Fitness and community feedbacks: the two axes that drive long-term invasion impacts

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Abstract

Many facets of ecological theory rely 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. We propose an analytical method to predict whether these impacts can be large, as a function of community structure and invader dynamical characteristics, applicable to a wide 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 is controlled by its invasion fitness, which depends on environmental conditions and direct interactions with resident species. But whether this invasion will cause significant transformations, such as extinctions or a regime shift, depends on a specific measure of indirect feedbacks that may involve the entire resident community. Using this metric, we investigate how the complexity, specialization and asymmetry of invader-resident and resident-resident interactions may affect the severity of invasion impacts. Our approach applies to arbitrarily complex communities, from few competing phenotypes to large nonlinear food webs, and hints at new questions to ask as part of any invasion analysis.

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Introduction

Predicting the outcome of a species or phenotype introduction in a resident community is key in answering fundamental ecological and evolutionary questions (Elton 1958). Invasion analysis is invoked to understand adaptation, species coexistence and ecosystem assembly (Law & Morton 1996, Chesson 2000, O'Sullivan *et al.* 2018), and is instrumental in guiding management and conservation efforts in relation to invasive species (Pimm 1991, Williamson 1999, Galiana *et al.* 2014). To analyse the initial stages of an invasion, powerful theoretical approaches exist, built on the notion of invasion fitness or invasibility (Turelli 1978, Metz *et al.* 1995, Geritz *et al.* 1998a, Guo *et al.* 2015, Grainger *et al.* 2019). In essence, these approaches ask: under which conditions can the invader 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 (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, MacDougall *et al.* 2009).

But knowing that an invasion can occur, can we predict its long-term consequences (Levine *et al.* 2003), 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 are not only tied to characteristics of the invader and its immediate interaction partners (predators, prey, competitors...). They can involve the whole web of interactions in the resident community (White *et al.* 2006, Hui & Richardson 2018, Rossberg & Barabás 2019). They may thus be highly unpredictable (Catford *et al.* 2019), both because of their complexity and also 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 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. When community feedbacks are positive, an invasion will cause an irreversible shift in the state of the community, signalling the existence of alternative stable states. The theory that we develop applies to arbitrary many-species stable community models, allowing for any interaction type, network structure and functional response.

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. We first demonstrate it in the simple case of two species, where it connects with known results of competition theory and adaptive dynamics (Roughgarden 1983, Metz *et al.* 1996, Dieckmann & Law 1996, Geritz *et al.* 1998b, Champagnat *et al.* 2002, Meszéna 2005, Meszéna *et al.* 2005, Brännström *et al.* 2013). We then explain how those results can be extended to apply to species-rich 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 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 communities, where only a few statistical features of the interaction network determine the behaviour at the community level (Barbier *et al.* 2018). We predict that asymmetry in the interaction structure of the invader-community system makes invaders less potent. Strikingly, this result contradicts common expectations from invasion biology (see, e.g., Frost *et al.* 2019)). We then demonstrate how this

method extends to nonlinear food web models. These results showcase the new insights that can be gained by accounting for feedback loops in invasion analysis.

Methods

Invasion analysis (Turelli 1978, Geritz *et al.* 1998a, Williamson 1999, Lewis *et al.* 2016, Barabás *et al.* 2018) proceeds as follows: we start from a stable resident community with abundance distribution $\mathbf{N}^* = (N_i^*)$, then add a rare species 0 (the invader), whose abundance we denote N_0. The growth rate of species 0, defined as

$$W_0(\mathbf{N}, N_0) = \frac{1}{N_0}\frac{\mathrm{d}N_0}{\mathrm{d}t}, \tag{1}$$

depends on the abiotic conditions experienced by the new species, as well as biotic conditions, determined by the abundances of resident species (e.g competitors or predators) and its own abundance (e.g., intra-specific competition). The invader's growth rate when rare,

$$w_0 = W_0(\mathbf{N}^*, 0), \tag{2}$$

is what is commonly called the invasion fitness. If $w_0 < 0$, the species cannot grow when rare. By construction, the invasion fitness describes short-term dynamics right after the species' introduction. It does not account for any feedbacks caused by the invading population itself, since it is assumed rare. The 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 mainly focus on this quantity (Turelli 1978, Metz *et al.* 1995, Geritz *et al.* 1998b, Williamson 1999, Lewis *et al.* 2016).

Here we propose that a second quantity, associated with long-term effects, can be revealed via a simple extension of the invasibility approach. As the invading population N_0 increases, it affects the abundance of other species, which feeds back on its own growth rate W_0. At first, this will represent an incremental change, expressed as the following linear approximation of the growth rate function:

$$W_0(\mathbf{N}(N_0), N_0) = w_0 + N_0 \left.\frac{\mathrm{d}W_0}{\mathrm{d}N_0}\right|_{N_0=0}. \tag{3}$$

The invasion ends when $W_0(\mathbf{N}(N_0^*), N_0^*) = 0$ (the invading population stops growing –cf. Fig. 1). If the invader has only weakly affected other species, causing no extinctions and settling at a small equilibrium abundance N_0^*, the above linear approximation should still hold and tells us that

$$N_0^* = v_0 w_0 \qquad \text{with} \qquad 1/v_0 = -\left.\frac{\mathrm{d}W_0}{\mathrm{d}N_0}\right|_{N_0}, \tag{4}$$

an expression that connects the invader's long-term abundance N_0^* to its initial growth rate w_0 via a prefactor v_0.

In the following sections, we will express v_0 in terms of invader-resident interactions and the sensitivity of the resident community to environmental perturbations (Meszéna *et al.* 2006, Barabás *et al.* 2014). For now, we may see v_0 as a measure of long-term feedbacks on the invading population. If the factor v_0 is large, the invader can tend to high abundances, even if has a low initial growth rate. This suggests that the invasion is transforming the biotic environment to be more favourable in the long term than it was at the time of introduction.

We interpret the inverse quantity $1/v_0$ as the effective density dependence of the invader's growth rate (Fig. 1). When it is large, the growth rate decreases rapidly with the population abundance N_0, and the linear approximation (3) holds up to equilibrium. Conversely, when $1/v_0$ is low and initial fitness w_0 is high, nonlinearities become important, signalling larger transformations in the community. In models with linear interactions (Lotka-Volterra dynamics, see below), nonlinearities imply resident species extinction. Even in other models, we find that large w_0 and v_0 correlate with extinction probability. Finally, if $1/v_0$ is negative, the growth rate W_0 first *increases* with abundance N_0, instead of decreasing towards equilibrium. Therefore, the assumption (4) of a weak impact on the community cannot hold, however small the invasion fitness w_0 may be. In that case, we predict the emergence of a tipping point resulting from the invasion dynamics: if abiotic and biotic conditions are such that $w_0 < 0$, the invading species cannot grow from rare, but as soon as the threshold $w_0 = 0$ is crossed, it will jump to high abundances and large impacts, driving the community into a qualitatively different state.

In brief, the factor v_0 encapsulates long-term reorganizations of the community (i.e changes in abundances or even extinctions) following the invasion. Invasion fitness w_0 and long-term feedbacks encapsulated in the factor v_0 thus constitute two complementary axes to describe and predict invasion scenarios.

