\partial R_0}{\partial N_0}. \quad (17)$$

In Lotka–Volterra models,  $f_0^{\text{fixed}} = f_0^{\text{alone}} = A_{00} \leq 0$  is a parameter of the model representing intraspecific regulation.

The difference between total and intraspecific feedbacks then represents indirect feedbacks going through the resident community

$$f_0^{\text{true}} - f_0^{\text{fixed}} = \sum_{i=1}^S \frac{\partial R_0}{\partial N_i} \frac{dN_i^*}{dN_0}. \quad (18)$$

These community feedbacks depend on the way that resident species abundances change in response to the addition of a fixed population  $N_0$ , which acts as a constant (press) perturbation. The feedback also depends on the sensitivity of the invading species to shifts in resident abundances (the term  $\partial R_0 / \partial N_i$ ). This last term can be interpreted as the effective per-capita strength of the interaction that species  $i$  exerts on the invading species 0. In a Lotka–Volterra

<sup>4</sup>The coexistence state where the invader remains rare is unstable (more precisely, it is unfeasible for positive invasion fitness, and unstable for negative fitness; see next section for concrete examples and Appendix for a more detailed analysis).

model, this is a parameter of the model, denoted  $A_{0i}$  above, which is negative if species  $i$  is a competitor or predator of the invader, and positive if it is a mutualist or prey.

To complete the analysis, we can decompose community feedbacks further. By the chain rule, we get that

$$f_0^{\text{true}} - f_0^{\text{fixed}} = \sum_{i,j=1}^S \frac{\partial R_0}{\partial N_i} \frac{\partial N_{i/0}^*}{\partial R_j} \frac{\partial R_j}{\partial N_0}, \quad (19)$$

where  $\partial N_{i/0}^* / \partial R_j$  represents how the equilibrium abundance of species  $i$  (in the absence of species 0) would change if we added an infinitesimal constant term to the growth function  $R_j$ . In Lotka–Volterra models, this can be expressed simply from interaction parameters (Table 1) as

$$f_0^{\text{true}} - f_0^{\text{fixed}} = \sum_{i,j=1}^S A_{0i} (-A_{i/0}^{-1})_{ij} A_{j0}. \quad (20)$$

This involves per-capita interactions between the invader and resident species, and the matrix  $-A_{i/0}^{-1}$  directly computed from the resident community interaction matrix  $A_{i/0} = (A_{ij})_{i,j>0}$  (Aufderheide et al., 2013; Barabás et al., 2014; Levins, 1974; Meszén et al., 2006; Yodzis, 1988). In general, the matrix  $V_{ij} = \partial N_i^* / \partial R_j$ , equal to  $-A_{i/0}^{-1}$  in Lotka–Volterra models, is the *environmental sensitivity matrix*, and integrates direct and indirect interaction pathways to determine the community's sensitivity to changes in species growth rates.

From (20), feedbacks in Lotka–Volterra models do not depend on resident species abundances, but only on community composition and interactions. This is true along the whole growth curve, not just at low invader density, and thus  $R_0^{\text{true}}$  is a piecewise linear function of  $N_0$ , changing slopes only when the species composition changes (see Figure 1a).

We have now arrived at a precise formulation of community feedbacks that lends itself to an intuitive interpretation. The invading population affects the growth rate of resident species, thus changing their equilibrium abundance, which in turn affects the invader's growth rate. Furthermore, the long-term response of resident species to shifts in their growth rates (the middle term) precisely reflects intrinsic stability properties of the community: its response to constant (press) environmental perturbations (Barabás et al., 2014).

These feedbacks depend on the state of the whole community (only its composition in Lotka–Volterra models), and will thus change along the course of the invasion, until the growth curve can vanish, and the invader reach a steady state. In Lotka–Volterra models, if total feedbacks are initially positive, community composition will have to change (via extinctions of resident species) until feedbacks become negative (cf. Figure 1).

## 2.5 | A quantitative indicator of long-term impacts

From the analysis of initial growth rates and slopes above, we can explain more precisely why the metric  $\mathfrak{F}$  defined in (14) is a measure of long-term abundance shifts. This metric was heuristically

constructed to quantify the relative deviations of growth curves. But we now know that the initial difference between the slopes of  $R_0^{\text{true}}$  and  $R_0^{\text{fixed}}$  coincides with community feedbacks. More precisely, from (18) this difference reads

$$(f_0^{\text{true}} - f_0^{\text{fixed}}) N_0 = \sum_{i=1}^S \frac{\partial R_0}{\partial N_i} \frac{dN_i^*}{dN_0} N_0, \quad (21)$$

and thus explicitly encodes the abundance shift  $\delta N_i = (dN_i^* / dN_0) N_0$  of resident species. It is proportional to a weighted average  $\delta N_i$  of these resident responses, where the weights are the effective per-capita interaction coefficients  $(\partial R_0 / \partial N_i)$  from resident to invader. We should then compare this effect to the unperturbed state. The difference in invasion fitness in the presence and absence of the community is a way to do so. Indeed, this difference is approximately (or exactly, in a Lotka–Volterra model)

$$r_0^{\text{true}} - r_0^{\text{alone}} \approx \sum_i \frac{\partial R_0}{\partial N_i} N_{i/0}^*. \quad (22)$$

It is thus proportional to a weighted average of the pre-invasion resident abundances  $N_{i/0}^*$ .

