How indirect interactions shape long-term invasion dynamics in complex ecological communities

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Abstract

Many facets of ecological theory rely on the analysis of invasion processes, and general approaches exist to understand a species' short-term ability to invade a community. However, predicting the long-term transformations of communities following an invasion remains –even in theory– a challenging endeavour. We propose a simple method to predict these impacts, as a function of community structure and invader dynamical characteristics, applicable to a vast class of dynamical models. Our approach reveals that short-term invasion success and long-term consequences are two independent axes of variation controlled by different properties of both invader and resident community. Whether a species can invade or not is controlled by its invasion fitness, which depends on environmental conditions and direct interactions between the invader and other species. But, whether this invasion will cause extinctions, or a even regime shift, depends on a specific measure of indirect interaction feedbacks that may involve the entire resident community. As an illustration of the new insights obtained by this method, we explore the interplay of invader specialization and community complexity, and discuss how asymmetrical invader-resident and resident-resident interactions can make communities less vulnerable to invasions.

Introduction

Predicting the outcome of a species or phenotype introduction in a resident community or population is central to many ecological and evolutionary questions (Elton, 1958): invasion analysis is often invoked to understand adaptation, species coexistence and ecosystem assembly (Law & Morton, 1996; Chesson, 2000; O'Sullivan *et al.*, 2018), and is also a central concern for management and conservation (Pimm, 1991; Williamson, 1999; Galiana *et al.*,

2014). General theoretical approaches exist, based on the notion of invasion fitness (or invasibility), to analyse the initial stages of this process (Turelli, 1978; Metz *et al.*, 1995; Geritz *et al.*, 1998; Guo *et al.*, 2015). These approaches essentially ask: under which conditions can the invader grow and spread from a small population?

But, knowing that an invasion can occur, can we predict its long-term consequences, such as whether it drives other species to extinction, or even causes an ecosystem regime shift (Scheffer *et al.*, 2001; Gaertner *et al.*, 2014; Kotta *et al.*, 2018)? These long-term consequences not only involve the invader's characteristics and those of its immediate interaction partners (predators, prey, competitors...). They ought to involve the whole web of interactions in the resident community (White *et al.*, 2006; Hui & Richardson, 2018), and may thus be highly unpredictable, given that few, if any, interaction networks are exhaustively known and accurately quantified (Frost *et al.*, 2019; Catford *et al.*, 2019). The question is, therefore, whether we can understand the essential features of invader and resident communities that control the qualitative nature of long-term impacts (e.g. benign effect or extinctions) and their magnitude.

We propose that the classical notion of invasion fitness (Metz *et al.*, 1992; Schreiber, 2000), and a novel measure of long-term feedback on the invading population, are two complementary dimensions that can be used to characterize the long-term impacts of invasions, across systems. We develop a general method for predicting how these dimensions together determine the impact of invasions and how they depend on invader and community properties. We illustrate this method on many-species community models, allowing for any interaction types and network structure in the resident-invader system.

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 (Jiménez-Valverde *et al.*, 2011; Blackburn *et al.*, 2011), and determine whether the biotic and abiotic environment is favourable to the invader (Guo *et al.*, 2015), and how that can be explained in terms of functional traits, niches, etc. (Eisenhauer *et al.*, 2013).

By contrast, we show that the feedbacks most relevant to invasion long-term impacts do not directly depend upon the abiotic environment, but involve indirect interaction pathways that may run through the whole resident community (White *et al.*, 2006). In particular, we show that when long term feedbacks are positive, an invasion will causes a shift between alternative stable states. Furthermore, our results suggest that positive feedbacks could explain why and when the initial size of the invader population, e.g. propagule pressure (Lockwood *et al.*, 2005), is essential in determining its invasion success .

We first show that by positioning an invader-community pair along the two axes of short-term invasion fitness and long-term feedbacks, our analysis takes an intuitive meaning in the simple case of two species, where it connects with known results of competition theory and adaptive dynamics (Roughgarden, 1983; Champagnat *et al.*, 2002). We then generalize the approach to many species resident communities. Using an invader-as-perturbation interpretation we reveal a direct connection between a community's stability in the face of environmental perturbations (Ives & Carpenter, 2007), and its its vulnerability to invasions.

This general method is our main contribution, and can be applied to a wide variety of ecological settings, from food webs to competitive or mutualistic communities. As an

illustration, we discuss its application to disordered (random) networks. We predict that asymmetry in the interaction structure of invader-community system makes invaders less potent. Strikingly, this result contradicts common expectations of invasion biology (see, e.g. Frost *et al.*, 2019)), and thus showcases the new insights that can be gained when accounting for entire feedback loops in the invasion analysis.

Methods

Invasion analysis (Turelli, 1978; Geritz *et al.*, 1998; Williamson, 1999; Lewis *et al.*, 2016; Barabás *et al.*, 2018) proceeds as follows: we start from a resident community at equilibrium (or more generally in a stationary state (Chesson & Warner, 1981; Schreiber *et al.*, 2011)), where each resident species i has abundance N_i^*, then add another species 0 –the invader– with small initial abundance N_0. For a vast class of community models (Barbier *et al.*, 2018), the equilibrium abundance of a resident species i will satisfy

$$N_i^* = K_i - \sum_j A_{ij} N_j^* \tag{1}$$

where K_i is the species' carrying capacity (its equilibrium abundance when alone), and A_{ij} is the per-capita interaction effect of species j on the focal species i. Competition is represented by $A_{ij} > 0$, meaning that j reduces species i's carrying capacity, while other sign patterns can denote mutualistic or trophic interactions. Per-capita effects A_{ij} can generally depend on species abundances. In our numerical illustrations below, we use the classic multi-species Lotka-Volterra model where the coefficients A_{ij} are constant, but our argument only requires that they change smoothly in the vicinity of the equilibrium (cf. Appendix S1 in Supporting Information).

Our approach is to compute the outcome of the invasion by assuming that it only acts as a small perturbation of the resident community. When the calculation yields an inconsistency, we can reject that hypothesis and affirm that the invasion *will* have a substantial long-term impact (e.g. extinctions of resident species or large biomass shifts across species).

We start with the the initial growth rate of the invader, written as

$$\frac{1}{N_0}\frac{dN_0}{dt} = \frac{r_0}{K_0} w_0 \tag{2}$$

where $r_0 > 0$ would be its intrinsic growth rate and K_0 its carrying capacity. The term

$$w_0 = K_0 - \sum_j A_{0j} N_j^* \tag{3}$$

is hereafter called the *invasion fitness* of species 0. If $w_0 < 0$, the species cannot invade when rare. The invasion fitness w_0 involves both the environmental conditions as directly perceived by the invader (represented as K_0), and the invader's direct interactions with resident species. The invasion fitness is a measure of how favourable the resident community is to the invader species, both in terms of abiotic and biotic conditions, and common explanatory approaches of invasion mainly focus on this quantity (Turelli, 1978; Metz *et al.*, 1995; Williamson, 1999; Lewis *et al.*, 2016).

By construction, the invasion fitness only describes short-term dynamics right after the species' introduction. It is only one of two essentially independent variables characterizing the outcome of invasion. The second variable is associated with long term effects and can be revealed via a simple reasoning. We first assume that the invasion has only weakly affected other species. Under this assumption, we can then compute the abundance N_0 of the invader in the post-invasion equilibrium, and see that it necessarily takes the form

$$N_0 = v_0 w_0 \tag{4}$$

with some factor v_0, that we identify below. When the initial conditions barely allow for invasion, i.e. if the species' invasion fitness w_0 is barely positive, we generally expect the invader to join the community with a low abundance. But if the factor v_0 is large, the invader should eventually attain high abundance, even with low initial growth rate. This can only happen if the invader has caused significant transformations in the community, so that the biotic environment has become much more favourable in the long term than it was at the time of introduction. Thus, our assumption of the invader having a weak impact cannot be true. It is then *likely* that some resident species have gone extinct in the process (cf. Appendices S2 and S3 of Supporting Information).

If the prefactor v_0 is negative, this means that the assumption of a small abundance for the invader cannot hold, however small its invasion fitness may be. This signals the instability of the coexistence state of the invader community system – If there is only one stable state per species compositions (the case for Lotka-Volterra models) this implies that invasion *necessarily* causes the extinction of some resident species – When v_0 is negative, as abiotic conditions change in favour of the invader, a tipping point is crossed at $w_0 = 0$, and the community eventually collapses on a qualitatively different state. In brief, the factor v_0 encapsulates long-term reorganizations of the community (i.e extinctions and/or changes in abundances) following the invasion. Invasion fitness w_0 and the factor v_0 (which we will interpret as a measure of long-term feedbacks) constitute two complementary axes to describe and predict invasion scenarios.

