A theory of ecological invasions and its implications for eco-evolutionary dynamics

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Predicting the outcomes of species invasions is a central goal of ecology, a task made especially challenging due to ecological feedbacks. To address this, we develop a general theory of ecological invasions applicable to a wide variety of ecological models: including Lotka-Volterra models, consumer resource models, and models with cross feeding. Importantly, our framework remains valid even when invading evolved (non-random) communities and accounts for invasion-driven species extinctions. We derive analytical expressions relating invasion fitness to invader abundance, shifts in the community, and extinction probabilities. These results can be understood through a new quantity we term "dressed invasion fitness", which augments the traditional notion of invasion fitness by incorporating ecological feedbacks. We apply our theory to analyze short-term evolutionary dynamics through a series of invasions by mutants whose traits are correlated with an existing parent. We demonstrate that, generically, mutants and parents can coexist, often by driving the extinction of low-abundance species. We validate theoretical predictions against experimental datasets spanning ecosystems from plants to microbial protists. Our work highlights the central role of ecological feedbacks in shaping community responses to invasions and mutations, suggesting that parent-mutant coexistence is widespread in eco-evolutionary dynamics.

I. INTRODUCTION

Invasion by a new species is a fundamental feature of ecosystems ranging from microbiomes to rainforests [1–3]. Ecological invasions also offer a powerful lens through which to view ecological and evolutionary processes [4, 5]. These include practical engineering tasks like ecosystem management [6] and designing probiotics [7], but also more general ecological questions regarding community function and resilience [8, 9]. More abstractly, a single step of evolution can also be viewed through the lens of invasions by viewing new mutations as invasions by highly related species [10–12].

Despite the importance of ecological invasions, our theoretical understanding remains limited [13–16]. This gap in our knowledge is even more pronounced when the communities of interest are diverse, evolved, and/or engage in complex behaviors such as cross-feeding [17]. Invasion outcomes are mediated by a variety of factors including invader characteristics, community interactions, and environmental conditions [5, 18–20]. A further complication that arises when thinking about invasions is that invaders fundamentally alter the ecosystem they invade [21, 22].

A prominent example of this is invasion-induced extinction of species originally present in the community [23–25]. Dealing with extinctions presents an especially challenging technical problem. It is hard to *a priori* predict whether an existing species will survive or go extinct after an invasion. This is especially true in context of evolution where the invader is highly correlated with an existing species in the community [10, 12].

To overcome these challenges, here we develop a general framework for modeling ecological invasions with species extinctions. Our framework allows us to predict invader abundances, which species go extinct, and changes in community abundances by solving a set of self-consistency equations relating these quantities to each other (see Fig. 1 (a)). The framework takes advantage of the fact that, for diverse ecosystems, we can view invasions as small perturbations. This allows us to understand invasion dynamics using linear-response theory [26], now augmented with the ability to account for invasion-induced extinctions.

A key advantage of our approach is its applicability to evolved communities and invaders with traits closely related to existing species in the ecosystem, which we henceforth refer to as correlated invaders. Such invaders arise during evolution, where mutants are highly-correlated with parents. We demonstrate that parent-mutant coexistence is mediated by interactions with the *entire community* through global eco-evolutionary feedbacks. A direct consequence of this is that for diverse communities, parents and mutants can often coexist despite being more phenotypically similar to each other than other community members.

Importantly, our theory is compatible with almost any niche-based ecological model where the species and resources reach a steady state (e..g, Lotka-Volterra and consumer resource models [27], models with cross-feeding [28–31], and models with more complex non-linearities [32]). Our theory also makes direct connection with experiments, highlighting its potential for connecting theoretical predictions with empirical observations.

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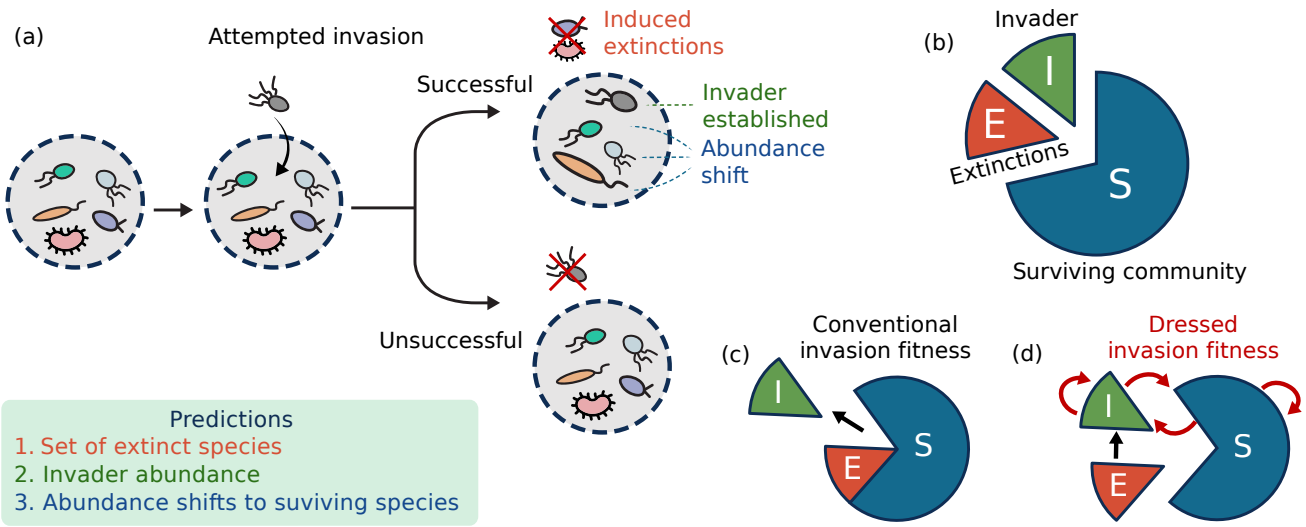

FIG. 1. **Predicting invasion outcomes in diverse ecological communities.** (a) Cartoon illustrating possible invasion outcomes. If an attempted invasion is unsuccessful, the community remains unchanged; if successful, the invader establishes, causing extinctions and abundance shifts among survivors. Our theory predicts all these three outcomes: the set of species that go extinct, the invader abundance, and the abundance shifts among surviving species. (b) We show that prediction requires partitioning a community into extinct and surviving species post-invasion (Eq (2)). (c) We introduce "dressed invasion fitness" (Eq (12)), which incorporates ecological feedbacks and show it predicts invasion outcomes better than conventional invasion fitness, which only considers direct community interactions.

II. THEORY OF ECOLOGICAL INVASIONS

Our goal is to describe how ecosystems respond to invasions by new species. We assume that the ecosystem being invaded is at steady state (i.e. resource and species dynamics are not changing in time) and ask about the new steady state reached by the system after invasion. As illustrated in the cartoon in Fig. 1 (a), there are two possible outcomes post-invasion: if the invasion fails, the system eventually recovers to the same ecological steady state as before; if the invasion succeeds, the invader proliferates and establishes itself within the system, leading to changes in community structure and the abundances of surviving species and resources.

In this work, we introduce a general framework to predict the new ecological steady state after an invasion, making use of the knowledge of the pre-invasion community and their interactions with the invader. The outcomes of successful invasions can be categorized by three experimentally measurable quantities: (1) the identity of species that go extinct, (2) the shifts in abundance among surviving species, and (3) the abundance of the invader itself. When the pre-invasion ecosystem is large and stable, invasions can be viewed as small perturbations to the existing ecosystems. Our framework exploits this observation to predict these outcomes systematically by developing a generalized linear-response theory for ecological invasions. Even though our assumption of invaders being small perturbations is justified only for large communities, our framework nevertheless successfully predicts invasion outcomes for small communities as well (see section V).

A. Predicting invasion outcomes

Our framework is broadly applicable to a wide range of ecological models but in the main text we focus on the generalized Lotka-Volterra model (GLV). The dynamics of the GLV model are given by

$$\frac{dX_i}{dt} \equiv X_i g_i(\vec{X}) = X_i \left(r_i - X_i - \sum_{j \neq i} A_{ij} X_j \right), \quad (1)$$

where i labels species from 1 to S, X_i is the abundance of species i and $g_i(\vec{X})$ is its net per capita growth rate in the presence of other species. $g_i(\vec{X})$ is a linear function of its naive growth rate r_i and the abundances of all species X_j. The interaction coefficients A_{ij} characterize how the presence of species j affects the growth rate of species i.

Throughout this study we assume that the dynamics converge to a stable steady state. Denote the pre-invasion abundances of the species in the community by X_j^{old}. We then ask what happens when we invade such an ecosystem by a new species, denoted by the distinguished index 0. Within GLV, the invader is fully characterized by specifying its interaction coefficients A_{0j} and A_{j0} and its growth rate r_0.

Our goal is to predict whether the invasion will be

successful, and if successful, the set of species that survive (denoted by the set $\mathcal{S}$), the set of species that go extinct (denoted by $\mathcal{E}$), the invader abundance X_0, and the abundances of surviving species post invasion $\vec{X}_{\mathcal{S}}^{\text{new}} = X_{\mathcal{S}}^{\text{old}} + \delta\vec{X}_{\mathcal{S}}$ for $j \in \mathcal{S}$. Note that the quantity $\delta\vec{X}_{\mathcal{S}}$ characterizes the shift in species abundances pre- and post-invasion.