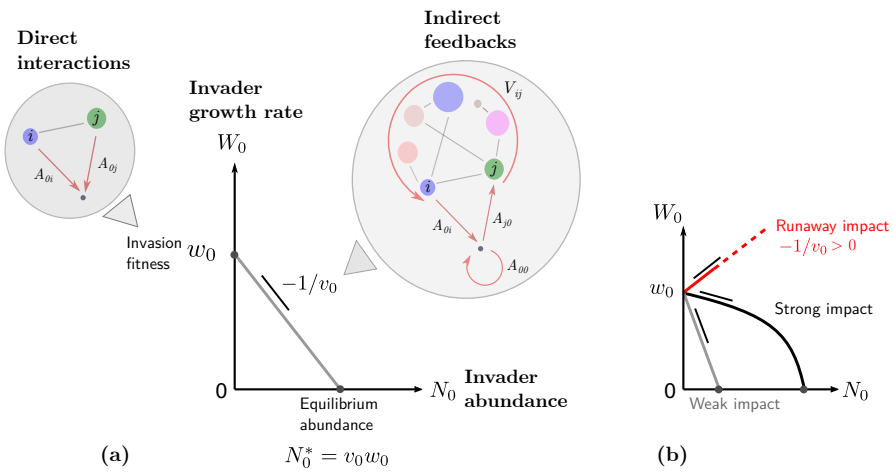

Figure 1: Invader's growth rate $W_0(\mathbf{N}, N_0)$ as a function of its abundance N_0 and that of resident species $\mathbf{N}(N_0)$. (a) Classic invasion analysis focuses on invasion fitness, $w_0 = W_0(\mathbf{N}^*, 0)$ the growth rate of invaders from low initial abundance, determined by the resident community state $\mathbf{N}^*$. We find that long-term effects of the invasion can be predicted using another quantity: the initial slope $1/v_0 = -\mathrm{d}W_0/\mathrm{d}N_0$ of the invader's growth rate, which represents how the invading population, by expanding and transforming its biotic environment, limits itself (if $v_0 > 0$) or accelerates its growth (if $v_0 < 0$). In insets, we show that w_0 arises from direct invader-resident interactions while v_0 encapsulates indirect feedbacks, as shown in (14). (b) For large $1/v_0$, the invader reaches a low equilibrium abundance N_0^*, given by the linear approximation $N_0^* = v_0 w_0$, and barely impacts the resident community. For lower or even negative $1/v_0$, nonlinearities become important. The invasion can cause large transformations and even extinctions of other species.

Two-species example

An illustration of the above reasoning is the example of one species invading a resident population of a second species. To make this preliminary analysis as simple as possible, we consider a Lotka-Volterra model with

normalized (i.e., unit) intraspecific competition, so that the growth rate of the invading species takes the explicit form

$$W_0(N_1, N_0) = r_0 - N_0 - A_{01}N_1, \tag{5}$$

where r_0 is the species growth rate when alone, encoding abiotic conditions, and the term A_{01} is the (constant) strength of resident to invader per-capita interaction. In this elementary example, our approach naturally connects with known results of competition theory (Roughgarden 1983, Tilman 1982, Meszéna *et al.* 2006) and adaptive dynamics (Metz *et al.* 1992, 1995, Geritz *et al.* 1998b, Meszéna 2005, Meszéna *et al.* 2005, Brännström *et al.* 2013). If the resident population is initially at carrying capacity K_1, the invasion fitness (2) of species 0 is

$$w_0 = r_0 - A_{01}K_1. \tag{6}$$

The sign of w_0 determines whether species 0 can invade from low abundance. If species 0 and 1 coexist, we have that

$$N_0^* = \frac{r_0 - A_{01}K_1}{1 - A_{01}A_{10}} = v_0 w_0 \qquad \text{with } 1/v_0 = 1 - A_{01}A_{10}. \tag{7}$$

We can see that v_0 represents the invader's long-term sensitivity to a change in its abiotic environment (e.g., addition of resources) *in the presence* of the resident species. More formally, $v_0 = \partial N_0/\partial r_0$. Its inverse measures the effective self-regulation (or density dependence) of the invader population via its interactions with the resident species. In contrast with the invasion fitness w_0, which only depends on the effect of species 1 on 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. 7). Thus $1/v_0$ measures the strength of the invader's regulatory feedback loop. As illustrated in Fig. 2, v_0 controls whether species actually coexist or exclude each other.

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 (e.g., increasing r_0 while keeping A_{01} and A_{10} fixed) will cause a smaller increase of N_0 than if it had been alone. This signals the occurrence of a strong *self-regulatory feedback* loop on species 0 via species 1. This is the case when a growing predator population limits its own 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. 2a).

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, but there is a range of conditions for which the two coexist (Fig. 2b).

In adaptive dynamics theory (Geritz *et al.* 1998b, Champagnat *et al.* 2002, Meszéna 2005, Brännström *et al.* 2013), the invader is a mutant phenotype, differing only slightly from one of the resident populations. This means that intra- and interspecific interaction strengths are almost exactly equal. By Eq. (7), this implies $1/v_0 \approx 0$. In this case, due to the oversensitivity of the dynamics, a coexistence state can only exist under special circumstances (Appendix S4; cf. Fig. 2c). Thus, in general, as soon as the mutant can invade (its invasion fitness w_0 is positive), it fixes in the community and drives the original resident population extinct.

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. 2d).

For two species, negative feedbacks require predator-prey interactions, and positive feedbacks can only be attained if interactions are competitive or mutualistic. We later 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 move on to an invader-community system with many species and arbitrarily complex, nonlinear interactions (e.g., food webs with predator interference or mutualistic communities with saturation), of the form

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = W_i(\mathbf{N}, N_0), \quad (i = 1, 2, ..., S) \tag{8}$$

$$\frac{1}{N_0}\frac{\mathrm{d}N_0}{\mathrm{d}t} = W_0(\mathbf{N}, N_0). \tag{9}$$

We start from a resident community where species coexist with equilibrium abundances $\mathbf{N}^* = (N_i^*)$, satisfying $W_i(\mathbf{N}^*, 0) = 0$ for all i from 1 to S. We can then define local per-capita interactions as

$$A_{mn} = -\left.\frac{\partial W_m}{\partial N_n}\right|_{(\mathbf{N}^*,0)} \quad (m, n = 0, 1, ..., S), \tag{10}$$

which can describe resident-resident (A_{ij}), invader-resident (A_{i0}) and resident-invader (A_{0i}) per-capita interactions, in the biotic context defined by the resident community. We denote w_0 the invasion fitness of species 0 as in Eq. (2). If $w_0 > 0$, invasion dynamics can take place. To predict if the invasion will have a substantial 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 abundance N_0^*, causes no extinctions, but acts as a weak additional source of growth or mortality for other species, i.e., a perturbation $\delta W_j = -A_{j0}N_0$ of their growth rates. Note that A_{j0} not only encodes direct invader-resident interaction, but also higher order effects representing how resident-resident interactions themselves are affected by the invasion. If the perturbation is weak, we may write its effect δN_i on resident species abundances as

$$\delta N_i = \sum_j \frac{\partial N_i^*}{\partial W_j}\delta W_j = -\sum_j V_{ij}A_{j0}N_0. \tag{11}$$

Here $V_{ij} = \frac{\partial N_i^*}{\partial W_j}$ is the long-term sensitivity of N_i to a change in the growth rate of species j. The whole matrix $V = (V_{ij})$, which we henceforth call *environmental sensitivity matrix*, can be computed from the resident interaction matrix $A_* = (A_{ij})$ $i, j = 1, ..., S$ as

$$V = A_*^{-1} \tag{12}$$

(Levins 1974, Yodzis 1988, Meszéna *et al.* 2006, Aufderheide *et al.* 2013, Barabás *et al.* 2014). The environmental sensitivity matrix encodes net resident-resident interactions, which integrate direct and indirect interaction pathways (see Appendix S1), and determines the community's sensitivity to environmental changes that affect species growth rates.