Two-species case

An enlightening illustration of the above reasoning is the example of one species invading a resident population of a second species. In this elementary example, our approach connects with known results of competition theory (Roughgarden, 1983; Tilman, 1982) and adaptive dynamics (Metz *et al.*, 1992, 1995; Champagnat *et al.*, 2002). Here species 0 is invading a resident population at carrying capacity ($N_1^* = K_1$). The invasion fitness (3) of species 0 is

$$w_0 = K_0 - A_{01} K_1 \tag{5}$$

Its sign determines whether species 0 can invade from low abundance. If species 0 and 1 coexist, the equilibrium abundance of the former is proportional to its invasion fitness,

$$N_0 = v_0 w_0 \tag{6}$$

with a multiplicative factor

$$v_0 = 1/(1 - A_{01} A_{10}) \tag{7}$$

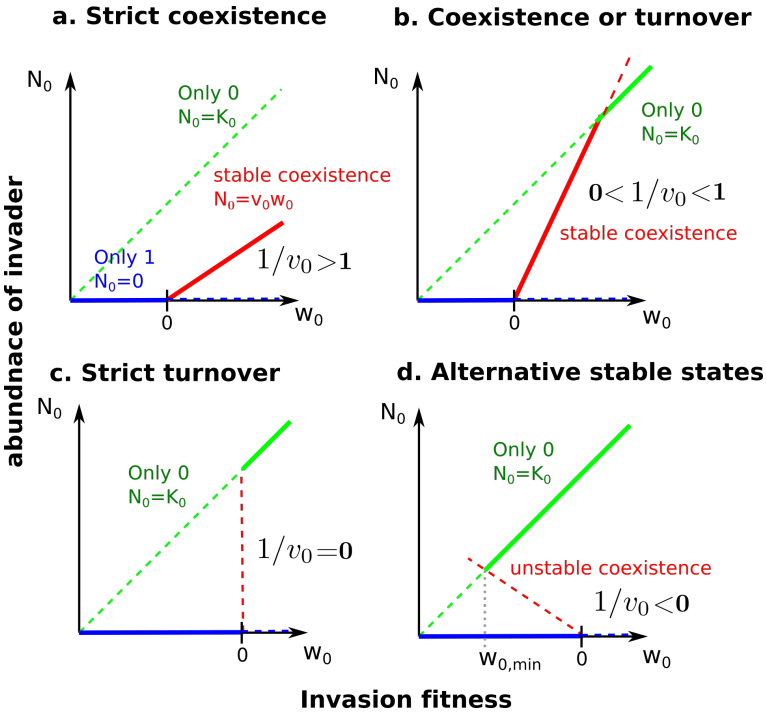

Figure 1: Bifurcation diagram of equilibrium abundance N_0 of species 0 as a function of its invasion fitness $w_0 = K_0 - A_{01}K_1$ into a resident population from species 1. Dashed lines represent unstable, and solid lines stable states. There are three possible states: (i) Species 1 persists alone, $N_0 = 0$ (blue line). (ii) Species 0 replaces species 2, $N_0 = K_0$ (green line). (iii) Coexistence, $N_0 = v_0 w_0$ (red line). If $w_0 < 0$, species 1 cannot invade. The feedback strength $v_0 = \partial N_0/\partial K_0$ defined in (7) gives the slope of the graph of $N_0(w_0)$ in the coexisting equilibrium. v_0 allows to determine which of the three possible states will be reached following the invasion. (a,b) if $1/v_0 > 0$ species can coexist either (a) for all positive values of w_0 or (b) only up to a threshold in w_0 beyond which the resident species is displaced. (c,d) If $1/v_0 \leq 0$, species exclude each other. (c) $1/v_0 = 0$ is the classical setting of adaptive dynamics, where a mutant phenotype fixes in the population as soon as its fitness is positive. (d) For $1/v_0 < 0$ the coexisting equilibrium is unstable and separates two alternate states (only species 0 survives, or only species 1). For $w_0 \in [w_{0,\min}, 0]$, these two states are both stable, meaning that 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).

This factor controls whether species actually coexist or exclude each other, see Fig. 1. In fact, $v_0 = \partial N_0/\partial K_0$, meaning that v_0 can be understood as the the invader's long-term sensitivity to a change of its abiotic environment (as represented by K_0, e.g. addition of resources), *in the presence* of the resident species. The inverse of v_0:

$$1/v_0 = 1 - A_{01}A_{10} \tag{8}$$

can be interpreted as a measure of the invader's indirect self-regulation via its interactions with the resident species. In contrast with invasion fitness w_0, which only depends on the interaction of species 1 to species 0, the indirect self-regulation $1/v_0$ depends on the whole interaction loop from species 0 to species 1 and back from species 1 to species 0 (represented by the product $A_{01}A_{10}$ in eq. 8). Thus $1/v_0$ measures the relative strength of the invader's regulatory feedback loop.

If $1/v_0 > 1$, interactions with the resident population are limiting the invader's long-term growth. Improving the abiotic environment of the invader (i.e. increasing K_0) will cause a smaller increase of N_0 than if it had been alone. This signals the occurrence of *self-regulatory feedback* of species 0 via species 1. This is the case when a growing predator population limits its growth by depleting its prey. In this case, the invasion can never cause the extinction of the resident species, even at high values of invasion fitness w_0 (Fig. 1a).

If $0 < 1/v_0 < 1$, interactions with the resident population are enhancing the invader's long-term growth. Increasing K_0 by some amount will cause a larger increase of N_0, indicating a *positive feedback* via species 1. This is the case when a species reduces the population of a competitor or increases that of a mutualist. As a consequence, if environmental conditions are sufficiently favourable (i.e if w_0 is large enough), the invader can drive the resident species to extinction (Fig. 1b).

In adaptive dynamics theory (Champagnat *et al.*, 2002), the invader is a mutant phenotype, often assumed to differ from the resident population only in terms of its adaptation to the abiotic environment. Intra- and inter-population interactions are equal so that $A_{01} = A_{10} = 1$ which, from eq. (8), implies $1/v_0 = 0$. Thus, as soon as it can invade (i.e. as soon as its invasion fitness w_0 is positive), it fixes in the population after driving the resident phenotype to extinction (Fig. 1c).

Finally if $1/v_0 < 0$, the invader no longer experiences indirect self-regulation. On the contrary, there is a positive feedback loop towards larger and larger abundance of the invading population, which signals the instability of the coexistence state. When the abundance of species 0 increases, it affects species 1, which causes 0 to increase even more, and so on. The only realistic scenario in which this can happen is mutual exclusion, when the diverging feedback loop ends with an extinction (Fig. 1d).

For two species systems, negative feedbacks require predator-prey interactions, and positive feedbacks can only be attained if interactions are competitive or mutualistic. We refine this intuition, and show that, in more complex communities, the nature of the feedback is not so strongly tied to the nature of interactions (i.e. the interaction sign pattern) but more to the patterns of symmetry of the interaction network.

General case

We now extend the approach to an invader-community system. We consider a resident community where all species coexist with abundances $N_i^* > 0$, and denote w_0 the invasion fitness of species 0, as defined in Eq. (3). If $w_0 > 0$, invasion dynamics can take place. To predict if the invasion will have a substantial (non-linear) impact, we proceed by *reductio ad absurdum*. We assume that the invader only acts a weak perturbation, and check if this assumption leads to a logical contradiction. We thus let species 0 invade, and assume that it eventually reaches a (small) equilibrium abundance N_0, causes no extinctions, but only slight abundance changes of the resident species. More precisely, the abundances of the latter become:

$$N_i = K_i + \delta K_i - \sum_{j \neq 0} A_{ij} N_j \tag{9}$$

where $\delta K_i = -A_{i0} N_0$ represents the effective environmental perturbation caused by the invasion. Equivalently, for all resident species in the post-invasion state, it holds that

$$N_i = N_i^* - N_0 \sum_j V_{ij} A_{j0} \tag{10}$$

where $V_{ij} = \frac{\partial N_i^*}{\partial K_j}$ is the *long-term sensitivity* of resident species i to an environmental change affecting another resident species j, which can also be interpreted as a measure of net, interspecific interactions, relative to the strength of intraspecific interactions. Similarly, diagonal terms V_{ii} represent net interspecific interactions. V_{ij} is the resident counterpart to the invader sensitivity eq. (13) derived in the two species example. Eq. (10) is a linear approximation (which applies to models other than Lotka-Volterra), which is consistent with our assumption of the invader having a small impact on resident species. The matrix $V = (V_{ij})$, which we henceforth call *environmental sensitivity matrix*, can be computed directly from the interaction matrix $A = (A_{ij})$ (see Appendix S1 in the Supporting Information). It encodes resident species' net interactions, and their long-term sensitivity to changes of abiotic conditions. With these notations at hand we have, from the perspective of the invader

$$N_0 = (K_0 - \sum_i A_{0i} N_i^*) + N_0 \sum_{ij} A_{0i} V_{ij} A_{j0} \tag{11}$$

The term in brackets is the invasion fitness w_0. Factorizing by N_0, we see that the invader's abundance can be expressed as a product of its short-term invasion fitness w_0 and a long-term modifier v_0

$$N_0 = v_0 w_0 \tag{12}$$

As in the two-species system, $v_0 = \frac{\partial N_0}{\partial K_0}$ so that it can be understood as the the invader's long-term sensitivity to a change of its abiotic environment, in the biotic context determined by the resident community. Its inverse

$$1/v_0 = 1 - \sum_{i,j} A_{0i} V_{ij} A_{j0} \tag{13}$$

can be interpreted as a measure of indirect self-regulation. It integrates both direct invader-community interactions, as well as indirect feedbacks through the entire community (Fig. 2).