To achieve our goal, we will write a set of perturbative self-consistency equations for our quantities of interest. Assume we know the outcome of the invasion, and in particular which species survive, $\mathcal{S}$, and which species go extinct, $\mathcal{E}$. Then we can split the pre-invasion interaction matrix of the community into four blocks,

$$A^{\text{old}} = \begin{pmatrix} A_{\mathcal{SS}} & A_{\mathcal{S\mathcal{E}}} \\ A_{\mathcal{E\mathcal{S}}} & A_{\mathcal{E\mathcal{E}}} \end{pmatrix}. \tag{2}$$

We also partition the pre-invasion species abundances and $\vec{r}_j$ into surviving and extinct species: $\vec{X}_{\mathcal{S}}^{\text{old}}$, $\vec{X}_{\mathcal{E}}^{\text{old}}$, and $\vec{r}_{\mathcal{S}}, \vec{r}_{\mathcal{E}}$. Having defined these partitions, the post-invasion steady-state condition becomes

$$g_{\mathcal{S}}(\vec{X}^{\text{new}}) = \vec{r_{\mathcal{S}}} - A_{\mathcal{SS}}\vec{X}_{\mathcal{S}}^{\text{new}} - A_{\mathcal{S}0}X_0 = 0. \tag{3}$$

We also know that extinct species have a negative invasion fitness, namely the will have a negative growth rate if they are re-introduced into the ecosystem

$$g_{\mathcal{E}}(\vec{X}^{\text{new}}) = \vec{r_{\mathcal{E}}} - A_{\mathcal{E\mathcal{S}}}\vec{X}_{\mathcal{S}}^{\text{new}} - A_{\mathcal{E}0}X_0 < 0. \tag{4}$$

Our key insight is to note that even though the abundances of extinct species $X_{\mathcal{E}}$ change abruptly to zero post-invasion, the post-invasion growth rates of extinct species $g_{\mathcal{E}}(\vec{X}^{\text{new}})$ change more smoothly from positive to negative and can hence still be calculated perturbatively. A related observation undergirds the use of slack variables in constrained optimization problems with inequality constraints [33]. Drawing on these observations, in Appendix A 3 we show the invader abundance can be expressed in terms of the quantities introduced above as

$$X_0 = \frac{r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{old}} - A_{0\mathcal{S}}A_{\mathcal{SS}}^{-1}A_{\mathcal{S\mathcal{E}}}\vec{X}_{\mathcal{E}}^{\text{old}}}{A_{00} - A_{0\mathcal{S}}A_{\mathcal{SS}}^{-1}A_{\mathcal{S}0}}, \tag{5}$$

and that the change in the abundances of surviving species is given by

$$\delta\vec{X}_{\mathcal{S}} = A_{\mathcal{SS}}^{-1}(-A_{\mathcal{S}0}X_0 + A_{\mathcal{S\mathcal{E}}}\vec{X}_{\mathcal{E}}^{\text{old}}). \tag{6}$$

The quantity in the bracket of Eq. (6) can be understood as an effective environmental perturbation that incorporates numerous ecological feedbacks resulting from invasion. This quantity can be decomposed into two parts: a term proportional to the invader abundance X_0 that captures the effects of feedbacks due to the invader and a term proportional to $\vec{X}_{\mathcal{E}}^{\text{old}}$ that captures changes in the environment due to invasion-induced extinctions. Notice that this environmental perturbation is converted to shifts in abundances by the *inverse* of the interaction matrix of surviving species $A_{\mathcal{SS}}^{-1}$. This is a global quantity that depends on the properties of *all the surviving species* $\mathcal{S}$, highlighting that the outcomes of invasion depend intricately on the structure of all community members in an extremely complicated and non-local manner.

To close this set of equations, we impose self-consistency. Namely, we require that surviving species $\mathcal{S}$ have positive abundances

$$\vec{X}_{\mathcal{S}}^{\text{new}} = \delta\vec{X}_{\mathcal{S}} + \vec{X}_{\mathcal{S}}^{\text{old}} > 0, \tag{7}$$

and that the invasion fitness of the extinct species are negative (Eq. (4)).

Collectively, Eqs. (4)-(7) define a set of self-consistent equations (a mix of equalities and inequalities) that must be satisfied by the post-invasion abundances. These equations play a role similar to the optimality equations in constrained optimization and hence can be solved iteratively by introducing auxiliary slack variables. Details of this procedure are outlined in the Appendix. We also show below that these equations have an natural ecological interpretation in terms of a new ecological quantity we call the "dressed invasion fitness" that generalizes the notion of invasion fitness to account for community-mediated ecological feedbacks.

B. Tests of model predictions

In the last section, we derived a set of self-consistency equations describing ecological invasions for the Lotka-Volterra model. In Appendix E, we show that self-consistency equations analogous to Eqs. (4)-(7) can be derived for a large class of niche-based ecological models, including most variants of consumer resource models. In this more general setting, the pairwise interaction matrix A is replaced by an inverse of a susceptibility matrix that captures how a perturbation in the abundance of one species affects the abundances of other species. In addition, for consumer resource models, the self-consistency equations for species must be augmented by additional equations describing the response of resources to invasion. Nonetheless, the qualitative logic, derivation, and structure of the self-consistency equations remains the same.

To demonstrate the generality of our framework, we compare our theoretical predictions to numerical simulations for three different classes of niche-based models in theoretical ecology: (i) the Generalized Lotka-Volterra model, (ii) the MacArthur consumer resource model ; and the (iii) Microbial consumer resource model with cross-feeding (see Fig. 2).

Lotka-Volterra models. We simulated 640 communities with 10 species and dynamics given by the generalized Lotka-Volterra equations in Eq. (1). We focused on ecosystems with symmetric interactions where the interaction coefficients A_{ij} were drawn from a random normal distribution (see Appendix H 1 for details of parameters). After running the dynamics until steady state, on average 8 of the 10 original species survived in our simula-

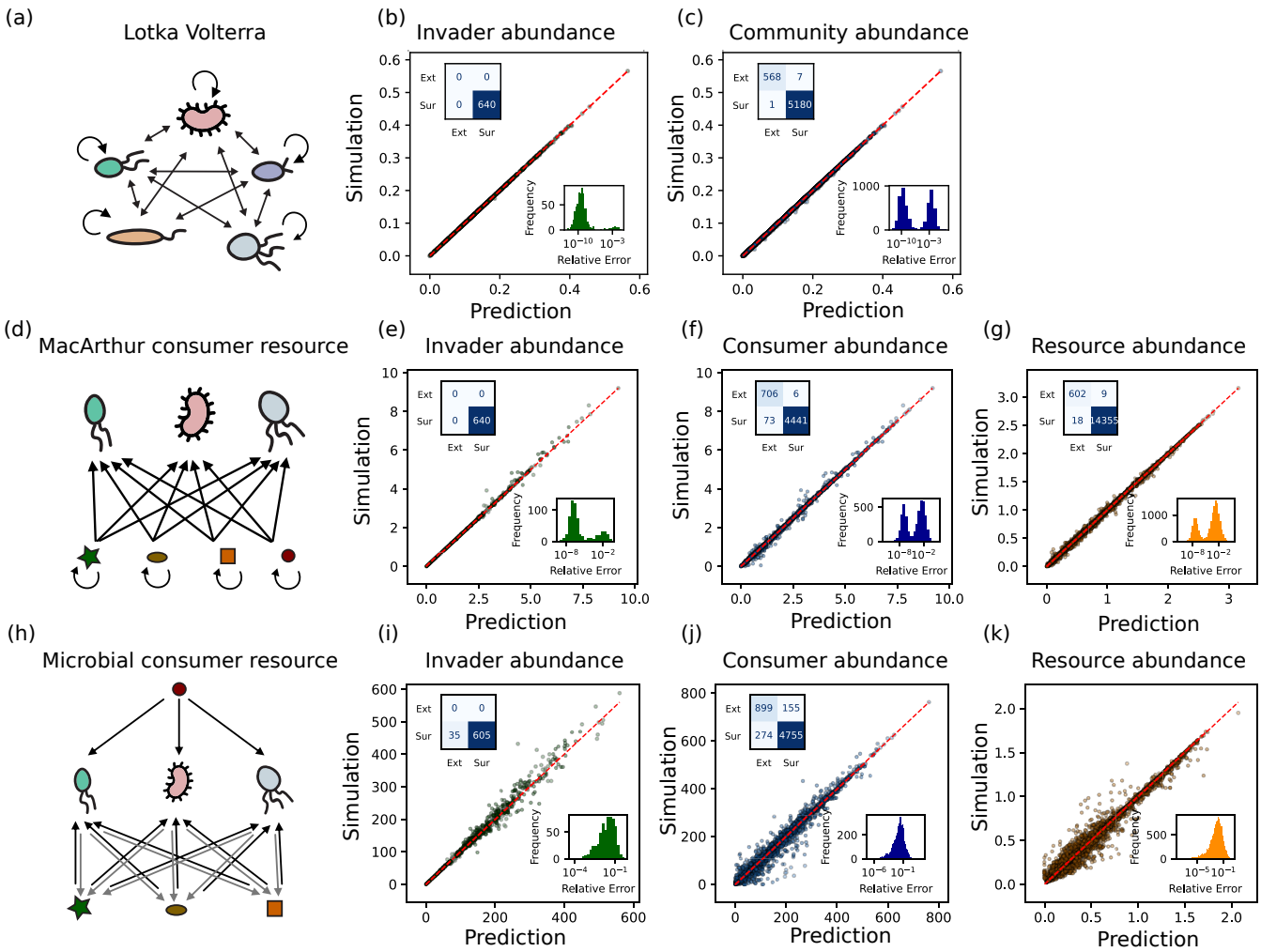

FIG. 2. **Theory makes accurate predictions across diverse ecological models.** Comparison between simulations theoretical predictions for (a–c) Lotka-Volterra models, (d–g) MacArthur consumer resource models, and (h–k) microbial consumer resource models with cross-feeding. Panels display simulated versus predicted abundances for invaders, community residents and resources respectively. Each data points indicate one species/resource. Insets for each panel show (1) matrices indicating qualitative prediction outcomes (extinct or surviving; rows indicate simulations, columns predictions); and (2) histograms of relative errors.