We thus see that  $\mathfrak{F}$ , the ratio of (21) and (22), is approximately equal to

$$\mathfrak{F} \approx \left| \frac{\langle \delta N_i \rangle}{\langle N_{i/0}^* \rangle} \right|, \quad (23)$$

the relative change of resident species abundances. To compute  $\mathfrak{F}$ , however, we have to specify  $N_0$  (in Equation 14). There are essentially three cases to consider:

1. If the invasion failed, then  $N_0 = 0$ .
2. Otherwise, if  $f_0^{\text{true}} < 0$  then we can use our linear expression for  $R_0$  to approximate  $N_0$  as  $N_0 \approx |r_0^{\text{true}} / f_0^{\text{true}}|$ .
3. Otherwise, if  $f_0^{\text{true}} > 0$  the growth function cannot stay linear, as it would imply diverging population dynamics. We can now only guess the order of magnitude of  $N_0$ . From dimensional considerations, we may choose  $N_0 \approx |r_0^{\text{alone}} / f_0^{\text{fixed}}|$ . In a competitive Lotka–Volterra model, this would amount to setting  $N_0$  to its carrying capacity.

## 2.6 | Limitations

- $\mathfrak{F}$  is related to average resident species abundance shifts  $\delta N_i$ , weighted by resident–invader interactions  $\frac{\partial R_0}{\partial N_i}$ . Without interactions from resident to invader, no impact can be detected this way. However, given the very general notion of interaction that we consider here, this is an unlikely scenario.
- $\mathfrak{F}$  is defined via a linear expansion, so it cannot stay accurate if there is a strong nonlinear response to the invasion. However, a strong nonlinear response requires large invader density. It is very

unlikely that a linear approximation would predict a low invader density when a large invader density is actually realized.<sup>5</sup> However, large predicted impacts might not imply large observed impacts, since the linear approximation will surely fail. This means that the proxy is likely to make false positives, but unlikely to make false-negative predictions.

Extending our quantitative analysis of the growth curves past invader rarity (thus more directly estimating Equation 8) would clearly lead to more precise predictions. We leave this as a future challenge, although we will later discuss empirical tests that implicitly amounts to considering mean feedbacks along the growth curve, and not initial ones, as we have done so far.

### 3 | APPLICATIONS

#### 3.1 | Simplest case: Two competing species

A species invading a resident population of a competing species provides an useful illustration of the theory, where it naturally connects with known results of competition theory (Meszéna et al., 2006; Roughgarden, 1983; Tilman, 1982) and adaptive dynamics (Brännström et al., 2013; Geritz et al., 1998b; Meszéna, 2005; Meszéna et al., 2005; Metz et al., 1992, 1995).

Suppose the growth rate of the invading species takes the linear form

$$R_0(N_1, N_0) = r_0^{\text{alone}} + A_{00}N_0 + A_{01}N_1. \quad (24)$$

Here  $r_0^{\text{alone}} > 0$  and all terms  $A_{ij}$  are negative, representing competitive intraspecific and interspecific per-capita interactions. If the resident population is initially at carrying capacity  $N_{1/0}^*$ , the invasion fitness (9) of species 0 is.

$$r_0^{\text{true}} = r_0^{\text{alone}} + A_{01}N_{1/0}^*. \quad (25)$$

The sensitivity matrix of the resident is a single number  $V_{11} = -A_{11}^{-1}$  so that the total feedbacks (16) experienced by the invader simply read:

$$f_0^{\text{true}} = A_{00} - A_{01}A_{11}^{-1}A_{10}. \quad (26)$$

where  $A_{00} < 0$  is also  $f_0^{\text{fixed}}$ , the intraspecific feedbacks, or self-regulation (12). We can then write the invasion growth rate as linear function of  $N_0$  only:

$$R_0^{\text{true}}(N_0) = r_0^{\text{true}} + f_0^{\text{true}}N_0. \quad (27)$$

We deduce in particular, that if species coexist, the invader will ultimately reach the abundance density  $N_0^* = -r_0^{\text{true}}/f_0^{\text{true}}$ .

Let us focus on the invasion scenarios listed in Box 1. We show in Appendix S1 that the x-y-axes and one curve, respectively:

$$\{r_0^{\text{true}} = 0\}; \{f_0^{\text{true}} = 0\}; \text{ and } \left\{ r_0^{\text{true}} = \frac{f_0^{\text{true}}}{f_0^{\text{fixed}} - f_0^{\text{true}}} \left( -A_{01}N_{1/0}^* \right) \right\}, \quad (28)$$

together delineate five regions in the fitness-feedback plane shown in Figure 3, with each region corresponding to one invasion outcomes listed in Box 1.

There cannot be coexistence if  $f_0^{\text{true}} > 0$ : the growth rate  $R_0$  will keep growing with invader abundance  $N_0$  until it causes the extinction of the resident species<sup>6</sup> (Figure 3 left). If  $r_0^{\text{true}} < 0$ , the invader cannot grow from rare, but it may be able to grow from finite abundance. Hence, the feedback through the resident species can create an Allee effect on the invader (Figure 3 centre). The state reached (invader or resident) then depends on initial conditions (yellow region in Figure 3 right).