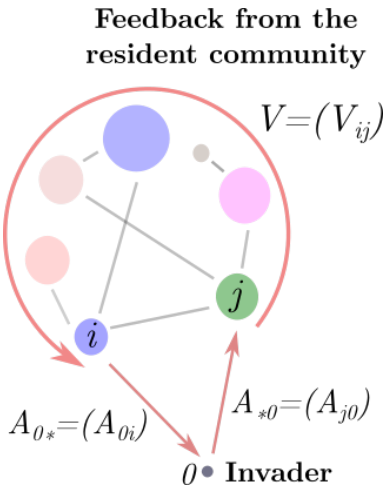

Figure 2: Representation of the direct interactions that determine short-term invasion success, and the feedback loop (13) through the resident community that determines the long-term impacts of the invasion. This cartoon also provides a graphical representation of the invader-as-perturbation interpretation that we propose in section C.

The fact that this term represents long term indirect feedbacks is made clear by the derivation above: we introduced species 0, estimated the induced long-term modifications of resident species abundances, before evaluating how these modifications, in turn, affected the invader's own abundance. As detailed in the next section, from the sign and magnitude of both w_0 and v_0 we either accept our assumption of the invader having a weak impact, or on the contrary, assert that it necessarily causes a discontinuous shift in the resident community.

Results

The fitness-feedback map

We show in Fig. 3 that the interpretation of w_0 and v_0 follows that of the two species case. We identify in Appendix S2 (Supporting Information), the thresholds on v_0 that decide the long-term impact of an invasion, and we see in Fig. 3 that the five possible outcomes (no invasion, coexistence, turnover, irreversible-turnover, and alternative stable states) are naturally ordered in a plane whose x and y axis correspond to the invader's indirect self-regulation $1/v_0$, and invasion fitness w_0, respectively.

For large enough $1/v_0$, the self-regulating feedbacks on the invading species are so strong that the invasion can never cause any extinction, no matter how favourable the biotic and abiotic conditions are to the invader (as represented by its invasion fitness w_0).

For smaller yet positive values of $1/v_0$, the larger the invasion fitness w_0, the more likely it is that the invasion will result in at least one extinction. In this case, an invasion may cause turn-over, but if environmental conditions change to reduce w_0, extinct species can rejoin the community and exclude the invader. In this sense, the consequences of the invasion are not irreversible. The singular point $1/v_0 = 0$, as in our two-species results, suggests perfect replacement: an invader with $w_0 > 0$ will replace a resident. We noted this possibility above

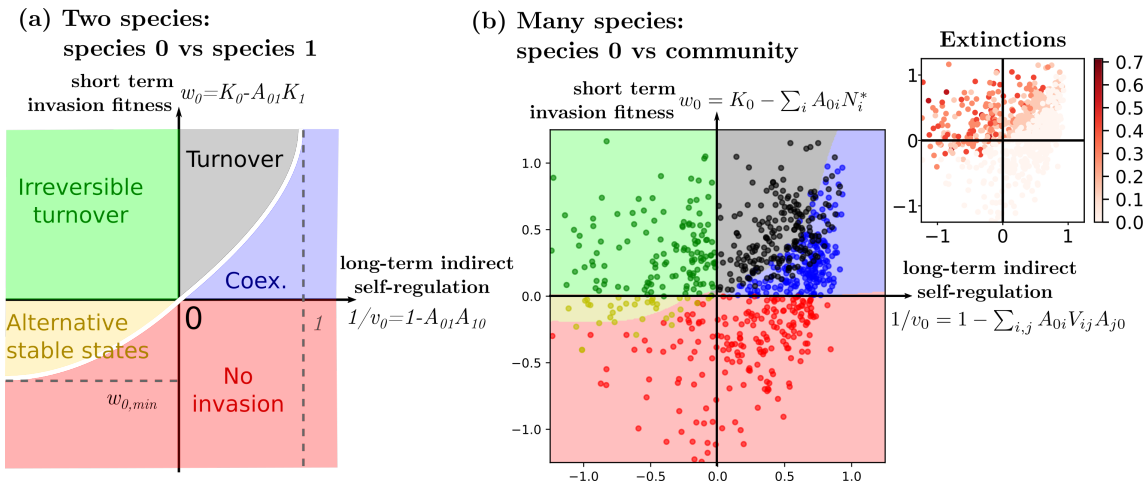

Figure 3: Fitness-feedback map for **(a)** species 0 in a two-species system (Sec.), and **(b)** in a large resident community, with pre-invasion abundances N^* and vulnerability matrix V (Sec.). The y-axis is the invader's short-term fitness w_0: the species can grow from a small initial abundance only if w_0 is positive. The x-axis represents indirect self regulation of the invading species $1/v_0$ (Fig. 2). We delineate four regions: no invasion, coexistence, turnover (when some resident species goes extinct), turnover and hysteresis and alternative stable states (see Fig. 1) where a invader can establish (and cause extinctions) only if its initial population is high enough (high propagule pressure). In (b), symbols are randomly-drawn invader-community pairs, and background colors are predictions from a support vector classifier. **Inset:** Fraction of resident species going extinct due to the invasion (see Appendix S3 of the Supporting Information for complete details of the simulation procedure).

for adaptive dynamics, and show in Appendix S4 (Supporting Information) that this can also arise in complex models of saturated resource competition (when all resources are being consumed).

Finally, negative values of $1/v_0$ imply that the invader experiences a positive feedback from the resident community. This signals the instability of the coexistence state. If there is a single equilibrium per species composition (the case in Lotka-Volterra models), at least one resident species will go extinct due to the invasion. Even in conditions that do not allow the invader to establish from rarity (i.e when $w_0 < 0$), it may still be able to invade if its initial population is large enough. There are thus two stable states, one where the invader is extinct, and one where it has established (and possibly pushed some species to extinction). When $1/v_0 < 0$, a successful invasion induces species turn-over and *hysteresis*: modifying environmental conditions to reduce its invasion fitness below 0 will not be enough to eradicate it. In this sense the invasion has caused irreversible long-term reorganization of the community.

Invader-as-perturbation and stability

We now focus on v_0, an uncharted dimension of description of invasions. Using an *invader-as-perturbation* interpretation, and notions of worst-case invader and largest community response to perturbations, we can showcase a fundamental relationship between community stability and long-term impact of invasions.

A resident community in which the environmental sensitivity matrix V has large elements

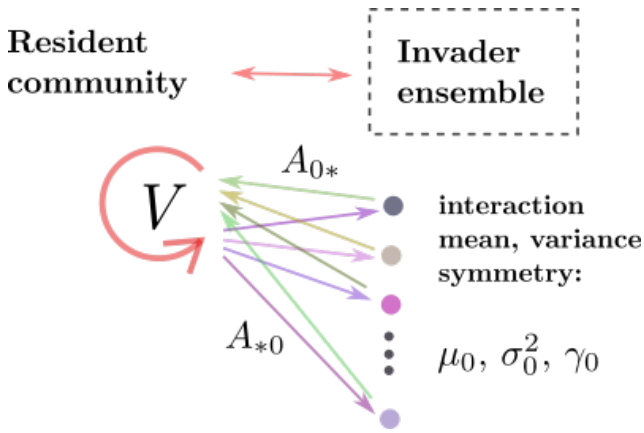

Figure 4: Pool of potential invaders associated with a given community. To ask how basic statistics of invader-resident interactions determine invasion outcomes, we seek the expected value of the indirect feedback that an invader, randomly chosen from the pool, will experience. The coefficient $-1 \leq \gamma_0 \leq 1$ controls the patterns of symmetry between invader-resident and resident-invader interactions, and requires some interaction variance (heterogeneity), σ_0, to be relevant. The variance in interaction strength can be interpreted as a metric of specialization of the invader.

is more likely to allow some invading species to experience positive indirect feedback (i.e. negative self-regulation $1/v_0 < 0$). Such a community is at risk for irreversible biological invasions. We can formalize this intuition by defining the *worst case* bound

$$1/v_0 \geq 1 - ||A_{0*}||\ ||V||\ ||A_{*0}|| \tag{14}$$

where $||\cdot||$ is the Euclidean norm for interaction vectors $A_{0*} = (A_{0j})$, $A_{*0} = (A_{i0})$, and the spectral norm for the environmental sensitivity matrix V (the max of $||Vu||$ over all normalized vectors u, see (Arnoldi *et al.*, 2016) for an application of this notion for ecological stability). At first sight, the contribution of the invader in this expression is straightforward: the stronger the invader-resident interactions, the larger the norms $||A_{0*}||$ and $||A_{*0}||$, thus the more likely the invasion it is to induce long-term, irreversible impacts. But the worst case expression also involves the environmental sensitivity matrix of the resident community, and its spectral norm $||V||$ measures the maximal response of the resident community to an environmental press perturbation.