tions. We then introduced an invader into the ecosystem and compared theoretical predictions to numerical simulations. We focused on three quantities: (a) predicting whether the invader would invade successfully, (b) the post-invasion invader abundance for successful invasions, and (c) the resulting shift in the species abundances (the community shift). As can be seen in Fig. 2 (b)-(c), the theory and simulations agree remarkably well.

MacArthur consumer resource models. Next, we applied our theoretical framework using the MacArthur consumer resource model (MCRM) [34, 35]. Like the Lotka-Volterra model, the MCRM is a foundational model of niche theory. In MCRMs, species with abundances N_i deplete resources with abundances R_α. Species i have preferences $C_{i\alpha}$ for resource α. We further assume that in the absence of consumers, the resource dynamics can be described by a Lotka-Volterra equation. Within this model, all interactions between species are mediated by competition for resources, with dynamics given by

$$\frac{dN_i}{dt} = N_i \left(\sum_\alpha C_{i\alpha} R_\alpha - m_i \right) \tag{8}$$

$$\frac{dR_\alpha}{dt} = R_\alpha \left(K_\alpha - \sum_\beta Q_{\alpha\beta} R_\beta \right) - \sum_j C_{j\alpha} N_j R_\alpha, \tag{9}$$

where m_i is the mortality rate of species i, K_α is the intrinsic growth rate of resource α, and $Q_{\alpha\beta}$ is the resource-resource interaction matrix. Fig. 2(d) presents a schematic representation of a typical MacArthur consumer-resource model.

To test these theoretical predictions, we simulated 640 communities using Eq. (9), with parameters drawn randomly (see Appendix H 2 for details). We initialized each community with 60 consumers and 30 resources and ran the dynamics to steady state. After this initial phase, we introduced an invader and simulated the post-invasion ecosystem until it reached a steady state. We then compared our theoretical predictions for invasion success, invader abundance, and the shifts in species and resource abundances with the results of our simulation (see Fig. 2 (e)-(g)). As in the Lotka-Volterra model, our theory for the MCRM recapitulates the simulation results.

Microbial consumer resource model with cross-feeding. Finally, to test our theory in a more complex ecological setting, we applied our framework to the Microbial consumer resource model (MiCRM) [31, 36]. The MiCRM extends traditional consumer resource models by explicitly modeling cross-feeding by microbial species — where metabolic byproducts produced by one species are consumed by others. As a result of this cross-feeding, the steady-state conditions of the MiCRM are non-linear. We show in the Appendix that we can still perturbatively derive self-consistency equations for invasion success, invader abundance, and the shifts in species and resource abundances. A detailed discussion of the MiCRM and this calculation can be found in Appendix E. Fig. 2(i-k) shows a comparison with good agreement between theory and simulation (see Appendix H 3 for numerical detail). These results suggest that our theory applies to a variety of ecological models and successfully predicts all key properties of invasion outcomes.

III. DRESSED INVASION FITNESS GOVERNS OUTCOMES

We now provide a simple ecological interpretation of the outcomes of our theory in terms of a new quantity we call the "dressed invasion fitness". As the name suggests, the dressed invasion fitness extends the classic concept of invasion fitness, the growth rate of an invader when it is initially introduced into a resident ecosystem, by incorporating the effects of ecological feedbacks.

Consider an invading an ecosystem governed by Eq. (1) by a new species 0 with naive growth rate r_0 and interaction matrix A_{0j}. The invasion fitness g_0^{naive} of species 0 is given by

$$g_0^{\text{naive}} = r_0 - \sum_j A_{0j} x_j^{\text{old}}, \tag{10}$$

where x_j^{old} is the pre-invasion abundance of species j. A negative invasion fitness ($g_0^{\text{naive}} < 0$) means that an invader cannot successfully invade an ecosystem. However, knowing an invader has a positive invasion fitness is not enough to predict its final abundance. This is because invasion fitness depends only on the pre-invasion state of the ecosystem and therefore is agnostic to the subsequent ecological dynamics resulting from feedback and extinction.

Nonetheless, ecological intuition suggests that there should be a relationship between the final invader abundance X_0 and the invasion fitness g_0^{naive} since species with a high initial growth rate are more likely to end up at high abundance once the ecosystem reaches its new post-invasion steady state. We find that this is indeed the case. As before, if we denote the set of species that survive after a successful invasion by $\mathcal{S}$ and the set of species which go extinct by $\mathcal{E}$, a straight forward calculation shows that it is possible to rewrite Eq. (5) for X_0 as

$$X_0 = g_0^{\text{dressed}} + \vec{c}_{\mathcal{E}} \cdot \vec{X}_{\mathcal{E}}^{\text{old}}, \tag{11}$$

where we have defined the "dressed invasion fitness"

$$g_0^{\text{dressed}} = \frac{g_0^{\text{naive}}}{A_{00} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}0}}, \tag{12}$$

$\vec{X}_{\mathcal{E}}$ is a vector of size $|\mathcal{E}|$ consisting of the pre-invasion abundances of species that go extinct during the invasion, and

$$\vec{c}_{\mathcal{E}} = \frac{A_{0\mathcal{E}} + A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}\mathcal{E}}}{A_{00} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}0}}. \tag{13}$$

Eq. (11) shows that the invader abundance post-invasion can be decomposed into a sum of two terms: (1) a term proportional to the invasion fitness, which we call the dressed invasion fitness g_0^{dressed}; and (2) a term due to species extinctions $\vec{c}_{\mathcal{E}} \cdot \vec{X}_{\mathcal{E}}^{\text{old}}$ (Fig. 3a). The dressed fitness, unlike naive fitness g_0^{naive}, accounts for the propagation of feedback from invader to surviving community and back to invader (the second term in the denominator of Eq. (12)). Figs. 3 (c-d) show the invader abundance X_0 as a function of invasion fitness g_0^{naive} and dressed invasion fitness g_0^{dressed}. As expected, both these quantities are correlated with invader abundance. The dressed invasion fitness is much more predictive of the final invader abundance, especially in the absence of species extinctions (Fig. 3d). This shows that the dressed invasion fitness which incorporates ecological feedbacks is really the "right" quantity to predict the fate of an invader.

Additionally, we can decompose the shift in the post-invasion abundances of surviving species $\delta\vec{X}_{\mathcal{S}}$ into two parts: a term caused directly by the invader and a term resulting from extinctions (the terms on the right-hand side of Eq. (6) proportional to X_0 and $X_{\mathcal{E}}$ respectively). Fig. 3(e) shows a plot of the observed community shift versus the first term of Eq. (6) that captures the portion of the community shift due to direct interaction with the invader. As expected, in the absence of extinctions, the predicted and observed values agree with deviations growing progressively larger as the number of extinctions increases.

Analogous interpretations exist for consumer-resource models, including the MiCRM (see Appendix D -F).