The singular case  $f_0^{\text{true}} = 0$  (y-axis) suggests perfect replacement: an invader with  $r_0^{\text{true}} > 0$  will replace a resident. Here a direct connection with adaptive dynamics theory (Brännström et al., 2013; Champagnat et al., 2002; Geritz et al., 1998b; Meszéna, 2005) can be made if the invading population is a mutant phenotype, differing only slightly from the resident (asexual) population. This means that intraspecific and interspecific interaction strengths are almost exactly equal. By Equation (26), this implies  $f_0^{\text{true}} \approx 0$ . In this case, a coexistence state can only exist under special circumstances (a branching point, see Appendix S2). In general, however, as soon as the mutant can invade, it fixes in the community and drives the resident population extinct.

#### 3.2 | General multispecies community models

We illustrate in Figure 4 how the results of the two species case are representative of the behaviour of more complex models. We generated many-species communities with random Lotka–Volterra interactions and two-level food webs with nonlinear (Holling Type 2) functional responses. For each community, we simulated population dynamics until an equilibrium was reached  $N_{i/0}^*$ . We then generated hundreds of invaders with randomly distributed interactions (see Appendix S3), and simulated the outcome of the invasion of each invader separately, monitoring the fraction of species extinctions, their change in abundance, but also checking whether the outcome depended on the initial invader abundance (i.e. multi-stability). We see in Figure 4 that the five possible regions (no invasion, coexistence, turnover, irreversible turnover and alternative stable states) identified in two-species case are still well ordered in the fitness-feedback plane  $(f_0^{\text{true}}, r_0^{\text{true}})$ . We explain in Appendix S1 why the boundaries in the fitness-feedback plane have a hyperbolic shape, but we do not attempt to match them quantitatively.

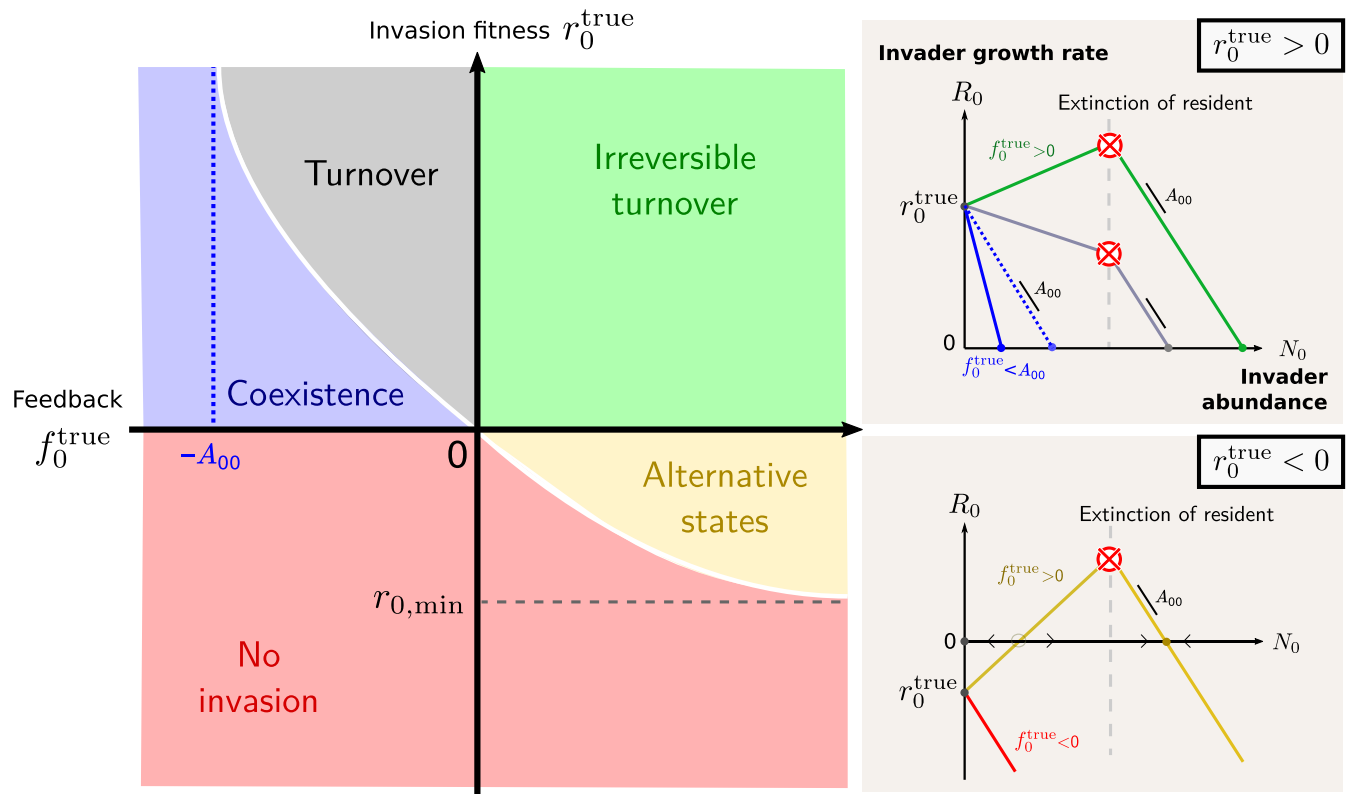
In Figure 5, we compare actual measures of invasion impact—fraction of resident extinctions and mean change of relative abundances—to the linear extrapolation of impact (14) based solely on

<sup>5</sup>One would need a high invasion fitness (to give nonlinearities a chance to manifest), yet strongly negative initial feedbacks (so that the linear approximation makes a low density prediction) that quickly become weak or even positive as invader density grows.