To elicit the largest long-term impact, the invader-community vector A_{0*} must align with the direction of the worst-case perturbation associated to this community. Then, the community-invader vector A_{*0} must align with the direction of the community response to the worst perturbation. This reasoning provides both an invader-as-perturbation interpretation, as represented in fig. 2, and a method to find the worst invader-community and community-invader interactions (see Appendix S1.1 of the Supporting Information for an exact expression). It showcases a formal link between stability in the face of perturbations (represented by $||V||$), and the long term impacts of biological invasions ($1/v_0$).

The worst-case invader is by definition a special case, and may not represent the typical outcome of an invasion. If we consider a whole pool of potential invaders, as illustrated in Fig. 4, we may wonder what would be the expected impact of an invader, chosen from this pool. The long term feedback that such an invader will experience is determined by

the projection of its interaction vectors along those of the worst case invader. But it will also critically depend on the projection along other particular directions of perturbation and responses of the resident community. Nonetheless, we show in Appendix S1.2 (Supporting Information) that an expression analogous to the worst-case Eq. (14) can be derived for this mean-case scenario, which only involves the first moments of invader-community interactions, and the resident environmental sensitivity matrix. The mean case approach is particularly useful to apply our method to invader-community systems for which only summary statistics of interactions are known. This is the focus on the following sections.

Generic drivers of invasion outcomes

So far, our analysis makes no assumption about the interaction structure of the invader-community system. In most ecological settings, however, we have little prior knowledge of how an invader will interact with resident species, or even how the latter interact amongst themselves. We may however want to know which basic features of the invader-resident system are likely to determine long-term impacts. From our analysis it follows that, to do so, we must ask how basic features of invaders and communities control v_0. We first consider the case where we have full knowledge of resident community interactions, but can only access summary statistics of invader-resident interactions, such as their mean, variance and symmetry. This will reveal the stabilizing role of the statistical asymmetry between invader-resident and resident-invader interactions, a prediction that contradicts common expectations. Then, we will consider the case where only summary statistics are known for both invader and community interactions. We will show that community complexity and symmetry are expected to allow for larger invader long-term impacts.

Generic invader characteristics

We consider a single resident community of S^* species, and a pool of potential invaders, as illustrated in Fig. 4. We then compute the expected feedback felt by an invader from this pool, given the mean of invader-community interactions $\mathbb{E}(A_{i0}) = \mathbb{E}(A_{0j}) = \mu_0/S^*$; their variance, $\mathrm{var}(A_{i0}) = \mathrm{var}(A_{0j}) = \sigma_0^2/S^*$; and importantly, the correlation coefficient $\mathrm{corr}(A_{i0}, A_{0i}) = \gamma_0$. The parameters μ_0 and σ_0 are scaled by S^* so that, for fixed μ_0 and σ_0, our results are independent of resident diversity. The correlation coefficient $-1 \leq \gamma_0 \leq 1$ controls the patterns of symmetry (around the mean) between invader-resident and resident-invader interaction strengths, provided that these interactions are heterogeneous, $\sigma_0 > 0$. Note that interaction heterogeneity σ_0 can also be interpreted as a metric of specialization of the invader (whether in a context of competition, mutualism, or trophic interactions).

From the general mean-case expression given in Appendix S1.2 (Supporting Information), we can compute the long-term feedbacks felt by a typical invader from the pool. At first order in $1/S^*$, we have that:

$$\mathbb{E}(1/v_0) = 1 - \mu_0^2 \langle V_{ij} \rangle - \sigma_0^2 \gamma_0 \langle V_{ii} \rangle \tag{15}$$

where $\langle V_{ij} \rangle$ is the mean over off-diagonal terms in V and $\langle V_{ii} \rangle$ is the mean over the diagonal. As noted, this expression depends on the resident diversity S^* only through μ_0 and σ_0. We see that the contribution of the mean invader-resident interaction strength μ_0 enters as a factor of net interactions between distinct resident species $\langle V_{ij} \rangle$. Thus, in the presence of

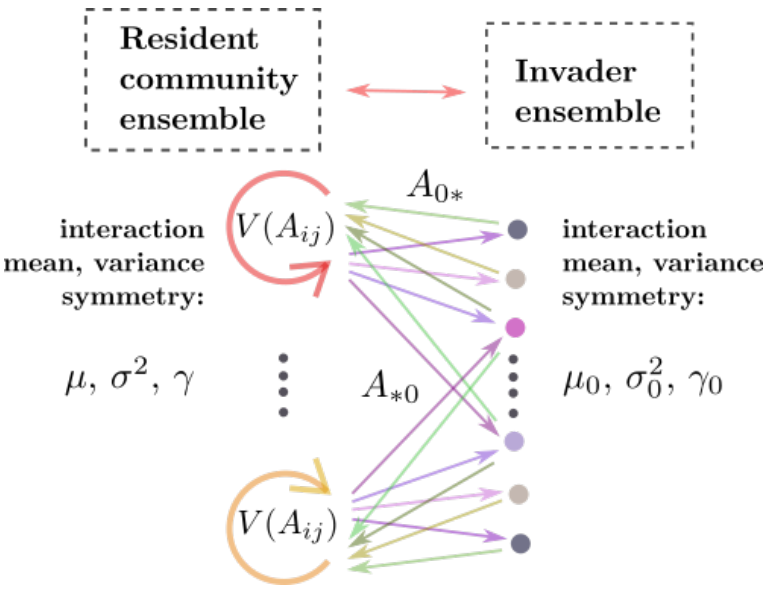

Figure 5: Representation of the random community and random invader approach. We seek the expected value of the indirect feedback that an invader chosen from the pool will experience, when introduced in a community assembled from another species pool, as a function of basic statistics of resident-invader interactions A_{i0} and A_{0j}, and resident-resident interactions A_{ij}.

negative net interactions between resident species (e.g. effective competition), increasing the mean interaction strength of the invader actually increases the self-regulatory feedbacks that it experiences, and so reduces its invasion potential. In the rightmost term we see the effect of the invader specialization and symmetry $\gamma_0\sigma^2$. Their contribution depends on net self-regulation $\langle V_{ii}\rangle > 0$ of resident species. We can thus deduce that, all else being equal, invaders with asymmetrical interactions ($\gamma_0 < 0$) will be less potent than invaders presenting symmetrical interactions ($\gamma_0 > 0$).

Generic community characteristics

Given that few, if any, interaction networks are exhaustively known and accurately quantified, we want to characterize how basic statistics of community interactions can influence invasion outcomes (Lurgi *et al.*, 2014). A powerful way to do so is to consider randomly-drawn invader and community interactions in the limit of high species richness (see fig. 5). In fact, many community-level properties of disordered –yet non-random– communities will behave as those of completely random ones, controlled by only three simple interaction statistics (Barbier *et al.*, 2018; Barbier & Arnoldi, 2017). These statistics are: mean interaction strength, $\mathbb{E}(A_{ij}) = \mu/S^*$, variance (or complexity sensu May (1972)), $\mathrm{var}(A_{ij}) = \sigma^2/S^*$ and symmetry, $\gamma = \mathrm{corr}(A_{ij}, A_{ji})$. Note how these expressions parallel the parametrization chosen for the invader ensemble, with the same scaling with resident diversity S^*. Once again, we can use the expression derived above for a typical invader, eq. (15). Bunin (2017), showed that the environmental sensitivity matrix of large random *assembled* communities satisfies

$$\langle V_{ij}\rangle \approx -\frac{\mu}{S^*} \text{ and } \langle V_{ii}\rangle \approx \frac{1-\sqrt{1-4\gamma\sigma^2}}{2\gamma\sigma^2} \tag{16}$$