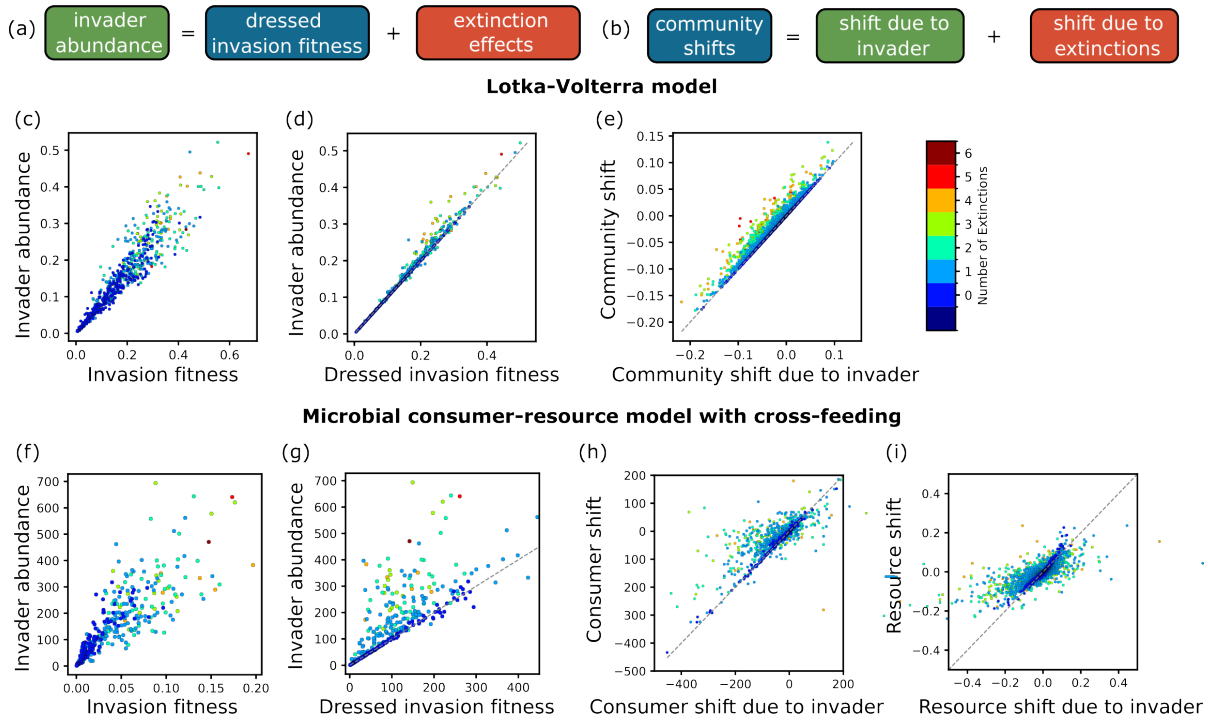

FIG. 3. **Dressed invasion fitness and extinction-induced feedbacks govern invasion outcomes.** Our theory shows that both (a) invader abundance and (b) shifts in community abundances can be decomposed into two parts: a direct contribution the invader — through the dressed invasion fitness — and an indirect contribution due to extinctions (Eqs (11)). (c–i) Both Lotka-Volterra and Microbial consumer resource model simulations that (c–d) invader abundance is generally correlated with naive invasion fitness, but (d) and (g) show that dressed invasion fitness — which correctly incorporates ecological feedbacks — is a much better predictor of invader abundance. Similarly (e) and (h–i) show that our theory can also generally predict shifts in community abundances through the invader's direct effect (dashed line and blue dots) in the absence of extinctions. To predict the effect of invaders that introduce more extinctions — which show deviations from direct effect-based predictions (colored dots) — we need to account for indirect effects as well (Eq. (6)).

Once again all relevant quantities can be decomposed into a contribution due to the invader and a contribution due to extinctions. As can be seen in Figs. 3 (f–i), these decompositions continue to hold in consumer resource models despite the presence of more complex dynamics.

IV. IMPLICATIONS FOR ECO-EVOLUTIONARY DYNAMICS

A particularly interesting application of our theoretical framework is using it to understand eco-evolutionary dynamics in microbial ecosystems [12]. In order to do so, we view the emergence of a mutant as an invasion by a new species that is highly correlated with an existing species in the community (the parent). We focus on the "strong-selection-weak-mutation" regime [37] in which a mutant either fixes or goes extinct before a subsequent mutation can occur. In this limit, evolution can be modeled as a sequence of invasions by successive mutations. Following each invasion, we run ecological dynamics to steady state and permanently remove any species that go extinct (see Fig. 4(a)). For simplicity, we neglect stochastic dynamics of the mutant; this is equivalent to assuming that the community has a large population size.

Our theoretical framework is especially well-suited for analyzing short-term evolutionary dynamics of this type because it makes no assumptions about invader characteristics or the ecosystem being invaded. This flexibility allows us to use our theoretical results to model eco-evolutionary processes despite the fact that evolution often generates complex correlations between species that co-exist in the ecosystem. An example of this is shown in Fig. 4(b) which shows how the consumer preferences of species in the MiCRM change as a community is evolved by successive attempted invasions by highly-correlated mutants (Methods). Remarkably, after just 40 successful mutations, the consumer preference matrices of the evolved and assembled communities looked qualitatively distinct (Fig, 4(b)). Quantifying these differences revealed two key distinctions: first, species in evolved communities exhibit much higher trait correlations, with the inter-species correlation histogram showing a second peak near 0.8 (Fig. 4(e)); second, evolved communities contain fewer low-abundance species (Fig. 4(d)). This second pattern emerges because low-abundance species

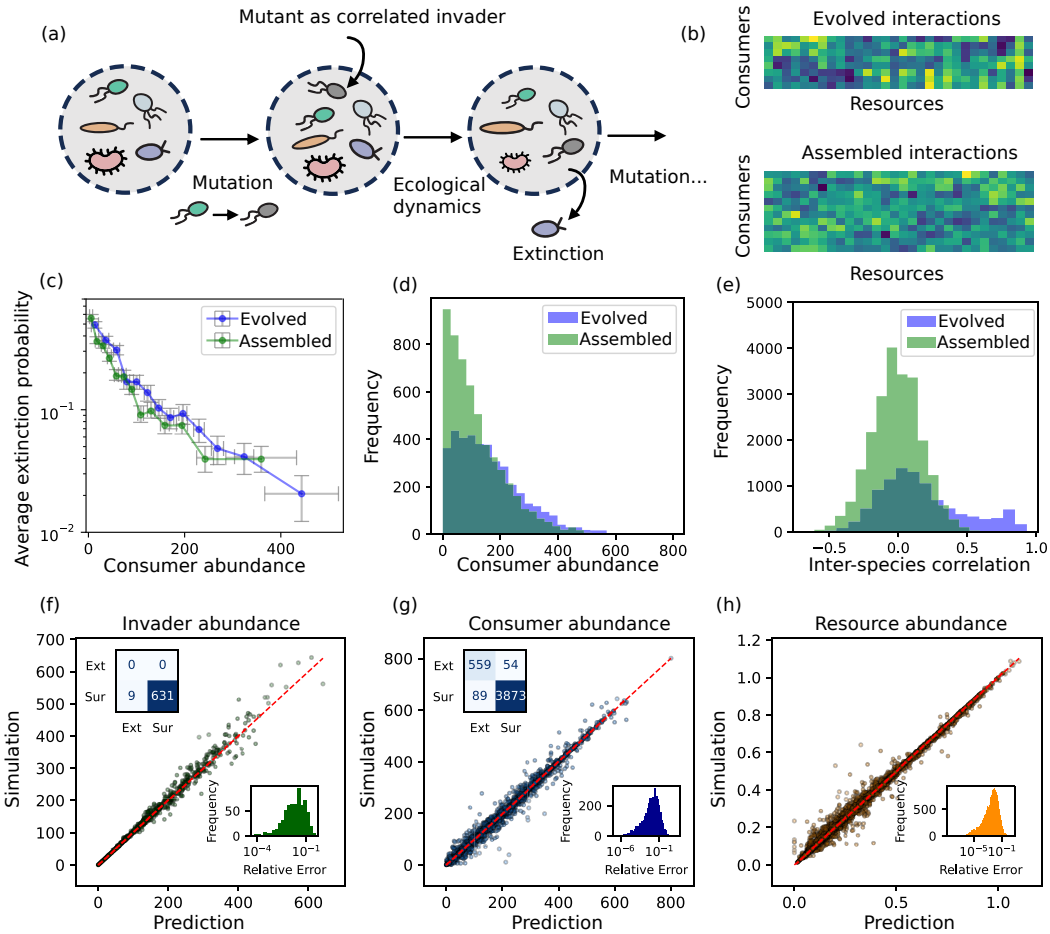

FIG. 4. **Evolved communities are markedly different from assembled communities, yet predictable.** (a) Schematic showing one step of community evolution; starting with a steady-state community, we invade communities with mutants — highly correlated with a randomly chosen parent in consumer preferences — one at a time till communities reach a new steady state. (b) Consumer preference matrices of the evolved community after 40 evolutionary steps (top) and the original assembled community (bottom); the evolved community matrix is more structured with correlated species coexisting. (c) Extinction probability as a function of pre-invasion abundance showing an exponential decay. The error bar shows the standard error. (d) Histogram of species abundances and (e) inter-species correlations for evolved and assembled communities showing statistical differences between them. Evolution replaces uncorrelated low-abundance species with more correlated ones. (f-h) Comparison between simulated and predicted abundances for the mutant, community members, and resources in evolved communities, similar to Fig. 2, showing our theory still makes accurate predictions despite evolved communities having complex correlations.

disproportionately go extinct following successful mutations (Fig. 4(c)), regardless of whether communities are evolved or assembled.

Given the very different structure of evolved and assembled communities and the fact that mutants are highly correlated with species that already exist in the community, we wanted to directly test whether our theoretical framework could be used to predict the outcome of a single step of evolution. To do so, we simulated the evolution of 640 distinct communities and then introduced a new mutant into each of these evolved communities (see Appendix H 4). We then used our theory to predict whether the the mutant would fix, and if it fixed, the abundance of the mutant as well as the abundances of the species and resources in the community. Despite the complexities introduced by evolutionary history, Fig. 4(f-h) shows that our theoretical predictions show remarkable agreement with simulations. These results demonstrate that evolutionary dynamics can be captured — despite complex evolutionary histories, mutant-parent correlations, and community diversity — as long as one incorporates ecological feedbacks.