<sup>6</sup>This is true for any model where there is at most one steady state per species compositions.



## Example: Two-species Lotka-Volterra model



**FIGURE 3** Illustration of the method on a linear two-species competitive system. Left panel: For positive invasion fitness  $r_0^{\text{true}}$ , there are four scenarios to consider, determined by the feedback  $f_0^{\text{true}}$ . If  $f_0^{\text{true}}$  is more negative than self-regulation  $A_{00} = f_0^{\text{fixed}}$ , the invader's growth is repressed by the resident and cannot displace it (coexistence, in blue also in rightmost panel). If  $f_0^{\text{true}}$  is negative but larger than  $A_{00} = f_0^{\text{fixed}}$ , the resident species is favouring the growth of the invader, at its expense. Coexistence is still possible but require invasion fitness to be small enough. Otherwise the resident is replaced (reversible turnover, in grey also in rightmost panel). If  $f_0^{\text{true}}$  is positive, this means that the invader accelerates its own growth, due to the presence of the resident. This diverging feedback loop ends with the exclusion of the resident (irreversible turnover, in green also in rightmost panel). The turnover is irreversible in the sense that there is presence of hysteresis (centre panel). Indeed, positive  $f_0^{\text{true}}$  allows for alternative stable states. In this case, for  $r_0^{\text{true}} \in [r_{0,\text{min}}, 0]$  species 0 will be able to invade only if its initial abundance is high enough (e.g. high propagule pressure is needed for invasion to take place). Furthermore, after a successful invasion, reversing abiotic conditions to those pre-invasion will not necessarily allow the resident to re-invade from rarity. The singular case  $f_0^{\text{true}} = 0$  (vertical axis in the rightmost panel) is the classical setting of adaptive dynamics, where a mutant phenotype fixes in the population as soon as its fitness is positive

our indicators of fitness and feedback. We see a good correlation of both metrics with our predictor. In the coexistence region (blue dots), resident species do not go extinct, but this does not mean that the invader has no impact—in fact, it may be precisely because of the impact on resident abundances that the invader's growth is limited (ER regime in Box 1).

Overall, invaders with higher fitness and weaker regulatory feedbacks will have larger impacts: in particular, in the Positive Feedback (PF) regime of Box 1 (green dots), many residents go extinct after invasion, while others might have their abundances increase dramatically. These highly nonlinear effects are poorly predicted by our linear extrapolation, yet—as expected—the latter makes no false negatives: we do not observe high impacts when low impacts are predicted.

In Figure S2 in the Appendix, we further illustrate the applicability of our theory. There, we assembled random Lotka-Volterra

communities made of 100 species, but only focused on the impact of invasions on the 10 most abundant ones (the designated resident species). All others species are then acting as unobserved latent variables. We find that our theory works just as well, and furthermore, that invasion fitness alone is not a good predictor of invasion impacts.

## 4 | DISCUSSION

Our study has proceeded in three steps, which we summarize here, and whose implications we discuss in greater detail below:

1. Reducing a high-dimensional problem—long-term invasion outcomes in a complex community—to the study of the single invading species' growth curves.

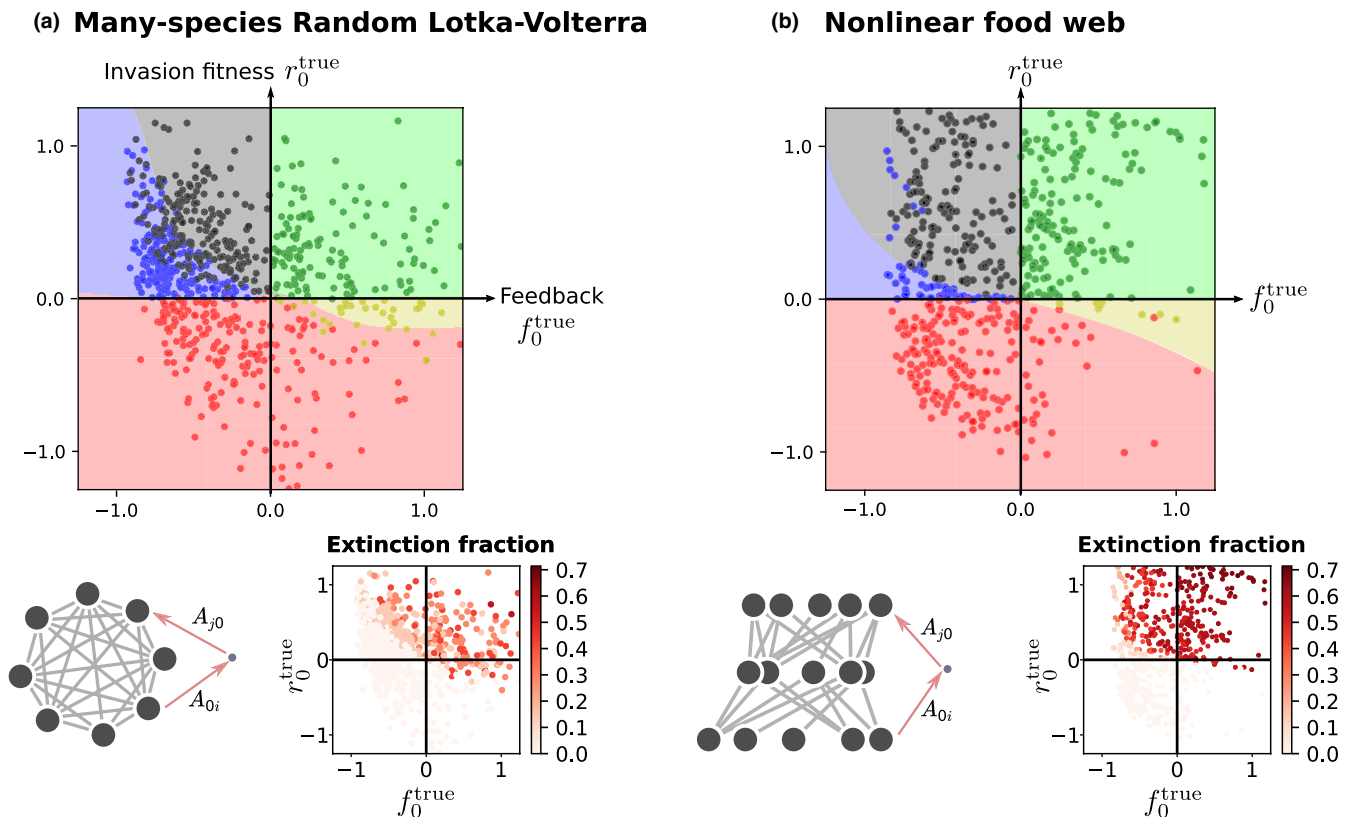
### BOX 1 Predicted scenarios of invasion dynamics (invader perspective): invasion fitness and feedbacks determine five invasion outcomes.