Now, to understand how the invasion will proceed, we must understand is impact on the growth rate W_0 of the invader itself, which was initially given by w_0. In other words, we must evaluate the quantity

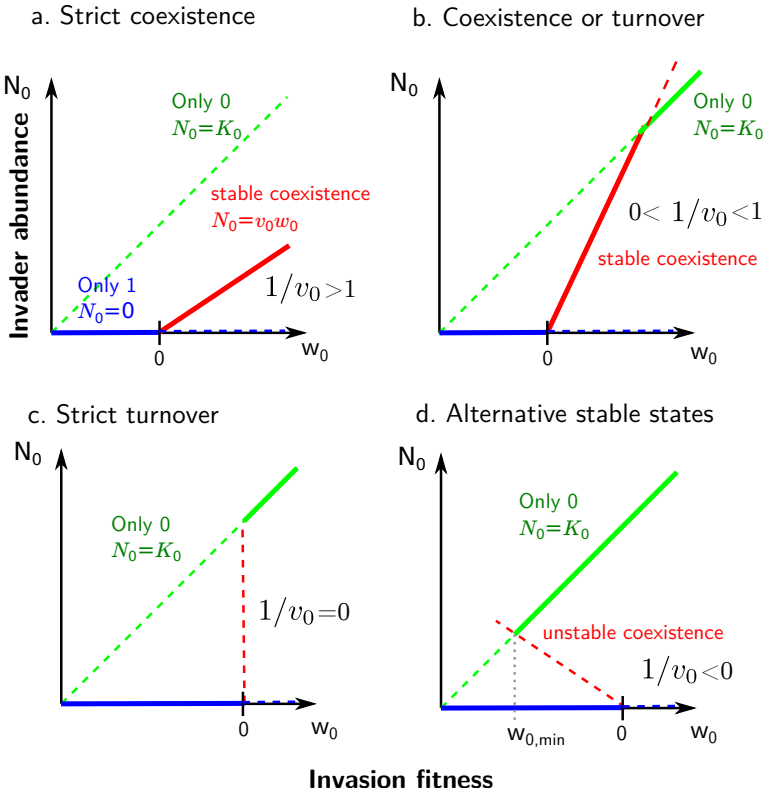

Figure 2: Bifurcation diagram of equilibrium abundance N_0 of species 0 as a function of its invasion fitness $w_0 = K_0 - A_{01}K_1$ into a resident population from species 1. Dashed lines represent unstable, and solid lines stable states. There are three possible states: (i) Species 1 persists alone, $N_0 = 0$ (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).

$\delta W_0 = N_0 \frac{\mathrm{d}W_0}{\mathrm{d}N_0}$ in Eq. (3). This change will depend on the intensity of self-regulation of the invading population A_{00}. But it will also critically depend on the impact δN_i that the invasion is having on resident species as it feeds back to species 0 via resident-invader interactions A_{0i}. Given the expression of δN_i from Eq. (11), we can have

$$\delta W_0 = -A_{00}N_0 - \sum_i A_{0i}\delta N_i = -\left(A_{00} - \sum_{i,j} A_{0i}V_{ij}A_{j0}\right) N_0. \tag{13}$$

From the reasoning that led us to Eq. (4), because the invader's growth rate must vanish when the invasion ends (thus when $\delta W_0 = -w_0$), we see that

$$N_0^* = v_0 w_0 \quad \text{with} \quad 1/v_0 = A_{00} - \sum_{i,j} A_{0i}V_{ij}A_{j0}. \tag{14}$$

This factorization of N_0^* is exact in a neighbourhood of the invasibility threshold $w_0 = 0$, but as explained in Appendix S1, a similar expression can be extended to any value of invasion fitness. It gives the equilibrium abundance of the invader *if it coexisted will all resident species.* 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 substantial change (e.g., extinctions) in the resident community.

As in the two-species example, v_0 is the invader's long-term sensitivity to a change of its abiotic environment, in the biotic context determined by the resident community. Conversely, its inverse $1/v_0$ quantifies the invader's self-regulatory feedback loop, integrating both direct invader-community interactions and the effect of the invasion on all interactions, but also long indirect feedbacks through the entire community (Appendix S1). 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.

Results

The fitness-feedback map

We illustrate in Fig. 3 how the outcomes of an invasion depend on fitness w_0 and feedback v_0, showing that the analysis of the two species case can be directly transposed to complex simulation models. We generate many-species communities with random Lotka-Volterra interactions and food webs with nonlinear (Holling Type 2) functional responses, then simulate species dynamics until they reach an equilibrium $\mathbf{N}^*$. For each community, we then generate hundreds of invaders with randomly distributed interactions (see Appendix S3), and simulate the outcome of the invasion of each invader separately. We see in Fig. 3 that the five possible outcomes (no invasion, coexistence, turnover, irreversible turnover, and alternative stable states, see below) are naturally ordered in a plane whose x- and y-axes correspond to the invader's indirect self-regulation $1/v_0$, and invasion fitness w_0, respectively. We identify in Appendix S2 the thresholds on v_0 that separate these five outcomes. We find that:

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 turnover, 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 (unless the dynamics are at an evolutionary branching point; see Appendix S4). We noted this possibility above for adaptive dynamics, and show in Appendix S3 (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 means that, 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. When the invasion fitness is positive, the invader always establishes at large abundance. There is thus a tipping point precisely at $w_0 = 0$. A successful invasion displays *hysteresis*: modifying environmental conditions to reduce its invasion fitness w_0 below 0 will not be enough to eradicate it. The invasion has caused an irreversible long-term reorganization of the community.

Invader-as-perturbation and stability

In contrast with invasion fitness, long-term feedbacks constitute an uncharted dimension of the description of invasions. For this reason, we now focus our attention on v_0. This will lead us to propose an *invader-as-perturbation* interpretation, introduce notions of worst-case invader and largest community response to perturbations, to finally showcase a fundamental relationship between community stability and long-term impacts of invasions.

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 (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

$$1/v_0 \geq A_{00} - ||A_{0*}||\ ||V||\ ||A_{*0}||, \tag{15}$$

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 to ecological stability). At first sight, the contribution of the invader in this expression is straightforward: the stronger the invader-resident interactions (relative to intra-specific competition), 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 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, 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 ($1/v_0$).