V. VALIDATION USING EXPERIMENTAL DATA

To test whether our framework could successfully predict invasion outcomes in experimental communities, we analyzed three datasets spanning diverse ecological sys-

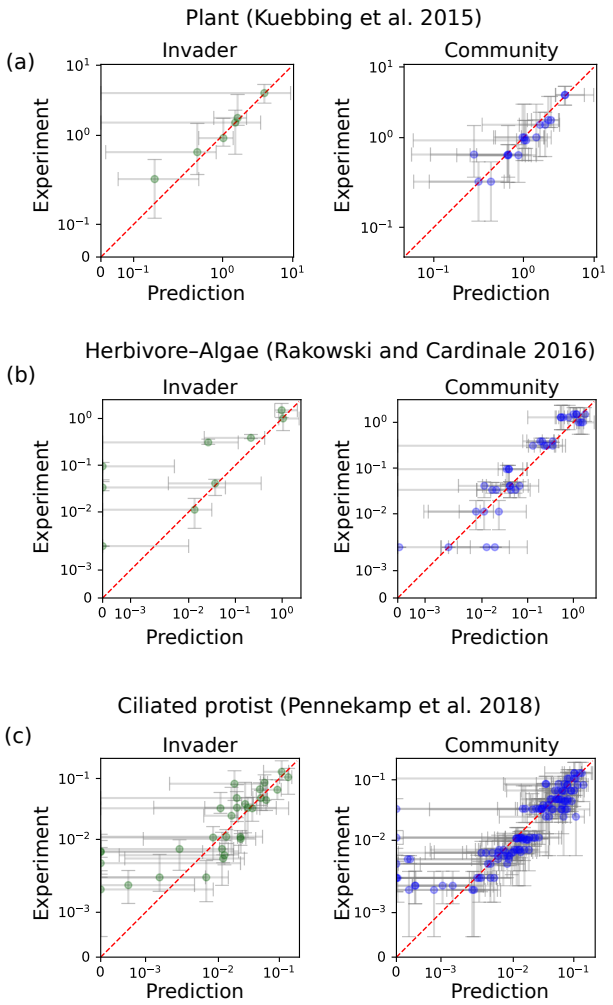

FIG. 5. **Theory accurately predicts invasion outcomes across diverse experimental ecosystems.** Scatter plots comparing experimentally measured abundances with theoretical predictions for three datasets assembling diverse ecological communities. We considered pairs of communities which differed from each other by the introduction of exactly one species, which we call the invader (Methods). Using our theory for the GLV model on these datasets, we predict both the invader abundance (left) and post-invasion community abundances (right). Points indicate median abundances for measurements, with error bars indicating variability across replicates. Both axes use a sym-log scale, with linear scaling applied below the smallest non-zero data point. The datasets span (a) plant communities [38], (b) herbivore–algae communities [39], and (c) ciliated protist communities [40].

tems (results in Fig. 5). Each dataset included species abundance measurements collected under consistent environmental conditions, with different combinations of species seeded in the ecosystem. Each ecosystem contained 4–5 species spanning different length scales and trophic levels: from plants to herbivore-algae to ciliated protists.

Even though these were not originally designed as invasion experiments, the large number of species combinations allowed us to probe invasion outcomes using a comparative approach. We took pairs of species combinations that differed from each other by the introduction of exactly one species. We then applied our framework viewing this one species as an invader. Thus, the community where this species was not introduced was the pre-invasion community, and the one where it was introduced was the post-invasion community. The large number of species combinations and relatively low community diversity allows one to infer species interactions matrices (assuming GLV dynamics) for each ecosystem. Thus, these experiments provide all the information needed to implement our framework, and comprise an ideal to test of our theory.

Applying our theoretical framework to all three datasets, we predicted: (a) whether the invader would successfully invade; if yes, the post-invasion (b) invader abundance and (c) resulting shift in community abundances (for details, see Methods in Appendix I). Fig. 5 shows results for all three datasets: (a) plant communities from the southeastern United States (data from Kuebbing et al. [38]); (b) herbivore-algae communities (data from Rakowski and Cardinale [39]); and (c) ciliated protist communities grown across a range of temperatures (15°C to 25°C; data from Pennekamp et al [40]). We found that predictions broadly agreed with measurements across all datasets. Specifically, while the median of our predictions agreed with the median of measurements, the size of the error bars varied across datasets. Generally, prediction errors decreased with the number of replicates. Errors were smallest for the plant community dataset (Fig. 5a), which had the largest number of replicates (10); and lowest for herbivore-algae communities (Fig. 5b) with the lowest number of replicates (5) . Further, deviations from measurements were more likely for species with low abundances (e.g., see points on the bottom-right of both panels of Fig. 5c). These deviations stem from several sources of error: measurement errors, biological variability, uncertainty in fitted interaction strengths, as well as GLV dynamics being an approximation of the true dynamics. Despite these assumptions, our framework demonstrates that invasion outcomes can be predicted and understood in diverse ecosystems spanning a range of environments, size scales, and trophic levels.

VI. DISCUSSION

In this paper, we develop a theory for predicting the outcomes of ecological invasions applicable to a wide variety of ecological models. Our framework treats invasions in diverse ecosystems as perturbations to existing communities, allowing us to predict which species go extinct, how surviving species' abundances shift, and the invader's final abundance. We validate our predic-

tions through both numerical simulations and analyses of experimental datasets spanning plant, herbivore-algae, and protist communities. Our theoretical framework is predictive across models with fundamentally different mathematical structures—from Lotka-Volterra to consumer resource models with and without cross-feeding—and across systems of different sizes—from small experimental communities with 4–5 species to large simulated ecosystems with 10s to 100s of species. This broad applicability lies in the generality of viewing invaders as perturbations near a steady state and the power of a linear response theory augmented with discontinuous extinction events.

A fundamental insight from our theory is the identification of a "dressed invasion fitness" as the central quantity governing invasion outcomes. Unlike conventional "naive" invasion fitness [34, 41] which only measures the initial growth rate of an invader in the resident community, the dressed invasion fitness incorporates ecological feedbacks between the invader and the resident community. We show that this distinction is crucial for accurately predicting both invasion success and the resulting community structure. This is because mathematically, the effect of an invader abundance decomposes into a contribution proportional to its dressed invasion fitness and a contribution from invasion-induced extinctions. Both these contributions incorporate ecological feedbacks between the invader and the full community into which it invades.

A direct implication of our framework is that eco-evolutionary dynamics in complex communities follow a pattern where successful mutants predominantly replace low-abundance community members rather than their parent species [10]. This stands in contrast to the canonical view from population genetics — where displacement occurs among closely related lineages — as well as pairwise niche overlap metrics [14]. The mathematical basis for this phenomenon lies in our self-consistency equations, particularly in how the dressed invasion fitness incorporates global feedbacks mediated by the entire community structure. The resulting extinction probabilities decay exponentially with pre-invasion abundance, effectively shielding abundant species while rendering rare species vulnerable regardless of their relatedness to the invader. This observation highlights how ecological feedbacks fundamentally reshape evolutionary trajectories in ways that cannot be captured by traditional models that ignore extinction-induced feedback.

Our theory also helps explain qualitative differences in invasion outcomes across different ecological models. In the Lotka-Volterra model with competitive interactions, species extinctions consistently increase overall community abundance because extinctions reduce negative interactions caused by competition. In contrast, extinctions in consumer-resource models can cause the abundance of surviving species to both increase or decrease. This difference arises because in consumer-resource models, interactions among consumers are mediated by resources, allowing for more diverse outcomes through complex resource-mediated feedback mechanisms.

In the future, it would be interesting to extend our theoretical framework to understand invasions in communities that exhibit time-varying dynamics such as limit cycles or chaos. Recent work shows that even in chaotic regimes, abundant species reach long-lived transient states that share many properties with steady states [42, 43]. This suggests that our framework might be adaptable to predict outcomes in dynamic regimes by viewing chaos as a series of epochs where the community is temporarily close to some steady state. Another promising direction would be to apply and extend our framework to community coalescence in which entire communities merge [44–46]. Our current theory assumes single-species invasions, whereas coalescence involves many simultaneous invaders.

Finally, while our work focuses primarily on short-term eco-evolutionary dynamics in the strong-selection-weak-mutation regime, it would be interesting to extend the framework to incorporate statistical predictions for long-term evolutionary dynamics. This would provide valuable insights into how ecological feedbacks shape community structure over long evolutionary time. The mathematical tools developed here provide a foundation for addressing these more complex scenarios while maintaining the conceptual clarity offered by linear response and perturbation theory.

METHODS

Please see SI Appendices for detailed Materials and Methods. These appendices contain: (1) derivations for our theoretical framework, including invasion outcomes for a variety of ecological models and all equations in the main text; (2) algorithms for implementing our theory for specific models, used as tests in Figs. 2–3; (3) methods for all simulations performed and parameters used; (4) extensions of our framework and generalization to multiple invaders and sources of environmental perturbations.

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Appendices for A theory of ecological invasions and its implications for eco-evolutionary dynamics

Appendix A: Derivation of linear response theory for Lotka-Volterra model

In this section, we provide a detailed derivation of Eq. (6) which relates community shift to invader abundance and the pre-invasion abundance of extinct species. Then we derive Eq. (5), which predicts invader abundance given the knowledge of pre-invasion community, invader-community interaction, and the knowledge of what survives after invasion. Finally, in the last subsection we go beyond the scope of the main text and extend the framework to allow multiple invaders and environmental perturbations.