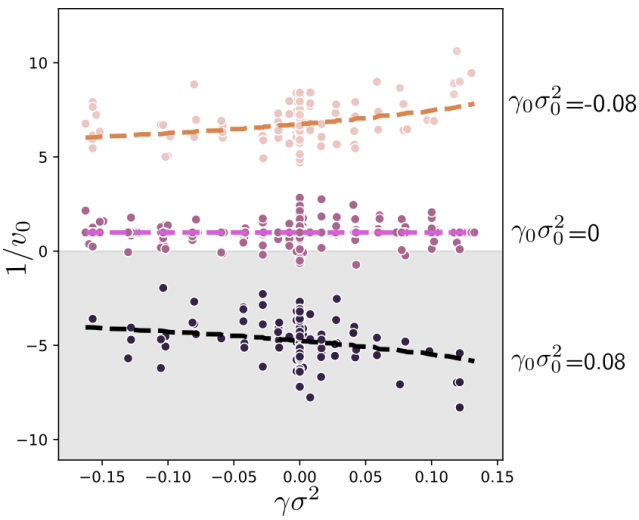

Figure 6: Combined contributions of invader and community interactions in the indirect self-regulation of the invader $1/v_0$ (y-axis, grey shaded region shows negative values), in random communities. At fixed mean interaction strength (μ and μ_0, see main text), we vary the statistical patterns of symmetry of resident-resident interactions (x-axis: $\gamma\sigma^2$) and invader-resident interactions (colors gradient from light to dark: $\gamma_0\sigma_0^2$). The three coloured curves correspond to the mean-case values associated to three pools of invaders (from top to bottom $\gamma_0\sigma_0^2 = -0.08, 0, 0.08$.)

This expression tells us that net interspecific interactions, $\langle V_{ii} \rangle$, increase with community symmetry $\gamma\sigma_0^2$. From eq. (15), we saw that this implies a reduction of the regulatory feedbacks on a given invader, thus increasing its potential impact. In fig. 6) we illustrate the combined effects of community and invader properties on the latter's self-regulating feedbacks, illustrating the synergistic combination of invader-resident and resident-resident interaction asymmetry (i.e going from the top left to bottom right corners of Fig. 6).

Discussion

The invasion dynamics of a species or phenotype can be a highly complex process, inducing significant transformations in the resident community. Classical invasion analysis mainly focuses on the initial stages of invasion, where a species is establishing in a resident community, and either grows and spread or goes extinct (Williamson, 1999; Blackburn *et al.*, 2011; Metz *et al.*, 1992). For theory (Lewis *et al.*, 2016), this perspective allows a local analysis: one only needs to know the biotic and abiotic environment that the invader perceives at the time of introduction, to predict whether the introduction will be successful.

Our contribution is to show that a similar local analysis can shed light on long-term impacts, and assess whether a successful invasion will act only as a slight perturbation of the community, or cause large shifts. While predicting the exact outcome of the invasion is generally out of reach, we can determine whether this outcome is likely to strongly alter the pre-existing community.

We revealed that, together with the classic notion of invasion fitness w_0, the analysis of a scalar quantity, v_0 allows a qualitative prediction of long-term invasion outcomes. v_0 encapsulates the indirect feedbacks experienced by the invading population, as it expands and

impacts the rest of the community. Negative feedbacks ensure that the invader will be quickly contained, and will coexist at moderate abundance with resident species. Positive feedbacks signal that the invader's growth will accelerate as the community undergoes significant transformations, such as species extinctions, until a qualitatively different equilibrium is reached. In the latter case, even an invader with a weak fitness advantage (or even negative) can achieve disproportional impacts in the long term on resident species, especially if its initial abundance is high.

We have shown that the metric v_0 depends on indirect interaction pathways. Its expression combines the invader's direct interactions with resident species, and stability properties of the resident community, encapsulated in its environmental sensitivity matrix V. The link between stability and invasion impacts is revealed by viewing the invader as an environmental press perturbation. If this perturbation causes a large response, it is likely to induce a strong feedback on the invader, thus allowing the latter to have substantial long-term impacts. This analysis thus brings together two important facets of ecological stability (Donohue *et al.*, 2016): resistance to environmental change and long-term response to invasions.

Alternative stable states in high-diversity communities

Our analysis is a step towards understanding when alternative stable species compositions can emerge from community dynamics (Fig. 3). Alternative stable states have mostly been discussed in the context of low-dimensional models of ecosystem functioning and regime shifts (Scheffer *et al.*, 2001). But many ecological phenomena hinge on the existence of alternative states in complex, high-dimensional communities (Gilpin & Case, 1976; Dakos, 2018; Bunin, 2018). Priority effects are a common feature of community assembly, and imply that different stable compositions can become established, depending on initial biotic conditions (Law & Morton, 1996; Fukami & Nakajima, 2011). 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.

From our work, it follows that those phenomena ought to be deeply entangled with the communities' long-term response to invasions (Gaertner *et al.*, 2014; Kotta *et al.*, 2018). 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 (species can be functionally redundant) but any regime shift must involve species invasions and extinctions.

Conversely, the alternative stable state perspective on invasions allows us to understand two essential phenomena which are not readily captured by classic invasion analysis. When there are positive feedbacks on the invader via the community ($1/v_0 < 0$) a minute change in environmental condition can have a disproportionate effect on the community, if it allows the invader to reach a positive invasion fitness. In other words, the invasion threshold $w_0 = 0$ is, in this case, a *tipping point* (Scheffer *et al.*, 2001). Furthermore, positive feedbacks create an emergent Allee effect, allowing a species to persist at a large abundance even if would not be able to invade from rarity. We can thus identify when invasion success depends on invader abundance, whether considered as an initial population (priority effect) or an influx from the outside (propagule pressure).

The two-fold stabilizing role of asymmetry

We have shown that long-term invasion impacts are influenced by a basic feature of species interactions: how correlated the effect of species i on j is with the effect of j on i, which we call interaction symmetry.

Asymmetric interactions have been studied in relation to stability and coexistence, in various contexts such as predator-prey interactions (Allesina & Tang, 2012) or intransitive competition (Soliveres & Allan, 2018). In complex communities, the dynamical effect of interactions are not directly tied to their nature (i.e. their sign patterns) but more to their patterns of symmetry (around a mean that can be positive or negative).

We found that asymmetrical interactions (e.g. commensalism or predator-prey interactions), either within the resident community or between the invader and resident species, increase the regulatory feedbacks experienced by an invading species. Asymmetry of a community's interactions increases its stability in the face of environmental perturbations, thus reducing the potentiality for a given invader to experience positive feedbacks. Furthermore, for a given community, asymmetrical invader-resident interactions promote regulating feedbacks on the invader. The synergistic combination of these two effects demonstrates a twofold stabilizing effect of asymmetry (Fig. 6).

Remarkably, this result runs counter to common expectation of invasion biology, where it has been suggested that species with asymmetrical interactions with residents are more likely to become invasive. This intuition may have come from the invasive fitness perspective, as the latter does not consider feedback loops. In this view, invaders experiencing positive effects from resident species (e.g. a predator invading a prey community) and having negative effects on residents (e.g. by predation) could be expected to be more potent invader than, say, an invading competitor (Dick *et al.*, 2017; Frost *et al.*, 2019). From the feedback perspective, however, the intuition is reversed and we have shown that the latter is a fundamental determinant of long-term impacts (Fig. 3).

Conclusion

Our work underlines the potential for cross-fertilization between the literature on 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 toward many-species networks and long-term feedbacks. Important qualitative properties, such as the possibility of alternate states (McNally & Jackson, 2013), or evolutionary branching (Geritz *et al.*, 1998; Doebeli & Dieckmann, 2000; Champagnat *et al.*, 2002)), could be within reach of a general approach in complex communities.

This general method lends itself to analyzing particular theoretical or empirical interaction networks. Studying diverse systems, from food webs to competitive guilds or complex microbial communities, could help test our predictions about the role of interaction asymmetry, and which features contribute more to short-term invasion success or long-term impacts. Our work constitutes a promising avenue to refine predictions on the role of other large-scale properties of an interaction network, such as conectance, directedness, nestedness or modularity (Lurgi *et al.*, 2014; Barbier *et al.*, 2018), on invasion vulnerability. While we interpreted our results in the context of ecological dynamics, this method is readily extended to other

biological dynamics, and could shed light on complex evolutionary dynamics in the presence of phenotypic diversity (Venkateswaran & Gokhale, 2019; Kotil & Vetsigian, 2018).

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How indirect interactions shape long-term invasion dynamics in complex ecological communities

Supporting Information

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The Supporting Information is organized as follows: Appendix S1 gives a general expression for the environemnatl sensitivity matrix, before deriving the associated worst and mean case invader interaction vectors. Appendix S2 provides a mathematical formulation for the boundaries between the possible invasion outcomes shown in Fig. 3 (coexistence, reversible turnover, irreversible turnover, multi-stability). Appendix S3 provides extensive details of the numerical procedures used to generates the figures of the main text as well as some additional insights into the behaviour of random Lotka-Volterra systems. Finally, Appendix S4 provides a detailed analysis of a general bipartite resource-consumer network, showing that $1/v_0$ is bounded above zero, so that no multi-stability can occur, only the replacement by one consumer by another (by competitive exclusion).