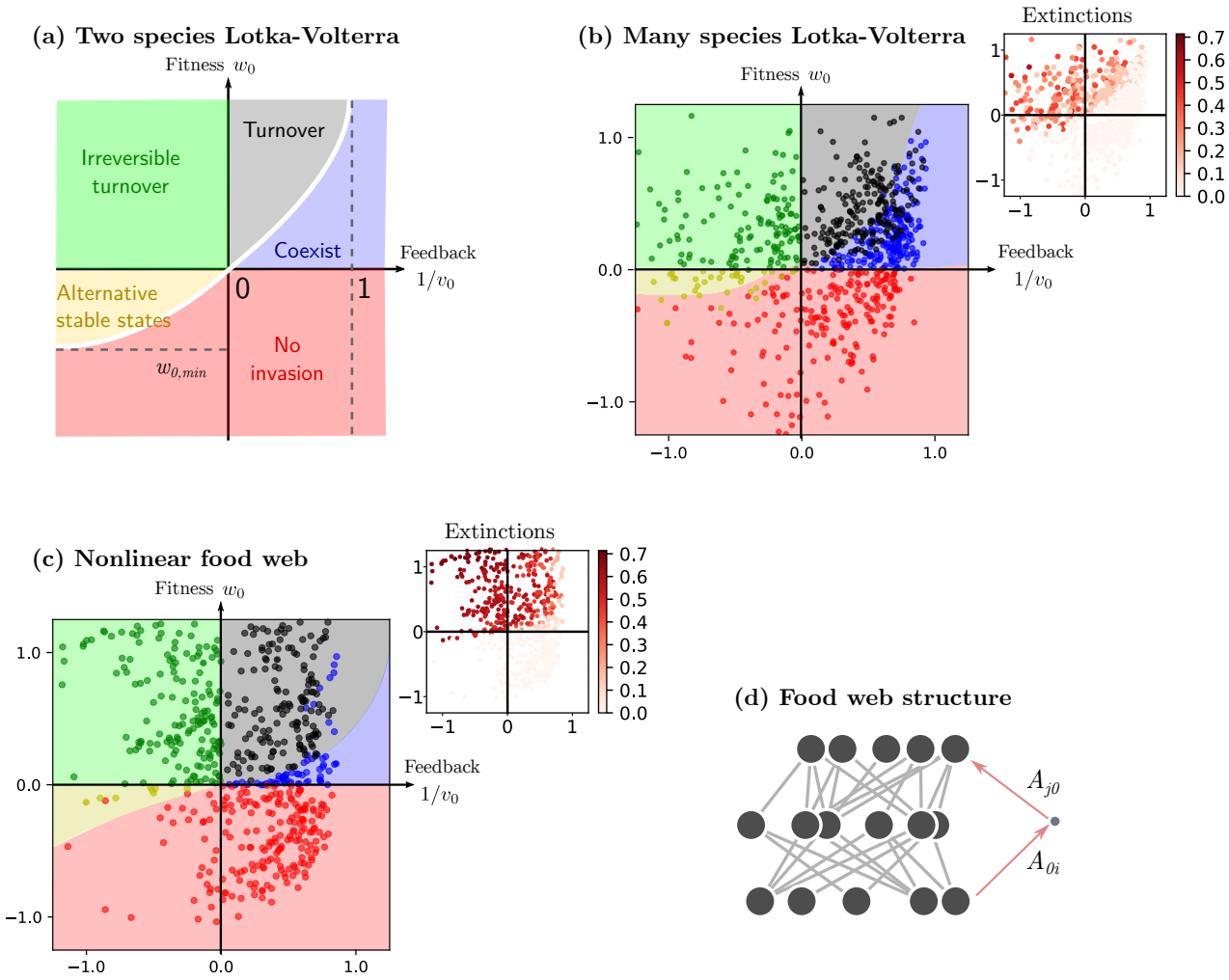

Figure 3: Fitness-feedback map for **(a)** species 0 in a two-species system, **(b)** in a large random community, and **(c)** in a food web with nonlinear functional responses. The y-axis is the invader's short-term fitness w_0: the species can grow from a small initial abundance only if w_0 is positive. The x-axis represents indirect self regulation of the invading species $1/v_0$ (Fig. 1). We delineate four regions: no invasion, coexistence, turnover (when some resident species goes extinct), turnover and hysteresis and alternative stable states (see Fig. 2) 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 S5 of the Supporting Information for complete details of the simulation procedure). Panel (c) shows similar results for a food web with nonlinear (Holling Type 2) interactions, whose structure is shown in panel (d).

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, 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. (15) 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 of 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 limited 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 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 asymmetry between invader-resident and resident-invader interactions, a prediction that contradicts previous 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. 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, at large S and fixed μ_0, σ_0, results become independent of resident diversity and will lead most naturally to the case where both invader and community interactions are only partially determined (but see Appendix S1.2 for the general expression). 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, $\sigma_0 > 0$. 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 high resident diversity it holds that

$$\mathbb{E}(1/v_0) = \mathbb{E}(A_{00}) - \mu_0^2 \langle V_{ij} \rangle - \sigma_0^2 \gamma_0 \langle V_{ii} \rangle \,, \tag{16}$$

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. 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 negative net interactions between resident species (e.g., effective competition), increasing the mean interaction strength of the invader actually increases the self-regulatory

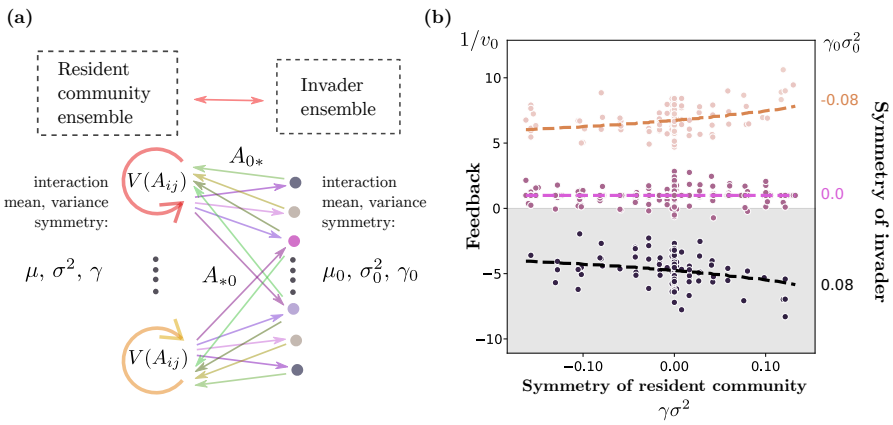

Figure 4: How invasion outcomes depend on basic statistics of invader-resident and resident-resident interactions in random communities. (a) We seek the expected value of the feedback v_0 that an invader, randomly chosen from the pool, will experience. The coefficient $-1 \leq \gamma_0 \leq 1$ controls the symmetry between invader-resident and resident-invader interactions, and requires some interaction variance (heterogeneity or specialization), σ_0. (b) Effective self-regulation of the invader $1/v_0$ (y-axis) in random communities. At fixed mean interaction strength (μ and μ_0, see main text), we vary the symmetry of resident-resident interactions (x-axis: $\gamma\sigma^2$) and invader-resident interactions (colors from light to dark: $\gamma_0\sigma_0^2$). The three coloured curves correspond to the mean-case predictions associated to three pools of invaders (from top to bottom $\gamma_0\sigma_0^2 = -0.08, 0, 0.08$. The grey shaded region shows negative values of $1/v_0$, i.e., strong long-term invasion impacts.)

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 interaction networks are exhaustively known and accurately quantified, we may 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. 4). Many community-level properties of disordered but non-random communities will behave as those of completely random ones (Wang 2018, Cui *et al.* 2019), controlled by only a few simple interaction statistics (Barbier *et al.* 2018, Barbier & Arnoldi 2017). For Lotka-Volterra models, these statistics are: mean interaction strength, $\mathbb{E}(A_{ij}) = \mu/S$, variance $\mathrm{var}(A_{ij}) = \sigma^2/S$ 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. (16). In addition, Bunin (2017) showed that the environmental sensitivity matrix of large communities assembled from a random species pool satisfies

$$\langle V_{ij}\rangle \approx -\frac{\mu}{S} \quad \text{and} \quad \langle V_{ii}\rangle \approx \frac{1-\sqrt{1-4\gamma\sigma^2}}{2\gamma\sigma^2}. \tag{17}$$

This expression tells us that net interspecific interactions, $\langle V_{ii}\rangle$, increase with community symmetry $\gamma\sigma^2$. From Eq. (16), we see that this implies a reduction of the regulatory feedbacks on a given invader, thus increasing

its potential impact. In Fig. 4 we illustrate the combined effects of community and invader properties on the latter's self-regulating feedbacks, showing the destabilizing effect of symmetry in invader-resident and resident-resident interactions (i.e going from the top left to bottom right corners of Fig. 4).