1. Primer: Environmental perturbations without extinctions

A simple primer to consider before considering invasion and extinction is when environmental perturbations alter species abundance without causing extinctions. The steady state before invasion X_j^{old} is given by linear equality $r_i - \sum_j A_{ij} X_j^{\text{old}} = 0$, solving the linear equation leads to

$$X_i^{\text{old}} = A_{ij}^{-1} r_j. \tag{A1}$$

Now suppose there is an environmental perturbation $r_i \to r_i + \delta r_i$, the new steady state condition is simply $r_i + \delta r_i - \sum_j A_{ij} X_j^{\text{old}} = 0$, leading to new abundance

$$X_i^{\text{new}} = A_{ij}^{-1}(r_j + \delta r_j). \tag{A2}$$

Therefore, the change in steady state abundance is simply

$$\delta X_i^{\text{no extinction}} = A_{ij}^{-1} \delta r_j. \tag{A3}$$

Here this relationship is exact instead of perturbative; the steady-state condition for surviving species in the Lotka-Volterra model is exactly linear.

2. Derivation of Eq. (6): Invasions and extinctions as effective perturbations

In this work, instead of actual environmental perturbation, we make use of the insight that in a background of large community, a species feels the addition of a new interaction or a deletion of an old interaction no differently than an environmental perturbation. More explicitly, solving Eq. (3) leads to

$$\vec{r_{\mathcal{S}}} - A_{\mathcal{SS}} \vec{X}_{\mathcal{S}}^{\text{new}} - A_{\mathcal{S}0} X_0 = 0, \tag{A4}$$

$$\vec{X}_{\mathcal{S}}^{\text{new}} = A_{\mathcal{SS}}^{-1}(\vec{r_{\mathcal{S}}} - A_{\mathcal{S}0} X_0) \tag{A5}$$

At the same time, the old steady state condition for these surviving species is

$$\vec{r_{\mathcal{S}}} - A_{\mathcal{SS}} \vec{X}_{\mathcal{S}}^{\text{old}} - A_{\mathcal{S}\mathcal{E}} \vec{X}_{\mathcal{E}} = 0 \tag{A6}$$

$$\vec{X}_{\mathcal{S}}^{\text{old}} = A_{\mathcal{SS}}^{-1}(\vec{r_{\mathcal{S}}} - A_{\mathcal{S}\mathcal{E}} \vec{X}_{\mathcal{E}}) \tag{A7}$$

Therefore, their change in abundance is

$$\delta \vec{X}_{\mathcal{S}} = \vec{X}_{\mathcal{S}}^{\text{new}} - \vec{X}_{\mathcal{S}}^{\text{old}} \tag{A8}$$

$$= A_{\mathcal{SS}}^{-1}(-A_{\mathcal{S}0} X_0 + A_{\mathcal{S}\mathcal{E}} \vec{X}_{\mathcal{E}}) \tag{A9}$$

This recovers Eq. (6). Moreover, comparison with Eq. (A3) shows the role of effective environmental perturbation played by invader and extinct species influence, $\vec{r}^{\text{eff}} = -A_{\mathcal{S}0} X_0 + A_{\mathcal{S}\mathcal{E}} \vec{X}_{\mathcal{E}}$.

3. Derivation of Eq. (5): Predicting invader abundance

The invader introduces an extra constraint on the steady state condition, namely

$$r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{new}} - A_{00}X_0 = 0 \tag{A10}$$

$$r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{old}} - A_{0\mathcal{S}}\delta\vec{X}_{\mathcal{S}} - A_{00}X_0 = 0 \tag{A11}$$

We can then substitute Eq. (6) to obtain

$$r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{old}} - A_{0\mathcal{S}}A_{\mathcal{SS}}^{-1}(-A_{\mathcal{S}0}X_0 + A_{\mathcal{SE}}\vec{X}_{\mathcal{E}}) - A_{00}X_0 = 0 \tag{A12}$$

Solving for X_0 arrives at

$$X_0 = \frac{r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{old}} - A_{0\mathcal{S}}A_{\mathcal{SS}}^{-1}A_{\mathcal{SE}}\vec{X}_{\mathcal{E}}}{A_{00} - A_{0\mathcal{S}}A_{\mathcal{SS}}^{-1}A_{\mathcal{S}0}}, \tag{A13}$$

which recovers Eq. (5)

4. Extended framework for multiple invaders and environmental perturbations

To extend our theory to accommodate multiple invaders, we need to separate indices of all species into those invading ($\mathcal{I}$), extinct ($\mathcal{E}$) and surviving ($\mathcal{S}$), illustrated in Fig. S1. In explicit block matrix notation, the interaction matrix of the new system consists of 9 block matrices,

$$A = \begin{pmatrix} A_{\mathcal{SS}} & A_{\mathcal{SI}} & A_{\mathcal{SE}} \\ A_{\mathcal{IS}} & A_{\mathcal{II}} & A_{\mathcal{IE}} \\ A_{\mathcal{ES}} & A_{\mathcal{EI}} & A_{\mathcal{EE}} \end{pmatrix}. \tag{A14}$$

This block structure and relationship with the self-consistency equations is illustrated in the diagram in Fig. S1 (b).

In general, any perturbation to the system is composed of 3 parts, including direct environmental perturbation, invasions, and extinctions respectively. These effects can all be absorbed into an effective environmental perturbation $\delta\vec{r}^{(eff)}$,

$$\delta\vec{r}^{\text{eff}} = \delta\vec{r} + \delta\vec{r}^{\text{inv}} + \delta\vec{r}^{\text{ext}}, \tag{A15}$$

where

$$\vec{r}^{\text{inv}} = -A_{\mathcal{SI}}\vec{X}_{\mathcal{I}}, \quad \vec{r}^{\text{ext}} = A_{\mathcal{SE}}\vec{X}_{\mathcal{E}}$$

The corresponding linear perturbations in abundance, the generalized version of Eq. (6), is

$$\delta\vec{X}_{\mathcal{S}} = A_{\mathcal{SS}}^{-1}\delta\vec{r}_{\mathcal{S}}^{(eff)} = \delta\vec{X}_{\mathcal{S}} = A_{\mathcal{SS}}^{-1}(\delta\vec{r}_{\mathcal{S}} - A_{\mathcal{SI}}\vec{X}_{\mathcal{I}} + A_{\mathcal{SE}}\vec{X}_{\mathcal{E}}). \tag{A16}$$

At the same time, abundance of surviving invaders needs to follow the set of new steady state conditions

$$r_0 - A_{0\mathcal{S}}\vec{X}_{\mathcal{S}}^{\text{new}} - A_{\mathcal{II}}\vec{X}_{\mathcal{I}} = 0 \tag{A17}$$

$$\tag{A18}$$

Substituting (A16) into (A18) like before, we obtain the generalized version of Eq. (5)

$$\vec{X}_{\mathcal{I}} = \mathbf{M}_{\mathcal{II}}^{-1}\left(\vec{f}_I + A_{\mathcal{IE}}\vec{X}_{\mathcal{E}} - A_{\mathcal{IS}}A_{\mathcal{SS}}^{-1}\delta\vec{r}_{\mathcal{S}} - A_{\mathcal{IS}}A_{\mathcal{SS}}^{-1}A_{\mathcal{SE}}\vec{X}_{\mathcal{E}}\right), \tag{A19}$$

$$\tag{A20}$$

where

$$\mathbf{M}_{\mathcal{II}} = A_{\mathcal{II}} - A_{\mathcal{IS}}A_{\mathcal{SS}}^{-1}A_{\mathcal{SI}}, \tag{A21}$$

$$\vec{f}_I = \vec{r}_{\mathcal{I}} - A_{\mathcal{IS}}\vec{X}_{\mathcal{S}} - A_{\mathcal{IE}}\vec{X}_{\mathcal{E}}. \tag{A22}$$