- **No Invasion (NI).** If  $r_0^{\text{true}} < 0$ , the invasion fails from rarity (but see AE below).
- **Enhanced Regulation (ER).** If  $f_0^{\text{true}} \leq f_0^{\text{fixed}}$  the community only enhances (or does not change) invader self-regulation. Unless  $r_0^{\text{true}}$  is large, the invasion likely ends with the establishment of a small invader population.
- **Reduced Regulation (RR).** If  $f_0^{\text{true}} \geq f_0^{\text{fixed}}$  community feedbacks reduce self-regulation. The invader population is modifying its biotic environment to its advantage. The larger  $r_0^{\text{true}}$  is, the larger this modification.

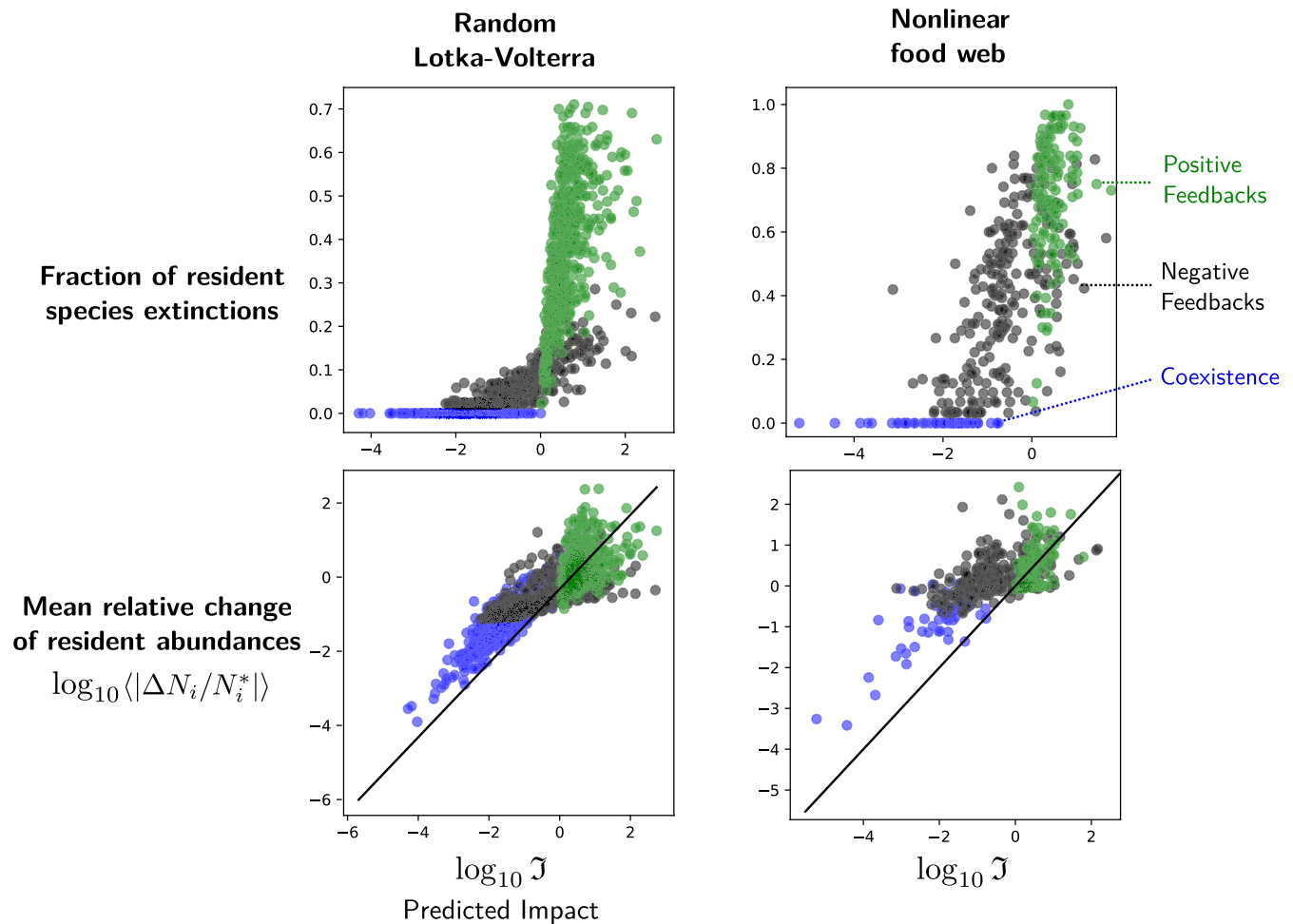
The two scenarios ER and RR allow **coexistence**, at least for low enough invasion fitness. If invasion fitness is large however, **turnover**, that is, replacement of some resident species, can occur. In the latter case, if abiotic conditions were modified to lower  $r_0^{\text{true}}$ , the resident species could re-establish.