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, when 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 another 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, an invader with a weak (or even negative) fitness advantage can achieve disproportionate 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 (since 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 conditions 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. 4).

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 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 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.* 1998a, 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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Fitness and community feedbacks: the two axes that drive long-term invasion impacts

Supporting Information

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The Supporting Information is organized as follows: Appendix S1 gives a general derivation of the fitness-feedback analysis of invasions, valid for any stable community model. We explain how to get the expressions used in the main text, as well as the more simple expression specific to Lotka-Volterra models. We then focus on the general environmental sensitivity matrix V and derive the associated worst and mean case invader interaction vectors. Appendix S2 then 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 General feedback-fitness analysis of invasions

Consider a general community model of the form

$$\frac{1}{N_i}\frac{dN_i}{dt} = W_i(\mathbf{N}) = r_i - \sum_{j=1}^{S_{\text{pool}}} a_{ij}(\mathbf{N})N_j \qquad (i = 1, ..., S_{\text{pool}}), \tag{S1}$$

where r_i denotes species' intrinsic growth (or mortality) rates, which are negative for strict consumers. The terms a_{ij} could encode any type of inter-specific interaction, and any functional response. The sign convention chosen is that a positive a_{ij} would be an antagonistic interaction (e.g., competition or predation). The diagonal terms a_{ii} denote self-interactions (e.g self-regulation when positive). However, we do not assume that there are direct self-interaction terms for all species. In food web models, for instance, one rarely assumes intra-specific interactions for predators (e.g., cannibalism). Before performing the invasion analysis, we do assume that the resident community has reached an equilibrium $N^* = (N_i^*)$ comprised of $S \leq S_{\text{pool}}$ persisting species. For conciseness we will write $a_{ij}(N^*) = a_{ij}^*$. If a new species is introduced with a small invasion fitness

$$\delta w_0 = r_0 - \sum_{j=1}^{S} a_{0j}^* N_j^*, \tag{S2}$$

it will grow form rarity. We assume that it eventually reaches a low abundance δN_0. Under this assumption, resident species abundances must have consequently changed by a small amount δN_i to satisfy

$$\sum_{j=1}^{S} a_{ij}(N_j^* + \delta N_j) + a_{i0}\delta N_0 = r_i;\ i = 1, ..., S \tag{S3}$$

to first order in δN_0 and δN_i. This expression implies that

$$\sum_{j=1}^{S}(a_{ij}^* + \sum_{k=1}^{S}\frac{\partial a_{ik}}{\partial N_j}N_k^*)\delta N_j = -(a_{i0}^* + \sum_{j=1}^{S}\frac{\partial a_{ij}}{\partial N_0}N_j^*)\delta N_0. \tag{S4}$$

We now define the effective resident interaction matrix $A = (A_{ij})$ as

$$A_{ij} = a_{ij}^* + \sum_k \frac{\partial a_{ik}}{\partial N_j}N_k^*. \tag{S5}$$

A_{ij} encodes both direct interactions between j and i as well as the effect that species j can have on other interactions affecting species i (e.g., higher order interactions). Also, this term encodes effective self-interactions, that can be non-zero even if $a_{ii} = 0$ (e.g., predator interference). Furthermore, we can directly generalize the above expression of A_{ij} to include effective interactions A_{i0} between invader and resident species. With these notations we get

$$\delta N_i = -\sum_j V_{ij}A_{i0}\delta N_0; \quad V = A^{-1}, \tag{S6}$$

where V_{ij} is also the environmental sensitivity matrix $\partial N_i/\partial \xi_j$ of the resident community. In other words, the invader acts as the following persistent perturbation of resident species growth parameters:

$$r_i \to \xi_i - A_{i0}\delta N_0. \tag{S7}$$

Taking the perspective of the invading species, its abundance δN_0 should satisfy:

$$\sum_{i=1}^{S} a_{0i}(N_i^* + \delta N_i) + a_{00}\delta N_0 = r_0, \tag{S8}$$

which, to first order in δN_0 and δN_i, becomes

$$\sum_{i=1}^{S}\left(a_{0i}^* + \sum_k \frac{\partial a_{0k}}{\partial N_i}N_k^*\right)\delta N_i + (\sum_{i=1}^{S}\frac{\partial a_{0i}}{\partial N_0}N_i^* + a_{00}^*)\delta N_0 = \delta w_0. \tag{S9}$$

We define the interactions A_{0i} from resident species to invader so that A_{0i} encompasses the effect that species i can have on the other interactions that can affect the invader. The self-interaction term A_{00} encodes direct intra-specific interactions as well as self-induced changes of interactions with other species. With these notations we finally get

$$\left\{A_{00} - \sum_{i=1}^{S} A_{0i}V_{ij}A_{i0}\right\}\delta N_0 = \delta w_0 \Leftrightarrow \delta N_0 = v_0^*\delta w_0, \tag{S10}$$

recovering the fitness-feedback factorization of the abundance of the invader. If the latter has finite (i.e., not infinitesimal) invasion fitness w_0, if it coexists with resident species its abundance will read

$$N_0 = \int_0^{w_0} v_0 dw_0 = \langle v_0 \rangle w_0, \tag{S11}$$

where $\langle v_0 \rangle$ is the average feedback over the fitness range $[0, w_0]$. In general there will be no closed form for $\langle v_0 \rangle$. We can expect however, that it will be strongly correlated with its value v_0^* near the bifurcation $w_0 = 0$. In particular, for Lotka-Volterra models $v_0 = v_0^*$, and, if all $a_{ii} > 0$, one can rescale all interactions so that $a_{ii} = 1$ and define a general carrying capacity (i.e allowing negative values) $K_i = r_i/a_{ii}$ for all species. In this simple case (i.e., Lotka-Volterra with self-regulation of all species) we can more simply write $1/v_0$ as

$$1/v_0 = 1 - \sum A_{0i}V_{ij}A_{j0}, \tag{S12}$$

where $A_{ii} = 0$ and $V_{ij} = \partial N_i / \partial K_j$. Furthermore,

$$V = (\mathbb{I} + A)^{-1} \tag{S13}$$

where $A_{ij} = a_{ij}/a_{ii}$ denotes relative direct interactions, and $\mathbb{I}$ is the identity matrix. This simple case, although restrictive, allows us to make a general statement: we can explain why v_0 depends on (long) indirect interaction pathways through the resident community. Indeed, in the self-regulating Lotka-Volterra case, we can write V in terms of the Neumann series

$$V = (\mathbb{I} + A)^{-1} = \mathbb{I} - A + A^2 + ... + (-1)^n A^n + \dots \tag{S14}$$

This means that

$$1/v_0 = 1 - \sum_{n \geq 0} (-1)^n \mathcal{L}_0^{(n)}, \tag{S15}$$

where $\mathcal{L}_0^{(n)}$ represents the sum of all invader-invader interaction loops of length $n+2$ trough the community:

$$\mathcal{L}_0^{(n)} = \sum_{i_1, \dots, i_n} A_{0,i_n} A_{i_n, i_{n-1}} ... A_{i_1,0}. \tag{S16}$$