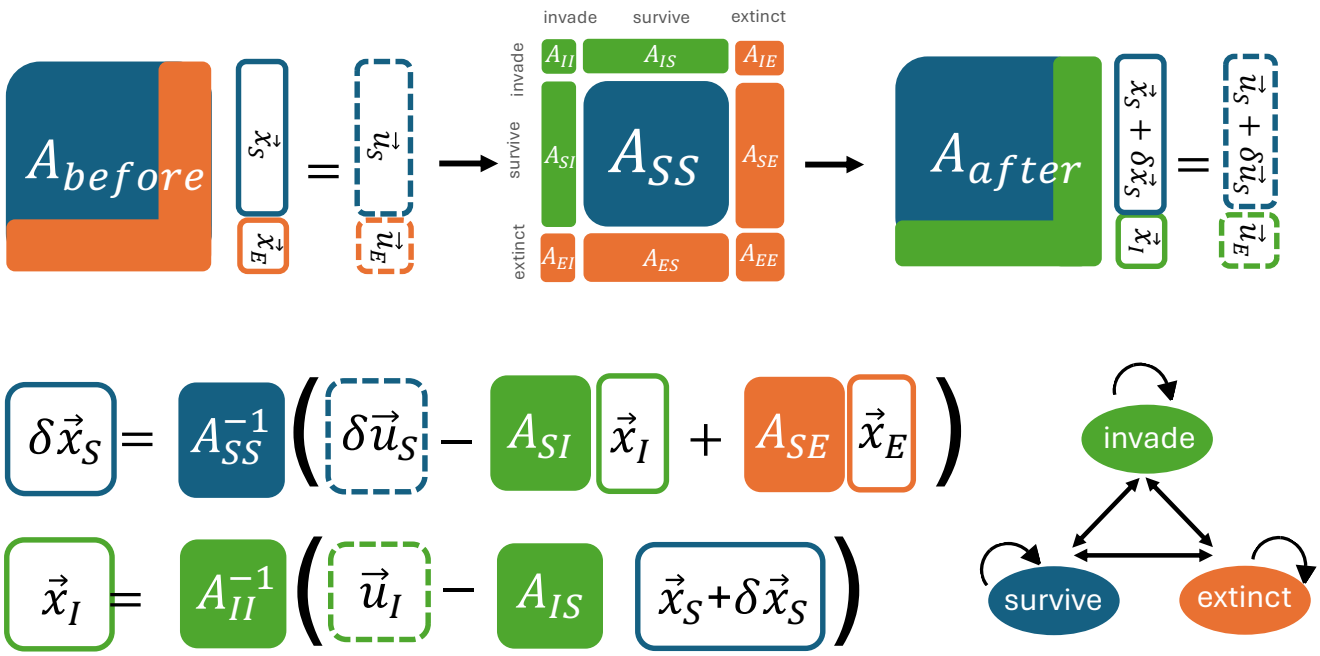

FIG. S1. Schematized equations showing how our theory partitions an ecosystem into invaders, survivors and extinct species. (a) shows how the structure of interactions changes in the Lotka-Volterra model before and after an invasion, and (b) shows how the community shifts and invader abundance is related to each part of the system shown in Eq. (A14)

Appendix B: General linear response theory

We propose the following generalized form of ecological models:

$$\frac{dX_i}{dt} = f_i(X_i)g_i(\vec{X},\vec{r}), \tag{B1}$$

where X_i represents the abundance of each species, and $\vec{r}$ parameterizes the environmental influences on growth. The function $f_i(X_i)$ governs species extinction dynamics. It is positive for surviving species, and it captures the concept of extinction for biotic species as $f_i(X_i)$ must satisfy one of the following conditions:

$$f_i(0) = 0, \quad \text{for biotic species,} \tag{B2}$$

It simply means that biotic species cannot grow again once their abundance reaches zero, as biotic species grow by reproduction, an organic self-replication. In most models, $f_i(X_i)$ is simply X_i. Instead, for abiotic species like nutrients or metabolites that grow through supply, extinction should not apply, and we can simply set $f_i(x) = 1$.

In contrast, the function $g_i(\vec{X},\vec{r})$ governs species growth and interactions. The steady-state condition for species abundance $\vec{X}^*$ is determined by:

$$g_i(\vec{X}^*,\vec{r}) \begin{cases} = 0 & \text{if species } i \text{ survives} \\ < 0 & \text{if species } i \text{ becomes extinct} \end{cases}, \tag{B3}$$

where the second condition corresponds to the stability to re-introduction by extinct species. This tells us that instead of linearizing the complete dynamics in Eq.(B1), it is more natural to linearize the steady-state condition if we consider perturbations to the ecosystem.

We first study the scenario where all species survive, following the first condition in Eq.(B3). We want to study the abundance change to each species, $\vec{X} \to \vec{X}^* + \delta\vec{X}$, in response to perturbation of environmental parameter $\vec{r} \to \vec{r} + \delta\vec{r}$. The new steady state needs to satisfy

$$g_i(\vec{X} + \delta\vec{X}, r_i + \delta r_i) = 0. \tag{B4}$$

Define the susceptibility matrices of the steady state condition,

$$\mathcal{A}_{ij} = \left.\frac{\partial g_i(\vec{X},\vec{r})}{\partial X_j}\right|_{\vec{X}=\vec{X}^*}, \quad \mathcal{B}_{ij} = \left.\frac{\partial g_i(\vec{X},\vec{r})}{\partial r_j}\right|_{\vec{X}=\vec{X}^*} \tag{B5}$$

Taylor expanding the new steady state condition in Eq.(B4) to first order results in

$$\mathcal{A}\delta\vec{X} + \mathcal{B}\delta\vec{r} = 0 \tag{B6}$$

Further simplifying by labeling the matrix product $A^{-1} = -\mathcal{A}^{-1}\mathcal{B}$. The abundance shift should satisfy

$$\delta\vec{X} = A^{-1}\delta\vec{r} \tag{B7}$$

To summarize, to predict the linear response of the steady state in any nonlinear model, the first step is to compute the susceptibility matrix, and compute the matrix inverse given by A^{-1}. Once this matrix is determined, the problem simplifies and becomes equivalent to a linear model with

$$g_i(\vec{X},\vec{r}) = r_i - \sum_j A_{ij}X_j, \tag{B8}$$

which has the exact same form as the steady state condition for the general Lotka-Volterra model. This simple exercise of Taylor expansion justifies the use of the Lotka-Volterra model despite its simplicity - it captures the linear response of ecosystems near their steady states. Finally, the result maps to the one derived for the general Lotka-Volterra model in Eq.(6). A similar derivation for Eq.(5) will require solving only the equation for invader steady state abundance, i.e., $g_{i\in\mathcal{I}}(\vec{X}^{\text{new}},\vec{r}^{\text{new}}) = 0$.

Appendix C: Extinct species have negative invasion fitness

If we do a perturbation around a stable steady state by adding a little bit of the extinct species i, the new growth rate follows

$$\frac{d}{dt}(x_i + \delta x_i) = (x_i + \delta x_i)(k_i - \sum_{j\neq i} A_{ij}x_j - A_{ii}\delta x_i)$$

for extinct species, $x_i = 0$, thus

$$\frac{d\delta x_i}{dt} = \delta x_i(k_i - \sum_{j\neq i} A_{ij}x_j - A_{ii}\delta x_i)$$

The terms in the bracket are almost the invasion fitness. It needs to be negative for a stable fixed point, i.e.,

$$(k_i - \sum_{j\neq i} A_{ij}x_j) < A_{ii}\delta x_i.$$

For a general model, the perturbation to extinct species is

$$\frac{d\delta X_i}{dt} = g_i(\vec{X},\vec{r})\frac{\partial f_i}{\partial X_i}\delta X_i + f_i(X_i)\frac{\partial g_i}{\partial X_i}\delta X_i$$

The analogous inequality is

$$g_i(\vec{X},\vec{r})\left.\frac{\partial f_i}{\partial X_i}\right|_{X_i=0} < 0 + f_i(X_i)\left.\frac{\partial g_i}{\partial X_i}\right|_{X_i=0} < 0$$

But $f_i(0) = 0$ by definition, and we should expect $\left.\frac{\partial f_i}{\partial X_i}\right|_{X_i=0} > 0$ because it needs to allow growth for positive abundance. Therefore, for the general model, an analogous quantity to invasion fitness is simply $\left. g_i(\vec{X},\vec{r})\right|_{X_i=\delta X_i}$

Appendix D: Derivation of linear response in CRMs

Notice that the consumer resource model can be reformulated in a matrix form

$$\begin{pmatrix} \frac{d\vec{N}}{dt} \\ \frac{d\vec{R}}{dt} \end{pmatrix} = \begin{pmatrix} \vec{N} \\ \vec{R} \end{pmatrix} \odot \left[\begin{pmatrix} -\vec{m} \\ \vec{K} \end{pmatrix} - \begin{pmatrix} 0 & -C \\ E^{\mathrm{T}} & Q \end{pmatrix} \begin{pmatrix} \vec{N} \\ \vec{R} \end{pmatrix} \right] \tag{D1}$$

Comparing with the Lotka-Volterra model in matrix form,

$$\frac{d\vec{X}}{dt} = \vec{X} \odot (\vec{r} - A\vec{X}) \tag{D2}$$

We have the mapping

$$\vec{X} = \begin{pmatrix} \vec{N} \\ \vec{R} \end{pmatrix}, \quad \vec{r} = \begin{pmatrix} -\vec{m} \\ \vec{K} \end{pmatrix}, \quad A = \begin{pmatrix} 0 & -C \\ E^{\mathrm{T}} & Q \end{pmatrix} \tag{D3}$$

For the surviving subset of species, interaction matrices are invertible, and can be derived in block matrix form

$$A^{-1}_{\mathcal{SS}} = -\begin{pmatrix} -I & B^{-1}C \\ Q^{-1}E^{\mathrm{T}} & I-P \end{pmatrix}_{\mathcal{SS}} \begin{pmatrix} B^{-1} & 0 \\ 0 & Q^{-1} \end{pmatrix}_{\mathcal{SS}} \tag{D4}$$

$$= \begin{pmatrix} B^{-1} & B^{-1}CQ^{-1} \\ Q^{-1}E^{\mathrm{T}}B^{-1} & (I-P)Q^{-1} \end{pmatrix}_{\mathcal{SS}} \tag{D5}$$

where B and P are defined to simplify the expressions

$$B = CQ^{-1}E^{T}, \quad P = Q^{-1}E^{T}A^{-1}C. \tag{D6}$$

For consumer invader, we have the invader

$$X_0 = \begin{pmatrix} \vec{N_0} \\ 0 \end{pmatrix}, \quad \vec{u_0} = \begin{pmatrix} -m_0 \\ 0 \end{pmatrix}, \quad A_{0S/E} = \begin{pmatrix} 0 & -C_{0S/E} \end{pmatrix}, \quad A_{S/E0} = \begin{pmatrix} 0 \\ E^{\mathrm{T}}_{S/E0} \end{pmatrix}$$