**Positive Feedbacks (PF).** If  $f_0^{\text{true}} > 0$ , the whole environment feeds back positively on the invading population. The density-dependent growth rate  $R_0^{\text{true}}$  first increases with  $N_0$ , instead of decreasing towards an equilibrium. This regime displays a tipping point at  $r_0^{\text{true}} = 0$  and hysteresis: modifying environmental conditions to let invasion fitness become positive will lead to a discontinuous jump in invader abundance. On the other hand, reducing  $r_0^{\text{true}}$  back below 0 after the invasion will not be enough to eradicate the invader, as it enters into the AE scenario (below).

**Allee Effect (AF).** If  $f_0^{\text{true}} > 0$  but  $r_0^{\text{true}} < 0$ , the invading species cannot grow if rare, but it may be able to grow from a larger population.



**FIGURE 4** Fitness–feedback maps the invader (species 0) in (a) a large random Lotka–Volterra community, and (b) a two-level food web with nonlinear functional responses (Holling Type 2), represented schematically in inset. The y-axis in the maps is the invasion fitness  $r_0^{\text{true}}$ . The x-axis represents total feedbacks  $f_0^{\text{true}}$  (Figure 1). Symbols are randomly drawn invader–community pairs, and we differentiate five outcomes: no invasion (red dots), coexistence (blue dots), turnover (black dots), irreversible turnover (green dots) and alternative stable states where an invader can establish (and cause extinctions) only if its initial population is high enough (high propagule pressure, gold dots). Background colours represent the most frequent outcome at each point of the map, as predicted by a support vector classifier (see Methods). Insets: Fraction of resident species going extinct due to the invasion (see Appendix S3 for details of the simulation procedure)



**FIGURE 5** Impact prediction based on the linear extrapolation of impact  $\mathfrak{J}$  (Equation 14) versus two actual outcomes of simulated invasions: (Top) fraction of extinctions and (down) mean change of relative abundance  $\langle |\Delta N_i/N_i^*| \rangle = \frac{1}{S} \sum_i \Delta N_i/N_i^*$ . As in Figure 3, we consider random Lotka–Volterra communities (Left), and two-level food webs with nonlinear functional responses (Holling Type 2, right). Dots correspond to randomly drawn invader–community pairs, and colours are associated with the domain in the fitness–feedback maps of Figure (3). Blue: coexistence, black: negative feedbacks, green: positive feedbacks. Spearman rank-order correlation coefficient  $\rho$  between predicted impact and fraction of extinction is  $\rho = 0.75$  for Lotka–Volterra communities, and  $\rho = 0.57$  for the nonlinear food-web ensemble. Correlation coefficient between predicted impact and mean abundance change is  $\rho = 0.60$  for the Lotka–Volterra communities, and  $\rho = 0.44$  for the nonlinear food-web ensemble. See Appendix S3 for details of the simulation procedure

2. Finding linearized indicators for small invading populations that are more tractable than the full growth curve.
3. Analysing these indicators to isolate contributions of more mechanistic parameters, in particular species interactions and stability properties of the resident communities.

This last point then allows us to shift our perspective, from understanding the invader through its impact on the community, to understanding the community through its response to invasions. This will shed light on connections between various important facets of ecological dynamics and stability. In particular, we discuss when a community is likely to create emergent negative or positive feedbacks on a species invading it, as positive feedbacks are a key element of qualitative regime shifts and alternative stable states. Finally, we will comment on how our theoretical analysis may be approached from an empirical viewpoint.

#### 4.1 | From complex many-species dynamics to the invader's growth curve

The invasion of a species or phenotype in an ecological community is often a highly complex dynamical process, that can be viewed through two lenses: either the outcome for the invading population, from failure to runaway growth, or the resulting impacts on resident species, which may benefit from the invasion, decline or even go extinct.

We have proposed that key features of this inherently high-dimensional problem, involving many species and abiotic factors, and their interactions, can be summarized in the analysis of a one-dimensional curve: simply asking how the invasion's impacts on the resident community are reflected in the growth of the invader population itself. We have given a precise theoretical formulation of this idea that allows general quantitative predictions. However, this first argument relies on mathematical objects (density-dependent

growth curves for the invader) that are usually inaccessible both empirically and theoretically.