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

$$1/v_0 \geq A_{00} - ||A_{0*}||\ ||V||\ ||A_{*0}||, \tag{S17}$$

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:

$$||V||^2 = \max_{||u||=1} ||Vu||^2 \tag{S18}$$

$$= \max_{||u||=1} \langle Vu, Vu \rangle \tag{S19}$$

$$= \max_{||u||=1} \left\langle (V^\top V)u, u \right\rangle. \tag{S20}$$

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_{dom}^2 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,

$$A_{*0}^{\text{worst}} = ||A_{*0}^{\text{worst}}|| \cdot u_{\text{dom}}. \tag{S21}$$

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

$$A_{0*}^{\text{worst}} = ||A_{0*}^{\text{worst}}|| \cdot \frac{Vu_{\text{dom}}}{s_{\text{dom}}}. \tag{S22}$$

S1.2 Mean-case invader

We now seek the expected value of the indirect feedback on a species randomly chosen from a pool of potential invaders. This requires prior knowledge on the first moments $M_{ij} = \mathbb{E}(A_{i0}A_{0j})$ and $d = \mathbb{E}(A_{00})$ of a statistical ensemble of invader-community interactions. Indeed, the long-term feedbacks on an invader reads

$$\mathbb{E}(1/v_0) = d - \mathbb{E}\sum_{i,j} A_{0i}V_{ij}A_{j0} \tag{S23}$$

$$= d - \sum_i (\sum_j V_{ij}\mathbb{E}(A_{j0}A_{0i})) \tag{S24}$$

$$= d - \sum_i (\sum_j V_{ij}M_{ij}) \tag{S25}$$

$$= d - \mathrm{Tr}(VM), \tag{S26}$$

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

$$M_{ij} = \frac{\mu_0^2}{S^{*2}} + \frac{\gamma_0\sigma_0^2}{S^*}\delta_{ij}, \tag{S27}$$

and $d = 1$. We also considered the hight diversity limit $S^* \to \infty$. From the above calculations we get

$$\mathbb{E}(1/v_0) = 1 - \sum_i (\sum_j V_{ij}M_{ij}) \tag{S28}$$

$$= 1 - \mu_0^2 \frac{1}{S^{*2}} \sum_{i,j} V_{ij} - \gamma_0\sigma_0^2 \frac{1}{S^*} \sum_i V_{ii} \tag{S29}$$

$$= 1 - \mu_0^2 \frac{1 - 1/S^*}{S^*(S^* - 1)} \sum_{i\neq j} V_{ij} - (\gamma_0\sigma_0^2 + \frac{\mu_0^2}{S^*}) \frac{1}{S^*} \sum_i V_{ii} \tag{S30}$$

$$= 1 - \mu_0^2\langle V_{ij}\rangle - \gamma_0\sigma_0^2\langle V_{ii}\rangle + \text{h.o.t.}, \tag{S31}$$

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 the 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,

$$1/v_0 = 1 - a_{01}a_{10}, \quad w_0 = K_0 - a_{01}K_1. \tag{S32}$$

Our analysis in one of transcritical bifurcations. As parameters change, transition between invasion outcomes (Fig. 3a in main text) occur when equilibria meet and exchange their stability. 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 invader state (no resident). Thus, when

$$\underbrace{N_0}_{v_0 w_0} = \underbrace{K_0}_{w_0 + a_{01}K_1}, \tag{S33}$$

we get the condition

$$w_0(v_0 - 1) = a_{01}K_1. \tag{S34}$$

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

$$w_0 \leq \left(\frac{1/v_0}{1 - 1/v_0}\right) a_{01}K_1, \tag{S35}$$

which behaves as $w_0 = a_{01}K_1/v_0$ 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

$$a_{01}K_1 = -\frac{dw_0}{dN_1} N_1|_{N_1=K_1} \stackrel{\text{def}}{=} u_{0/1}. \tag{S36}$$

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

$$w_0 = \left(\frac{1/v_0}{1 - 1/v_0}\right) u_{0/1}. \tag{S37}$$

S2.2 General case

In the general multi-species case we can make a similar argument: the transition between invasion outcomes coincide with transcritical bifurcations which occurs when equilibria meet and exchange their stability (cf. Fig. S1). Assuming that there is at most one stable state per species composition, the coexistence state can become unstable (or vice versa) when it meets a state where one species, say i, is absent, i.e., when

$$\underbrace{N_0}_{\langle v_0\rangle w_0} = \underbrace{N_{0/i}}_{\langle v_{0/i}\rangle w_{0/i}}. \tag{S38}$$

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

$$w_{0/i} \approx w_0 \underbrace{-\frac{dw_0}{dN_i} N_i|_{N_i=N_i^*}}_{u_{0/i}}. \tag{S39}$$

This expression is exact for the Lotka-Volterra case because fitness is a linear function of abundances. However, it will remain a good approximation in more general models when the first species to go extinct due to the invasion has a small abundance, thus justifying this linear approximation. The intersection condition thus reads

$$w_0 \approx \left(\frac{1/\langle v_0\rangle}{1 - \langle v_{0/i}\rangle/\langle v_0\rangle}\right) u_{0/i}, \tag{S40}$$

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

$$1/\langle v_0\rangle \geq \frac{1}{\min_i \langle v_{0/i}\rangle}, \tag{S41}$$

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

$$-\max_i u_{0/i} \leq w_0 < 0. \tag{S42}$$

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

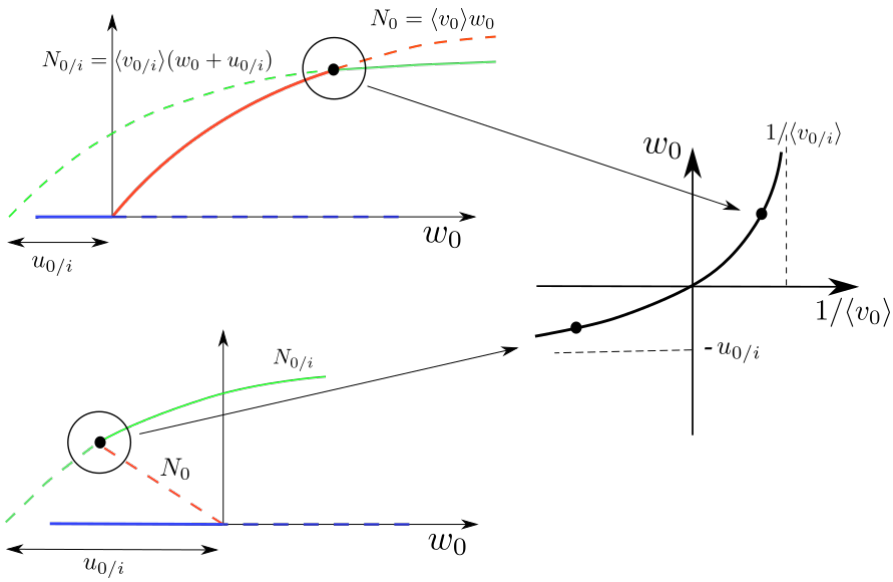

Figure S1: Illustration of the derivation of regime boundaries. Left panels: y-axis represents the possible equilibrium abundances of the invader as a function of its invasive fitness w_0. Coloured dashed lines denote unstable states, continuous lines stable states. Top: the case where $v_0 > 0$. As long as the invasion fitness is not too large, the coexistence state remains stable. As w_0 increases, coexistence looses its stability when it crosses another state where the invader can persist (here a state where one species i has been led to extinction). If the feedback is small enough, however, the invader will not cross any other states, no matter how large its invasion fitness is (vertical asymptote on the right panel) Consequently, it will not cause extinctions. Bottom right, the case where $v_0 < 0$. In this case the coexistence state is unstable, no matter how small the invasion fitness is, so that if the invasion fitness is positive, the community will shift to a different state. At negative values of invasion fitness, the unstable coexistence state delineates the basin of attraction of two alternative stable states: one where the invader is extinct (in blue) and one where it persists, at the expense of one (or more) species. At sufficiently negative values of w_0 there is no stable state of the community in which the invader can persist (horizontal asymptote on the right panel).