S1 A community's environmental sensitivity matrix and associated worst- and mean-case invaders

Given the equilibrium condition:

$$N_i^* = K_i - \sum_k A_{ik} N_k^* \tag{S1}$$

we seek a general expression for the *environmental sensitivity matrix* $V = (V_{ij})$, where $V_{ij} = \partial N_i^* / \partial K_j$. From Eq. (S1) above, we have

$$V_{ij} = \delta_{ij} - \sum_k A_{ik} V_{kj} - \sum_k \frac{\partial A_{ik}}{\partial K_j} N_k^* \tag{S2}$$

$$= \delta_{ij} - \sum_k A_{ik} V_{kj} - \sum_{k,l} N_k^* \frac{\partial A_{ik}}{\partial N_l} V_{lj} \tag{S3}$$

In matrix notation, if we write $(N\partial A)_{ij} = \sum_k N_k^* \frac{\partial A_{ik}}{\partial N_j}$, and $\mathbb{I}$ the identity matrix we get

$$V = \mathbb{I} - AV - N\partial AV \tag{S4}$$

$$V = (\mathbb{I} + A + N\partial A)^{-1} \tag{S5}$$

In Lotka-Volterra models the interaction matrix is independent of species abundance, in this case the environmental sensitivity matrix takes the simple and explicit form $V = (\mathbb{I} + A)^{-1}$, which is independent of abiotic factors (modelled by (K_i)). In general however (e.g in the case of a type II-III functional response) the term $N\partial A$ does not vanish and explicitly depends on the equilibrium abundances and thus, will implicitly depends on abiotic factors.

S1.1 Worst-case invader

A resident community in which the environmental sensitivity matrix V has large elements is more likely to allow some invading species to experience positive indirect feedback. Such a community is at risk for irreversible biological invasions. In the main text we formalized this intuition by defining the worst case bound

$$1/v_0 \geq 1 - ||A_{0*}||\ ||V||\ ||A_{*0}|| \tag{S6}$$

where $||\cdot||$ is the Euclidean norm for interaction vectors $A_{0*} = (A_{0j})$, $A_{*0} = (A_{i0})$, and the spectral norm for the environmental sensitivity matrix V (the max of $||Vu||$ over all normalized vectors u). The larger the norms $||A_{0*}||$ and $||A_{*0}||$, thus the more likely the invasion it is to induce long-term, irreversible impacts. But the worst case expression also involves the environmental sensitivity matrix V. Here we give a method to compute the worst-case invader. We start from the expression of the spectral norm of V:

$$||V||^2 = \max_{||u||=1} ||Vu||^2 \tag{S7}$$

$$= \max_{||u||=1} \langle Vu, Vu \rangle \tag{S8}$$

$$= \max_{||u||=1} \left\langle (V^\top V)u, u \right\rangle \tag{S9}$$

From this expression we deduce that the max is obtained by choosing $u = u_{\text{dom}}$ where u_{dom} is the (normalized) eigenvector associated with the dominant (i.e largest) eigenvalue s^2_{dom} of the positive definite matrix $V^\top V$. We also deduce that $||V|| = s_{\text{dom}}$ (which is why this norm is called "spectral"). To elicit the largest long-term impact, the invader-community vector A_{*0} must align with the eigenvector u_{dom}. Thus

$$A^{\text{worst}}_{*0} = ||A^{\text{worst}}_{*0}|| \cdot u_{\text{dom}} \tag{S10}$$

Then, the community-invader vector A_{*0} must align with the direction of the associated community response Vu_{dom}. Thus

$$A^{\text{worst}}_{0*} = ||A^{\text{worst}}_{0*}|| \cdot \frac{Vu_{\text{dom}}}{s_{\text{dom}}} \tag{S11}$$

S1.2 Mean-case invader

We now seek the expected value of the indirect feedback on an invader randomly chosen from a pool of potential invaders. This requires prior knowledge on the first moments $M_{ij} = \mathbb{E}(A_{i0}A_{0j})$ of a statistical ensemble of invader-community interactions. Indeed, the long-term

feedbacks on an invader reads

$$\mathbb{E}(1/v_0) = 1 - \mathbb{E}\sum_{i,j} A_{0i}V_{ij}A_{j0} \tag{S12}$$

$$= 1 - \sum_i (\sum_j V_{ij}\mathbb{E}(A_{j0}A_{0i})) \tag{S13}$$

$$= 1 - \sum_i (\sum_j V_{ij}M_{ij}) \tag{S14}$$

$$= 1 - \mathrm{Tr}(VM) \tag{S15}$$

where $\mathrm{Tr}(B)$ stands for the trace of a given matrix B. In the main text we chose a particularly simple pool of invaders, corresponding to

$$M_{ij} = \frac{\mu_0^2}{S^{*2}} + \frac{\gamma_0\sigma_0^2}{S^*}\delta_{ij} \tag{S16}$$

and considered the hight diversity limit $S^* \to \infty$. From the above calculations we get

$$\mathbb{E}(1/v_0) = 1 - \sum_i (\sum_j V_{ij}M_{ij}) \tag{S17}$$

$$= 1 - \mu_0^2\frac{1}{S^{*2}}\sum_{i,j} V_{ij} - \gamma_0\sigma_0^2\frac{1}{S^*}\sum_i V_{ii} \tag{S18}$$

$$= 1 - \mu_0^2\frac{1-1/S^*}{S^*(S^*-1)}\sum_{i\neq j} V_{ij} - (\gamma_0\sigma_0^2 + \frac{\mu_0^2}{S^*})\frac{1}{S^*}\sum_i V_{ii} \tag{S19}$$

$$= 1 - \mu_0^2\langle V_{ij}\rangle - \gamma_0\sigma_0^2\langle V_{ii}\rangle + \text{h.o.t} \tag{S20}$$

where "h.o.t" stands for "higher order terms" in $1/S^*$, that vanish at high diversity. The above expression is the one used in teh main text to deduce generic drivers of invader indirect self-regulation.

S2 Analytical predictions for regime boundaries

S2.1 Two-species case

In the two species case treated in the main text,

$$1/v_0 = 1 - A_{01}A_{10};\ w_0 = K_0 - A_{01}K_1 \tag{S21}$$

As parameters change, the transition between invasion outcomes (Fig. 3a in main text) occurs at the intersection between equilibrium branches. This is where the stability of an equilibrium can change (qualitatively). For instance, the resident state (no invader) becomes unstable at ($w_0 = 0$) which is where it crosses the coexistence state. On the other hand, the extinction of the resident occurs when the coexistence becomes unstable (and vice-versa) after crossing the the invader state (no resident), thus when

$$\underbrace{N_0}_{v_0w_0} = \underbrace{K_0}_{w_0+A_{01}K_1} \tag{S22}$$

We thus get the condition

$$w_0(v_0 - 1) = A_{01}K_1 \tag{S23}$$

We see that for $v_0 \leq 1$, there is no possible crossing, hence the invasion cannot cause the exclusion of the resident. On the other hand, at negative values of v_0 (i.e. when coexistence is unstable) the alternative stable state region ends when

$$w_0 \leq \left(\frac{1/v_0}{1 - 1/v_0}\right) A_{01}K_1 \tag{S24}$$

which behaves as $w_0 = A_{01}K_1 \times 1/v_0$ near $1/v_0 = 0$, and as $-A_{01}K_1$ for $1/v_0 \to -\infty$. The boundaries between regions in the fitness-feedback plane (shown in Fig. 3) are thus functions of carrying capacities and interactions, except for the $1/v_0 = 0$ and $w_0 = 0$ boundaries which are universal –as well as the $1/v_0 = 1$ asymptote, but, as we shall see, this is specific to the two-species case.