## 4.2 | From growth curves to linearized indicators

In a second stage, we have derived simple linearized indicators that only involve the growth rate of a small invading population. These indicators are more tractable, and still allow drawing qualitative scenarios of long-term invasion outcomes and impacts, as we demonstrated in both simple mathematical models and more complex simulations. While precise predictions are generally out of reach, we can determine whether an invasion is likely to strongly alter the pre-existing community.

Our approach generalizes classic invasion analysis, which traditionally focuses on the initial stages of invasion, when a species is establishing in a resident community, and either grows and spreads, or goes extinct (Blackburn et al., 2011; Metz et al., 1992; Williamson, 1999). In theoretical terms, this perspective allows a local analysis (Lewis et al., 2016): one only needs to know the biotic and abiotic environments that the invader perceives at the time of introduction to predict whether the invasion will be successful. Together with this classic notion of invasion fitness,  $r_0$ , our analysis introduces a new quantity,  $f_0$ , that encapsulates the long-term indirect feedbacks experienced by the invading population, while still small, as it impacts the rest of the community.

## 4.3 | From invader-based indicators to community stability

In a third stage, we have shown that our novel indicator is deeply connected to the resident community's dynamical stability. We have identified which properties of the community are likely to lead to an invader experiencing strong negative feedbacks (being quickly contained), or strong positive ones.

Our perspective brings together two important facets of ecological stability (Donohue et al., 2016): it showcases a formal link between stability in the face of environmental perturbations (represented by the environmental sensitivity matrix  $V_{ij} = \partial N_i^* / \partial R_j$ ), and the long-term impacts of biological invasions.

In particular, a resident community that is more sensitive to environmental change is also more likely to create a positive feedback  $f_0^{\text{true}} > 0$ . It is widely recognized that positive feedbacks are a key ingredient for an important set of ecological dynamics: alternative stable states, tipping points and regime shifts (Scheffer et al., 2001). This leads us to discussing the relationship between emergent feedbacks and alternative stable states in ecological communities.

## 4.4 | Emergent feedbacks and alternative stable states in ecological communities

The fact that resident species can create density dependence for invaders, with consequences such as Allee effects, tipping points and

hysteresis, has been discussed in various theoretical and empirical contexts (Anic et al., 2015; Courchamp et al., 1999, 2008; Kramer & Drake, 2010). In most cases, these discussions have focused on a small number of resident species, in direct interaction with the invader.

Here, we gave more general conditions for when the invader can experience emergent density dependence (positive or negative feedbacks on growth), distinct from the one seen in a bare environment, because of its impacts on a complex resident community. This stresses the possibility that runaway growth and alternative stable states in the invader's dynamics could reflect properties of the community as much as, or even more than, properties of the invader. In that case, they will likely be associated with dramatic shifts in the state of the resident community itself.

Let us first recall this phenomenology from the invader's viewpoint. A parallel can be drawn with studies of ecosystem engineers—organisms that alter the abiotic features of ecosystems (Wright & Jones, 2006). The population growth of an ecosystem engineer is subject to a feedback from the modified abiotic environment (Cuddington et al., 2009). Here, this idea is transposed to transformations of the *biotic* environment. Negative feedbacks ensure that the invader will be quickly contained and will typically coexist at moderate abundance with resident species. Positive feedbacks signal that the invader's growth accelerates as it transforms its environment. This induces two forms of discontinuities in the invasion dynamics. On the one hand, it creates an emergent Allee effect, allowing a species to persist at a large abundance even if it would not be able to invade from rarity (Taylor & Hastings, 2005). On the other hand, a minute change in environmental conditions can have a disproportionate effect on the community, if it allows the invader to reach a positive invasion fitness, as the invader population will then suddenly become able to grow to large abundance. In other words, the invasion threshold  $r_0^{\text{true}} = 0$  acts as a *tipping point* (Scheffer et al., 2001). Invasion success is thus highly sensitive to population density (priority effects, propagule pressure) and parameter changes.

Alternative stable states may also be seen at different levels of organization. They are often discussed at the level of ecosystem functioning, in the context of regime shifts such as desertification or eutrophication (Scheffer et al., 2001). But multi-stability in community composition has long been discussed or assumed, in relation to many ecological phenomena in complex, high-dimensional communities (Bunin, 2018; Dakos, 2018; Gilpin & Case, 1976). Priority effects are a common feature of community assembly, and imply that different stable compositions can become established depending on initial biotic conditions (Fukami & Nakajima, 2011; Law & Morton, 1996). Sharp spatial boundaries (ecotones) can arise between alternate communities in a homogeneous or smooth environment (Liautaud et al., 2019), and a perturbation can push a community from one state to the other. All these phenomena suggest that the community structure itself may favour alternative stable states, and respond strongly to invasions, not only by exotic species, but also

by species of its own regional pool<sup>7</sup> (Gaertner et al., 2014; Kotta et al., 2018).

## 4.5 | Empirical implications

Many of the concepts and quantities involved in our theoretical analysis may be challenging to approach empirically: difficulties due to uncertainties and stochasticity are faced even in the study of the simpler invasion growth rates (Pande et al., 2020b). We comment here on two possible connections: first, we wish to suggest how the quantities discussed here, or some proxies, might be accessed in an empirical setting. Second, we discuss how, even if these core indicators are inaccessible, they may inspire new empirical thinking, for example, on using invaders as probes of the community's stability and environmental response.