S3 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

$$\frac{\mathrm{d}R_a}{\mathrm{d}t} = R_a(s_a - R_a - \sum_j \xi_{ja} N_j), \tag{S43}$$

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \left(-m_i + \epsilon \sum_b \xi_{ib} R_b \right). \tag{S44}$$

The equilibrium condition for resources is

$$R_a = s_a - \sum_j \xi_{ja} N_j, \tag{S45}$$

which can be inserted in the equilibrium condition for consumers:

$$0 = \epsilon \sum_b \xi_{ib} s_b - m_i - \epsilon \sum_j N_j \sum_b \xi_{ib}\xi_{jb}. \tag{S46}$$

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

$$0 = \left(\epsilon \sum_b \xi_{ib} s_b - m_i\right) - \epsilon \left(\sum_b \xi_{ib}^2\right) N_i - \epsilon \sum_{j\neq i} N_j \left(\sum_b \xi_{ib}\xi_{jb}\right) \tag{S47}$$

$$= r_i - \alpha_{ii} N_i - \sum_{j\neq i} \alpha_{ij} N_j. \tag{S48}$$

We can now perform our invasion analysis. We take the perspective of the consumers, whose abundances N_i satisfy

$$0 = r_i - \sum_j \alpha_{ij} N_j. \tag{S49}$$

We can define the environmental sensitivity matrix V to encode the response of the community to a change of growth rate (rather than carrying capacity as in the main text and section S1). Thus,

$$V_{ij} = \frac{\partial N_i}{\partial r_j} = (\alpha^{-1})_{ij}. \tag{S50}$$

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:

$$\alpha_{0*} = (\alpha_{0i}), \quad \alpha_{*0} = (\alpha_{i0}). \tag{S51}$$

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

$$0 = r_0 - \alpha_{00} N_0 - \sum_{i\neq 0} \alpha_{0i} N_i, \tag{S52}$$

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

$$0 = r_0 - \alpha_{00} N_0 - \sum_i \alpha_{0i} N_i + \sum_{ij} \alpha_{0i} V_{ij} \alpha_{j0} N_0 \tag{S53}$$

$$\Leftrightarrow N_0 = \frac{r_0 - \sum_i \alpha_{0i} N_i}{\alpha_{00} - \sum_{ij} \alpha_{0i} V_{ij} \alpha_{j0}} = v_0 w_0, \tag{S54}$$

Where, in matrix notation,

$$1/v_0 = \alpha_{00} - \alpha_{0*}^\top \alpha^{-1} \alpha_{*0}. \tag{S55}$$

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

$$\alpha_{ij} = \epsilon \sum_b \xi_{ib}\xi_{jb}, \qquad \alpha = \epsilon\xi\xi^\top, \tag{S56}$$

$$\alpha_{0i} = \epsilon \sum_b \xi_{0b}\xi_{ib}, \qquad \alpha_{0*} = \epsilon\xi_0\xi^\top, \tag{S57}$$

$$\alpha_{j0} = \epsilon \sum_b \xi_{jb}\xi_{0b}, \qquad \alpha_{*0} = \epsilon\xi\xi_0^\top, \tag{S58}$$

$$\alpha_{00} = \epsilon \sum_b \xi_{0b}\xi_{0b}, \qquad \alpha_{00} = \epsilon\xi_0\xi_0^\top. \tag{S59}$$

The consequence is that

$$\alpha_{0*}^\top\alpha^{-1}\alpha_{*0} = \epsilon\xi_0\xi^\top(\xi\xi^\top)^{-1}\xi\xi_0^\top \tag{S60}$$

$$=^? \epsilon\xi_0\xi_0^\top = \alpha_{00}, \tag{S61}$$

where the equality sign in (S61) 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. This implies, in particular, that the number of surviving predators is equal to the number of preys, hence that the community is "saturated". Assuming that (S61) holds, we find that

$$1/v_0 = \alpha_{00} - \alpha_{0*}^\top\alpha^{-1}\alpha_{*0} = 0. \tag{S62}$$

In other words, the structure of resource competition has a peculiar effect: it constrains the coexisting equilibrium to the limit case $1/v_0 = 0$, 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, however, 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 $v_0 = 1/\alpha_{00}$ is finite).

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 (S60) is in fact not equal to line (S61), 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.

S4 v_0 and the principle of limiting similarity

According to Eq. (14) in the main text, the invader's equilibrium density $N_0^* = v_0 w_0$ is the product of the invasion fitness w_0 and the sensitivity v_0, where

$$1/v_0 = A_{00} - \sum_j \sum_k A_{0j}V_{jk}A_{k0}. \tag{S63}$$

Here we show that if the invader has identical interaction coefficients to another species (let that be species 1 without loss of generality), then $1/v_0 = 0$ implying infinite sensitivity.

Indeed, using the fact that $V = A^{-1}$ is the environmental sensitivity matrix (Eq. S6; see also Meszéna *et al.* 2006, Barabás *et al.* 2014), we can write $1/v_0$ as

$$1/v_0 = A_{00} - \sum_j \sum_k A_{0j}(A^{-1})_{jk}A_{k0}. \tag{S64}$$

Since the invader (species 0) and species 1 have identical interaction coefficients by assumption, the zero subscripts can be replaced with ones:

$$1/v_0 = A_{11} - \sum_j \sum_k A_{1j}(A^{-1})_{jk}A_{k1}. \tag{S65}$$

Focusing on just $\sum_k (A^{-1})_{jk}A_{k1}$, this is the product of the inverse of a matrix and the first column of the original matrix. The result, by definition, is a column vector with 1 as its first entry and 0s everywhere else. We therefore have

$$1/v_0 = A_{11} - \begin{pmatrix} A_{11} & A_{12} & A_{13} & \dots \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \\ \vdots \end{pmatrix} = A_{11} - A_{11} = 0, \tag{S66}$$

yielding infinite sensitivity.

Eq. (S66) was derived assuming the invader's interactions A_{0i} and A_{i0} are identical to those of one of the resident species. Since $1/v_0$ is a continuous function of the matrix entries, for an invader with nonidentical but highly similar interaction structure to that of a resident, $1/v_0$ will be close to zero, giving a very large (though finite) sensitivity. Being sufficiently different from all residents is therefore a necessary condition for v_0 not to be too large and thus for the approximation $N_0^* = v_0 w_0$ to work.