To make the argument more general, it is useful to realize that the sensitivity of invasion fitness w_0 to a change of abundance (N_1) of the resident species is $\frac{dw_0}{dN_1} = -A_{01}$. Thus

$$A_{01}K_1 = -\frac{dw_0}{dN_1} N_1|_{N_1=K_1} \stackrel{\text{def}}{=} u_{0/1} \tag{S25}$$

With this notation the intersection between the coexistence state and the monospecific one becomes

$$w_0 = \left(\frac{1/v_0}{1 - 1/v_0}\right) u_{0/1} \tag{S26}$$

S2.2 General case

In the general –multi-species– case we can make a similar argument: the transition between invasion outcomes occurs at the intersection between equilibrium branches, where the stability of equilibria can change, for stable to unstable or from unstable to stable. In particular, where the coexistence state can become unstable (or vice versa) when it meets a state where one species, say i, is absent, i.e. when

$$\underbrace{N_0}_{v_0 w_0} = \underbrace{N_{0/i}}_{v_{0/i} w_{0/i}} \tag{S27}$$

We can focus on $w_{0/i}$, the invasion fitness of species 0 in the absence of species i. We have

$$w_{0/i} = w_0 \underbrace{-\frac{dw_0}{dN_i} N_i|_{N_i=N_i^*}}_{u_{0/i}} \tag{S28}$$

This expression holds quite generally because we can expect the first species to go extinct due to the invasion to have small abundance, and that this extinction does not require a large

abundance for the invader, thus justifying the above linear approximations. The intersection condition thus reads

$$w_0 = \left(\frac{1/v_0}{1 - v_{0/i}/v_0} \right) u_{0/i} \tag{S29}$$

where we recognize a similar expression to the one derived in the two-species case. The vertical asymptote, that defines a bound on the turn-over region in the fitness-feedback map is

$$\frac{1}{v_0} \geq \frac{1}{\min_i v_{0/i}} \tag{S30}$$

and the alternative state regime is limited to $v_0 < 0$ and

$$0 > w_0 \geq -\max_i u_{0/i} \tag{S31}$$

These bounds are not universally determined by v_0 and w_0. The complex functions of dynamical parameters $\max_i u_{0/i}$ and $\min_i v_{0/i}$ play an explicit role, and cannot be expected to be independent of v_0 and w_0. This is why the transitions can be smooth in Fig. 3b of the main text.

S3 Random Lotka-Volterra simulations

In the main text, numerical results shown in Fig. 3 and 6, as well as the cartoon in Fig. 1, were obtained from the Lotka-Volterra model, whose dynamics are given by

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \left(K_i - N_i - \sum_{j \neq i} A_{ij} N_j \right) \tag{S32}$$

with r_i the growth rate of species (or strategy) i. For simplicity, we assumed that $r_i = K_i$. In fact growth rates have no impact on equilibrium abundances and the qualitative features of long-term dynamics. This model was chosen as a simple test for our analysis, and we discuss its specificities in the following section. We now describe the procedure for generating the numerical results shown in the text.

S3.1 Generating Figure 3

Using the parameters defined in "Generic community characteristics", we generate a random community of $S = 10$ species with normally distributed interactions A_{ij} with statistics $\mu = 5$, $\sigma = 0.8$ and $\gamma = 1$, and all carrying capacities $K_i = 1$. We simulate the dynamics defined by Eq. (S32) and measure the number of survivors S^* (species with abundances above $N_c = 10^{-10}$ at time 10^5) and their equilibrium abundances N_i^*.

We then draw 2500 random invaders with $K_0 = 1$ and symmetric interactions $A_{0i} = A_{i0}$, drawn from a normal distribution. The statistics of this distribution are chosen to ensure that we get both positive and negative values of w_0 and $1/v_0$:

- $\mathbb{E}(A_{0i}) = u_1 / \sum_j N_j^*$ with u_1 a uniform random number drawn in the interval $[0.7, 1.3]$

- $\mathrm{std}(A_{0i}) = u_2\sqrt{\mathbb{E}(A_{0i})]^2 \sum_{ij} V_{ij}/\mathrm{Tr(V)}}$ with u_2 drawn uniformly in the interval $[0, 2]$.

For each invader independently, we add it to the original community equilibrium and simulate its dynamics from two initial conditions: $N_0 = 1/S^* \min_i(N_i^*)$ and $N_0 = S^* \max_i(N_i^*)$, to test for multistability.

We then measure the number of extinctions as a result of invasion, the existence of alternate states, and the values of v_0 and w_0 for each invader, and use these properties to locate each invader on our map (Fig. 3) and label them with the different categories: no invasion, coexistence, turnover, irreversible turnover, and alternative stable states. The color background of Fig. 3 is obtained by training a Support Vector Classifier on these labelled data, predicting the label for each point in a grid covering the $(1/v_0, w_0)$ plane, and assembling these predictions in a contour plot, using Python and the scikit-learn library.

S3.2 Generating Figure 6

We generate random communities (see previous section) with $S = 60$ species, $\mu = 1$, all carrying capacities $K_i = 1$, and iterate over all combinations of 20 values of σ regularly drawn over the interval $[0.05, 0.8]$, and three values $\gamma \in [-1, 0, 1]$. As before, we simulate their dynamics until equilibrium to obtain the number of survivors S^* and their equilibrium abundances.

For each community, we draw 100 random invaders with $K_0 = 1$, $\mu_0 = \mu S/S^*$, and γ_0 and σ_0 drawn at random from all the possible values of γ and σ. In the main text, we only show a small subset of parameter values.

S3.3 Specificities of the Lotka-Volterra model

Much of our analysis holds for a wide range of possible models, but illustrations in the main text are based on the Lotka-Volterra model, which is the simplest possible model of interacting biological populations. Its foremost particularities are that species can go to extinction ($N_i = 0$ is always a solution), and equilibrium abundances for the S^* surviving species are linearly determined by their carrying capacities and interactions

$$N_i^* = \sum_j^{S^*} (\mathbb{I} + A^*)^{-1}_{ij} K_j \tag{S33}$$

where A^* is the interaction matrix A restricted to surviving species.

As a consequence of this linear expression, we can, for any equilibrium, represent the abundance of any species N_i as a function of any carrying capacity K_j by a straight line, as in our bifurcation diagram (Fig. 1). In other models, these solutions (or "branches") will be nonlinear and may recurve in complex ways, meaning that our formulas remain quantitatively correct only close to the invasion point, where the curve can be approximated by a line. Nevertheless, our qualitative interpretation, that $1/v_0$ implies the existence of an unstable branch (and therefore of multistability), remains true much more generally.

Since v_0 is a sole property of interactions of the community-invader system, we need not consider environmental conditions nor simulate the dynamics to know whether a community

is prone to irreversible invasions. We can directly characterize this vulnerability from resident-resident and invader-resident interactions. By contrast, to determine *if* such invasions happen, we would need to know the abundance of those resident species which directly interact with the invader, as well as the latter's carrying capacity (which represents abiotic conditions at the time of invasion). This is the focus of the majority of invasion analysis and adaptive dynamics, revolving around the notion of invasion fitness.

S3.4 Fraction of irreversible invaders in a random simulation

Let us generate a random matrix A with coefficients A_{ij} distributed with mean μ, variance σ^2 and symmetry $\gamma = \text{corr}(A_{ij}, A_{ji})$. Now, we can draw the interactions A_{0i} and A_{i0} with an additional species 0, using the same parameters $\mu_0 = \mu$, $\sigma_0 = \sigma$ and $\gamma_0 = \gamma$. We plot in Fig. S2 the fraction of such additional species which would be irreversible invaders ($1/v_0 \leq 0$) provided that their initial growth rate was positive. We see that this fraction increases dramatically for large μ and large σ, and reaches one as $\mu \to 1$, meaning that all invaders are irreversible in a neutral community (where $A_{ij} = A_{ii}$).

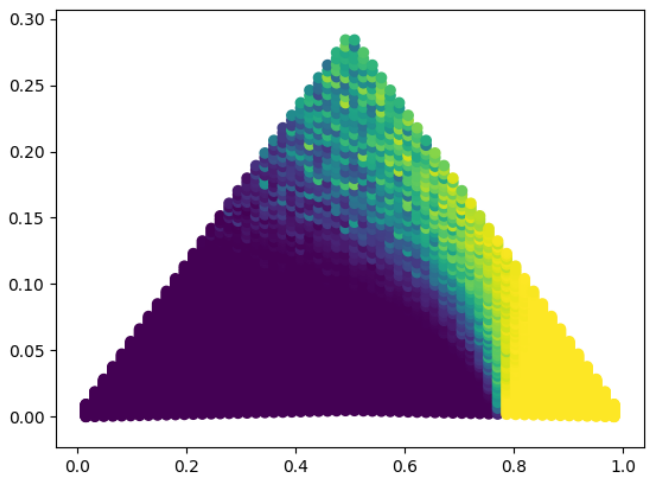

Figure S1: Fraction of irreversible ($1/v_0 \leq 0$) invaders among randomly drawn species, from 0 (blue) to 1 (yellow), as a function of mean μ (x-axis) and standard deviation σ (y-axis). Here the community and invaders all have symmetrical interactions $A_{ij} = A_{ji}$ drawn from the same uniform distribution.