We started with a general argument for estimating invasion impacts on a community by looking only at changes in the invader's density-dependent growth rate, even if we cannot access any information on the community itself. The study of density-dependent growth curves echoes a long-standing practice in empirical population ecology (Arim et al., 2006; Sibly et al., 2005). Our argument could, in principle, be tested experimentally by reconstructing the three curves of Figure 1. This would require observation of the population dynamics of the invading species in different contexts (alone or at least in a known biotic context, and in the community of interest).

Let us consider an experimental setting with various communities of resident plant species growing in the same abiotic conditions, and control plots devoid of these resident species. We now make invasion experiments where a single novel plant species is seeded in the various communities as well as in the control environment. Discarding cases where the invasion fails, we can measure the initial growth rate (i.e. invasion fitness) and long-term abundance of the invader, as well as the long-term impact it had on the resident community.

The most important growth curve in our theory ( $R_0^{\text{true}}$  in Equation 1) may not be directly accessible, as it requires that the invader abundance be kept fixed while resident species equilibrate. If this manipulation is not possible, we can still draw a line connecting invasion fitness to the long-term invader abundance. The slope of this line is the mean total feedbacks over the course of the invasion. The slope drawn in the absence of the resident community gives a proxy for intraspecific feedbacks. Subtracting this slope to the ones measured in the presence of the resident species would quantify the strength of community feedbacks. We may then test whether, across systems, invasion impact will be better explained by our indicator  $\mathfrak{F}$  that accounts for community feedbacks, than by invasion fitness alone.

We also proposed less systematic but more accessible proxies of community response. As noted above, our analysis relates invasion outcomes to the sensitivity of the resident community to environmental changes. It is however essential to remark that we define community sensitivity as the degree to which species interactions amplify or attenuate the reaction of individual species. It may be that certain ecosystems appear more sensitive because each species, on its own, reacts more strongly to the environmental change; and we do not expect this to relate to invasion impacts. Therefore, to empirically validate our prediction, we will have to carefully tease apart the component of stability that is due to species interactions. This being done, we predict that invasions should have greater impacts in ecosystems that are less stable to environmental changes, and conversely, that response to an invasion could be used a probe to predict the effect of other perturbations.

## 5 | CONCLUSIONS

The contribution of our work is twofold. On the one hand, we have proposed a novel way of synthesizing and predicting long-term outcomes of invasion processes. We have done so by expressing mathematically a simple intuition: we can estimate an invader's impacts on resident species, even without observing or modelling them explicitly, by seeing how these impacts feed back onto the invader's own growth. On the other hand, this has led us to understand how stability properties of the resident community can determine both the strength of these impacts, and whether the invader subsequently experiences negative or positive feedbacks. Strong positive feedbacks indicate the possibility of abrupt dynamical transitions such as regime shifts.

Our work underlines the potential for cross-fertilization between the literature on ecological community stability, and the many ecological and evolutionary approaches based on invasion analysis. These approaches, such as adaptive dynamics (Metz et al., 1995), have often focused on few species models and short-term outcomes. Our results suggest that extensions can be made towards many species networks and long-term dynamical outcomes.

We did not consider here spatial dynamics, which are often the focus of invasion biology studies. Additionally, our method assumes that the resident community is at a fixed point, both before and after the invasion. Weak stochasticity would not change our method, but its current form is not meant to handle resident communities along limit cycles or in more complicated attractors (Hastings et al., 2018; Roy et al., 2020). Fortunately, such complications, as well as spatial structure, have been considered within a sensitivity-based framework before (Barabás et al., 2012, 2014; Barabás & Ostling, 2013; Szilágyi & Meszén, 2009a, 2009b). These results ought to be easily co-opted for our invasion-based description as well, generalizing the approach further.

We believe that this is a first step towards a broader understanding of which features of species and communities may generically

<sup>7</sup>This connection is strongest when there is at most one equilibrium per species composition. Alternative stable states are then necessarily associated with different compositions, and shifts between states can be triggered by invasions. In this case, a compositional shift may or may not imply an ecosystem regime shift (since species can be functionally redundant) but any regime shift must involve species invasions and extinctions.



favour large invasion impacts, strong positive feedbacks and qualitative transitions, due not to any idiosyncratic mechanism, but to robust complexity effects. While we interpreted our results in the context of ecological dynamics, this method is readily extended to other biological settings, and could shed light on complex evolutionary dynamics in the presence of phenotypic diversity (Venkateswaran & Gokhale, 2019, Kotil & Vetsigian, 2018. We may hope that important qualitative properties, such as the possibility of alternate states (McNally & Jackson, 2013) or evolutionary branching (Champagnat et al., 2002; Doebeli & Dieckmann, 2000; Geritz et al., 1998a) could eventually be within reach of a general approach in complex communities.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

J.-F.A. and M.B. carried out the theoretical analysis and the numerical simulations. All authors contributed to the design of the study and writing of the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13735>.

## DATA AVAILABILITY STATEMENT

Python code used to generate the figures of the main text and Appendix is freely available at <https://github.com/mrcbarbier/invasions> (Arnoldi et al., 2021).

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