This result is in line with the theory of adaptive dynamics (Metz *et al.* 1996, Dieckmann & Law 1996, Geritz *et al.* 1998b, Meszéna 2005, Meszéna *et al.* 2005, Brännström *et al.* 2013), and our intuition of natural selection in general. If two species are exactly identical, then the slightest advantage to one of them (say, a mutation which reduces mortality by 0.1% on average) will cause it to establish and drive its competitor extinct. The fact that in the deterministic limit an arbitrarily small such parameter perturbation can change the identity of the winning species is reflected in the sensitivity v_0 being infinitely large. In the terminology of adaptive dynamics, mutant phenotypes that are very similar to a resident one will either go extinct, or themselves become resident, replacing the original resident phenotype. The only exception is at an evolutionary branching point (Geritz *et al.* 1998b), where two competing phenotypes may start diverging from one another without competitive exclusion. However, the way such branching points permit the temporary stable coexistence of arbitrarily similar phenotypes is not by making v_0 smaller, but having the fitness difference w_0 between phenotypes be fine-tuned so that $v_0 w_0$ will remain bounded thus coexistence, even when v_0 is arbitrarily large.

In summary, an invading species that is very similar to a resident has very large sensitivity v_0, rendering the approximation $N_0^* = v_0 w_0$ incompatible with the assumption of small N_0^*. This is because such a "mutant" phenotype either goes extinct or replaces the original resident. Neither scenario conforms to the assumption of the invader establishing at a low density and affecting the resident community only slightly. Whether the mutant invader will replace the resident can be determined via the methods of adaptive dynamics; e.g., by comparing their invasion growth rates. The only exception to this rule of competitive exclusion is when the dynamics are exactly at an evolutionary branching point, where the special parameter settings required to offset the effect of a large v_0 are automatically established.

S5 Many-species simulations

In the main text, numerical results shown in Fig. 3 and 4, as well as the cartoon in Fig. 2, were obtained from the Lotka-Volterra model (or a nonlinear extension, see below), whose dynamics are given by

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = \frac{r_i}{K_i} N_i \left(K_i - N_i - \sum_{j \neq i} A_{ij} N_j \right), \tag{S67}$$

with r_i the growth rate of species (or strategy) i. For simplicity, we assume $r_i = K_i$. 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.

S5.1 Generating Figure 3b

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. (S67) 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 500 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.

S5.2 Generating Figure 3c

For the food webs considered in Fig. 3c, we first draw niche positions $n_i \in [1, 2, 3]$ at random for $S = 20$ species. We then generate the matrix of predator-prey fluxes with randomly distributed coefficients (following the uniform distribution $\mathcal{U}$)

$$F_{ij} = \begin{cases} \mathcal{U}(0,2) & \text{with probability 0.4 if } n_i - n_j = 1, \\ 0 & \text{otherwise.} \end{cases} \tag{S68}$$

We then simulate the dynamics

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \left(r_i - N_i + \epsilon \sum_j \frac{F_{ij} N_j}{1 + \theta^{-1} \sum_k F_{ik} N_k} - \sum_j \frac{F_{ji} N_j}{1 + \theta^{-1} \sum_k F_{jk} N_k} \right), \tag{S69}$$

with $\epsilon = 0.4$, $\theta = 0.1$, and intrinsic growth rate

$$r_i = \begin{cases} 1 & n_i = 1, \\ -0.1 & n_i > 1. \end{cases} \tag{S70}$$

Invaders were not drawn according to the same structure, but with direct non-trophic interactions as in the previous section, so as to be able to visit the plane $(1/v_0, w_0)$ in a less constrained way. Since interactions were indiscriminate of trophic level, they were often relatively strong against low-abundance predators, and all successful invasions caused species extinctions in the community, so we set the threshold for blue dots

("coexistence") to less than 10% extinctions. Despite this quantitative difference, the same qualitative pattern held as in random Lotka-Volterra communities.

S5.3 Generating Figure 4

We generate random communities (see Sec. S5.1) 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.

S5.4 Fraction of irreversible invaders in a random community

In the main text, we independently vary invader and community properties. Here, we consider what happens when invaders and resident species are drawn from the same species pool. Let us generate a random matrix with coefficients A_{ij}, as well as the interactions A_{0i} and A_{i0} with an additional species 0, using the same parameters. We plot in Fig. S3 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 $\langle A \rangle$ and large $\mathrm{std}(A)$, and reaches one as $\langle A \rangle \to 1$, meaning that all invaders are on the threshold in a neutral community (where $A_{ij} = A_{ii}$).

We demonstrate this in simulations in Fig. S3, 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

$$K_0 = \epsilon + \sum_i A_{0i} N_i^*, \tag{S71}$$

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

$$|\Delta N|^2 = N_0^2 + \sum_j (N_j - N_j^*)^2. \tag{S72}$$

A reversible invader creates small changes in the community,

$$\Delta N \sim \epsilon, \tag{S73}$$

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

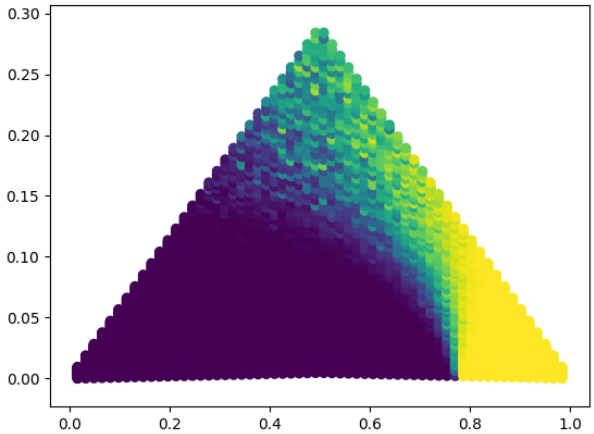

Figure S2: Fraction of irreversible ($1/v_0 \leq 0$) invaders among randomly drawn species, from 0 (blue) to 1 (yellow), as a function of mean $\langle A \rangle$ (x-axis) and standard deviation std(A) (y-axis) of interactions. Here the community and invaders all have symmetrical interactions $A_{ij} = A_{ji}$ drawn from the same uniform distribution.

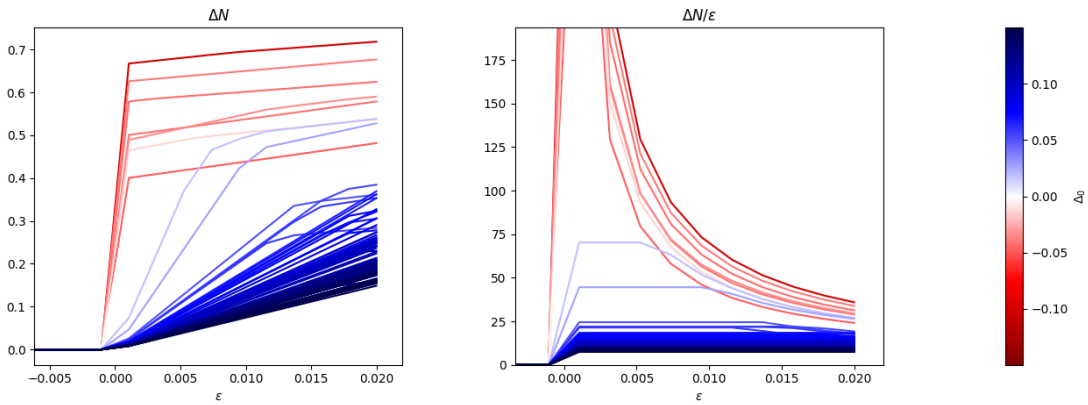

Figure S3: Change in equilibrium composition $\Delta N = (N_0^2 + \sum_j (N_j - N_j^*)^2)^{1/2}$ after the invasion of species 0, as a function of $w_0 = \epsilon$ the invasion fitness. Each line corresponds to a randomly drawn invader with $\Delta_0 = 1/v_0$ shown by colors. **Left:** We see that for 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.