We demonstrate this in simulations in Fig. S2, where we assemble a community, then randomly draw many invaders (i.e. generate the coefficients A_{0i} and A_{i0} at random, with the same rules used to generate the community). To test their impact right at the invasion threshold, we assign them a carrying capacity

$$K_0 = \varepsilon + \sum_i A_{0i} N_i^* \tag{S34}$$

varying ε from negative to positive, so that their initial growth rate (invasion fitness) is given by $w_0 = \varepsilon$. Finally, we measure the impact of the invasion on the equilibrium by the total

change in equilibrium abundances

$$|\Delta N|^2 = N_0^2 + \sum_j (N_j - N_j^*)^2 \tag{S35}$$

A reversible invader creates small changes in the community,

$$\Delta N \sim \varepsilon \tag{S36}$$

while an irreversible invader causes a sudden jump $\Delta N \gg \varepsilon$ right at the threshold $\varepsilon > 0$.

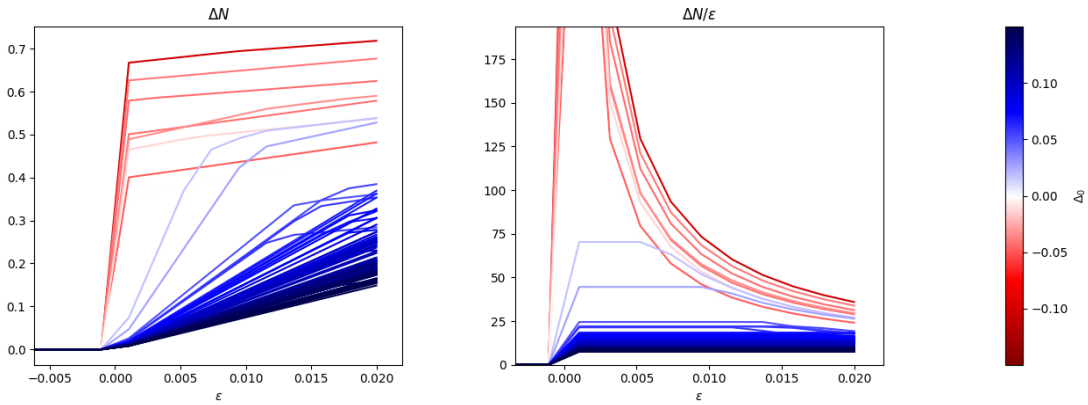

Figure S2: Change in equilibrium composition $\Delta N = \sqrt{N_0^2 + \sum_j (N_j - N_j^*)^2}$ after the invasion of species 0, as a function of $w_0 = \varepsilon$ the invasion fitness. Each line corresponds to a randomly drawn invader with $\Delta_0 = 1/v_0$ shown by colors. **Left:** We see that for reversible invaders (blue, $v_0 > 0$) the equilibrium starts to change smoothly at the invasion threshold $w_0 = 0$, whereas for irreversible invaders (red, $v_0 < 0$) there is a sudden jump. **Right:** For reversible invaders $\Delta N/w_0$ tends to a constant when $w_0 \to 0$, reflecting the fact that the change in community is smooth and proportional to w_0, while it diverges for irreversible invaders.

S4 Competitive exclusion in resource-consumer networks

Consider a bi-partite trophic network, where consumers (with indices i, j) feed on many resources (with indices a, b), following

$$\begin{cases} \dfrac{dR_a}{dt} = & R_a(s_a - R_a - \sum_j \xi_{ja} N_j) \\ \\ \dfrac{dN_i}{dt} = & N_i\left(-m_i + \varepsilon \sum_b \xi_{ib} R_b\right) \end{cases} \tag{S37}$$

The equilibrium condition for resources is

$$R_a = s_a - \sum_j \xi_{ja} N_j \tag{S38}$$

which can be inserted in the equilibrium condition for consumers

$$0 = \varepsilon \sum_b \xi_{ib} s_b - m_i - \varepsilon \sum_j N_j \sum_b \xi_{ib} \xi_{jb}. \tag{S39}$$

We thus find an effective Lotka-Volterra-like equilibrium for consumers:

$$0 = \left(\varepsilon \sum_b \xi_{ib} s_b - m_i\right) - \varepsilon \left(\sum_b \xi_{ib}^2\right) N_i - \varepsilon \sum_{j \neq i} N_j \left(\sum_b \xi_{ib}\xi_{jb}\right) \tag{S40}$$

$$= r_i - \alpha_{ii} N_i - \sum_{j \neq i} \alpha_{ij} N_j \tag{S41}$$

from which we can recover the expression in main text by using $K_i = r_i/\alpha_{ii}$ and $A_{ij} = \alpha_{ij}/\alpha_{ii}$. Since interactions have a rather complicated expression, we retain r and α instead of switching to K and A as we did in the main text. We can now perform our invasion analysis. We take the perspective of the consumers, whose abundances N_i satisfy

$$0 = r_i - \sum_j \alpha_{ij} N_j. \tag{S42}$$

We can define a (transformed) environmental sensitivity matrix $\hat{V}$ representing the response of the community to a change of growth rate (rather than carrying capacity as in the main text and section S1). Thus

$$\hat{V}_{ij} = \frac{\partial N_i}{\partial r_j} = (\alpha^{-1})_{ij} \tag{S43}$$

We add an invading species 0, whose interactions with the rest of the community are given by two vectors of coefficients which we denote as follows

$$\alpha_{0*} = (\alpha_{0i}), \qquad \alpha_{*0} = (\alpha_{i0}) \tag{S44}$$

If the invader can coexist with all species present, its equilibrium will read

$$0 = r_0 - \alpha_{00} N_0 - \sum_{i \neq 0} \alpha_{0i} N_i \tag{S45}$$

and as before, we assume a small effect of the invader on the existing community, so that

$$0 = r_0 - \alpha_{00} N_0 - \sum_i \alpha_{0i} N_i + \sum_{ij} \alpha_{0i} \hat{V}_{ij} \alpha_{j0} N_0 \tag{S46}$$

$$\Leftrightarrow N_0 = \frac{r_0 - \sum_i \alpha_{0i} N_i}{\alpha_{00} - \sum_{ij} \alpha_{0i} \hat{V}_{ij} \alpha_{j0}} = \hat{v}_0 \hat{u}_0 \tag{S47}$$

Where, in matrix notations,

$$1/\hat{v}_0 = \alpha_{00} - \alpha_{0*}^\top \alpha^{-1} \alpha_{*0} \tag{S48}$$

The interaction coefficients, however, have a very particular structure, inherited form the consumption coefficients ξ_{ia}. Indeed, we have, if $\xi_0 = (\xi_{0a})$, that

$$\alpha_{ij} = \varepsilon \sum_b \xi_{ib}\xi_{jb}, \qquad \alpha = \varepsilon \xi \xi^\top \tag{S49}$$

$$\alpha_{0i} = \varepsilon \sum_b \xi_{0b}\xi_{ib}, \qquad \alpha_{0*} = \varepsilon \xi_0 \xi^\top \tag{S50}$$

$$\alpha_{j0} = \varepsilon \sum_b \xi_{jb}\xi_{0b}, \qquad \alpha_{*0} = \varepsilon \xi \xi_0^\top \tag{S51}$$

$$\alpha_{00} = \varepsilon \sum_b \xi_{0b}\xi_{0b}, \qquad \alpha_{00} = \varepsilon \xi_0 \xi_0^\top \tag{S52}$$

The consequence is that

$$\alpha_{0*}^{\top}\alpha^{-1}\alpha_{*0} = \varepsilon\xi_0\xi^{\top}(\xi\xi^{\top})^{-1}\xi\xi_0^{\top} \tag{S53}$$

$$=^{?} \varepsilon\xi_0\xi_0^{\top} = \alpha_{00} \tag{S54}$$

where the equality sign in (S54) is marked as a question, because going from the preceding line to this one is not so obvious: it requires all the involved matrices being invertible, which implies that the number of surviving predators is equal to the number of preys). Assuming that (S54) holds, we find that

$$1/\hat{v}_0 = \alpha_{00} - \alpha_{0*}^{\top}\alpha^{-1}\alpha_{*0} = 0 \tag{S55}$$

In other words, the structure of resource competition has a peculiar effect: it constrains the coexisting equilibrium to the limit case $1/v = 0$, where a better competitor will always exclude a poorer one on the same resources, and mutual exclusion (in fact, any kind of multistability) is impossible. In this calculation, we used matrix notations in a fairly cavalier way. Imagine for instance that species 0 consumes only one resource that no other species is consuming. Then, $\alpha_{0i} = \alpha_{i0} = 0$ while $\alpha_{00} \neq 0$, so the previous calculation cannot hold (and $v = 1/\alpha_{00}$ is well-defined). More generally, if there are more resources than species at the pre-invasion equilibrium N^*, then $(\xi\xi^{\top})^{-1}$ may have a nonzero kernel, meaning that line (S53) is in fact not equal to line (S54), but the corresponding sum is missing some terms. This corresponds to the case where invader 0 is somehow "innovating" by consuming an unused resource or mix of resources, in such a way that it potentially becomes an equal competitor to others in the community, rather than being excluded by another or excluding them.