We can substitute these block-form Lotka-Volterra quantities to Eq. (5) and Eq. (6) to obtain

$$A_{0\mathcal{S}}A^{-1}_{\mathcal{SS}}A_{\mathcal{S}0} = C_{0\mathcal{S}}(1-P)Q_{\mathcal{SS}}E^{\mathrm{T}}_{\mathcal{S}0}, \tag{D7}$$

$$A_{0\mathcal{S}}A^{-1}_{\mathcal{SS}}A_{\mathcal{S}\mathcal{E}} = C_0E^{T}B^{-1}C_{\mathcal{S}\mathcal{E}}\vec{R}_{\mathcal{E}} - C_{0S}(1-P)Q_{\mathcal{S}\mathcal{E}}\vec{N}_{\mathcal{E}}, \tag{D8}$$

$$A_{\mathcal{I}\mathcal{E}}x_{\mathcal{E}} = -C_{0\mathcal{E}}R_{\mathcal{E}}, \tag{D9}$$

$$\tag{D10}$$

which pieces together the invader abundance

$$N_0 = \frac{g_0 - C_{0\mathcal{E}}R_{\mathcal{E}} - C_{0\mathcal{S}}E^{T}_{\mathcal{SS}}B^{-1}C_{\mathcal{S}\mathcal{E}}\vec{R}_{\mathcal{E}} + C_{0\mathcal{S}}PQ_{\mathcal{S}\mathcal{E}}\vec{N}_{\mathcal{E}}}{-C_{0\mathcal{S}}PE^{\mathrm{T}}_{\mathcal{S}0}} \tag{D11}$$

where invader fitness is $-m_0 + C_{0\mathcal{E}}R_{\mathcal{E}} + C_{0\mathcal{S}}R_{\mathcal{S}}$ And the abundance shifts to consumers and resources are

$$\begin{pmatrix} \delta N \\ \delta R \end{pmatrix} = \begin{pmatrix} B^{-1}C_{\mathcal{SS}}Q^{-1}_{\mathcal{SS}} \\ P \end{pmatrix} E^{\mathrm{T}}_{\mathcal{S}0}N_0 + \begin{pmatrix} B^{-1} & B^{-1}C_{\mathcal{SS}}Q^{-1}_{\mathcal{SS}} \\ Q^{-1}_{\mathcal{SS}}E^{\mathrm{T}}_{\mathcal{SS}}B^{-1} & P \end{pmatrix} \begin{pmatrix} 0 & -C_{\mathcal{S}\mathcal{E}} \\ E^{\mathrm{T}}_{\mathcal{S}\mathcal{E}} & Q_{\mathcal{S}\mathcal{E}} \end{pmatrix} \begin{pmatrix} N_{\mathcal{E}} \\ R_{\mathcal{E}} \end{pmatrix} \tag{D12}$$

Expanding, we have

$$\delta N_{\mathcal{S}} = B^{-1}C_{\mathcal{SS}}Q^{-1}_{\mathcal{SS}}E^{\mathrm{T}}_{\mathcal{S}0}N_0 - B^{-1}C_{\mathcal{S}\mathcal{E}}R_{\mathcal{E}} + B^{-1}C_{\mathcal{SS}}Q^{-1}_{\mathcal{SS}}(E^{\mathrm{T}}_{\mathcal{S}\mathcal{E}}N_{\mathcal{E}} + Q_{\mathcal{S}\mathcal{E}}R_{\mathcal{E}}) \tag{D13}$$

$$\delta R_{\mathcal{S}} = PE^{\mathrm{T}}_{\mathcal{S}0}N_0 - Q^{-1}_{\mathcal{SS}}E^{\mathrm{T}}_{\mathcal{SS}}B^{-1}C_{\mathcal{S}\mathcal{E}}R_{\mathcal{E}} + P(E^{\mathrm{T}}_{\mathcal{S}\mathcal{E}}N_{\mathcal{E}} + Q_{\mathcal{S}\mathcal{E}}R_{\mathcal{E}}) \tag{D14}$$

Appendix E: Linear response of nonlinear consumer resource model

We can apply the linearization framework to specially non-linear consumer resource models, similarly to how we map general nonlinear ecological models to general Lotka-Volterra models.

Consider nonlinear consumer resource models

$$\frac{dN_i}{dt} = f_i^N(N_i) g_i^N(\vec{N}, \vec{R}, \vec{m}) \tag{E1}$$

$$\frac{dR_\alpha}{dt} = f_\alpha^R(R_\alpha) g_\alpha^R(\vec{N}, \vec{R}, \vec{k}) \tag{E2}$$

The steady state condition for surviving species is

$$0 = g_i^N(\vec{N}, \vec{R}, \vec{m}) \tag{E3}$$

$$0 = g_\alpha^R(\vec{N}, \vec{R}, \vec{k}) \tag{E4}$$

The new steady state condition is

$$0 = g_i^N(\vec{N} + \delta\vec{N}, \vec{R} + \delta\vec{R}, \vec{m} + \delta\vec{m}) \tag{E5}$$

$$0 = g_\alpha^R(\vec{N} + \delta\vec{N}, \vec{R} + \delta\vec{R}, \vec{k} + \delta\vec{k}) \tag{E6}$$

The linear expansion leads to

$$\sum_j \frac{\partial g_i^N(\vec{N}, \vec{R}, \vec{m})}{\partial N_j}\bigg|_{\vec{N}=\vec{N}_{SS}} \delta N_j + \sum_\alpha \frac{\partial g_i^N(\vec{N}, \vec{R}, \vec{m})}{\partial R_\alpha}\bigg|_{\vec{R}=\vec{R}_{SS}} \delta R_\alpha + \sum_j \frac{\partial g_i^N(\vec{X}_{SS}, \vec{m}_i)}{\partial m_j} \delta m_j = 0. \tag{E7}$$

$$\sum_j \frac{\partial g_\alpha^R(\vec{N}, \vec{R}, \vec{m})}{\partial N_j}\bigg|_{\vec{N}=\vec{N}_{SS}} \delta N_j + \sum_\alpha \frac{\partial g_\alpha^R(\vec{N}, \vec{R}, \vec{m})}{\partial R_\beta}\bigg|_{\vec{R}=\vec{R}_{SS}} \delta R_\beta + \sum_j \frac{\partial g_\alpha^R(\vec{X}_{SS}, \vec{m}_i)}{\partial k_\beta} \delta k_\beta = 0. \tag{E8}$$

Defining each susceptibility matrix,

$$\frac{\partial g_i^N(\vec{N}, \vec{R}, \vec{m})}{\partial N_j}\bigg|_{\vec{N}=\vec{N}_{SS}} = \mathcal{Q}_{ij}^N, \quad \frac{\partial g_i^N(\vec{N}, \vec{R}, \vec{m})}{\partial R_\alpha}\bigg|_{\vec{R}=\vec{R}_{SS}} = \mathcal{C}_{i\alpha}, \quad \frac{\partial g_i^N(\vec{X}_{SS}, \vec{m}_i)}{\partial m_j} = \mathcal{B}_{ij}^N. \tag{E9}$$

$$\frac{\partial g_\alpha^R(\vec{N}, \vec{R}, \vec{m})}{\partial N_j}\bigg|_{\vec{N}=\vec{N}_{SS}} = -\mathcal{E}_{\alpha j}, \quad \frac{\partial g_\alpha^R(\vec{N}, \vec{R}, \vec{m})}{\partial R_\alpha}\bigg|_{\vec{R}=\vec{R}_{SS}} = -\mathcal{Q}_{\alpha\beta}^R, \quad \frac{\partial g_\alpha^R(\vec{X}_{SS}, \vec{m}_i)}{\partial k_\beta} \delta k_\beta = \mathcal{B}_{\alpha\beta}^R. \tag{E10}$$

In matrix notation the linear equation becomes

$$\mathcal{Q}^N \delta\vec{N} + \mathcal{C}\delta\vec{R} + \mathcal{B}^N \delta\vec{m} = 0. \tag{E11}$$

$$-\mathcal{E}\delta\vec{N} - \mathcal{Q}^R \delta\vec{R} + \mathcal{B}^R \delta\vec{k} = 0. \tag{E12}$$

$$\begin{pmatrix} Q^N & C \\ -E & Q^R \end{pmatrix} \begin{pmatrix} \delta\vec{N} \\ \delta\vec{R} \end{pmatrix} = \begin{pmatrix} \mathcal{B}^N & 0 \\ 0 & \mathcal{B}^{\mathcal{R}} \end{pmatrix} \begin{pmatrix} \delta\vec{m} \\ \delta\vec{k} \end{pmatrix} \tag{E13}$$

$$\begin{pmatrix} (\mathcal{B}^N)^{-1} & 0 \\ 0 & (\mathcal{B}^{\mathcal{R}})^{-1} \end{pmatrix} \begin{pmatrix} Q^N & C \\ -E & Q^R \end{pmatrix} \begin{pmatrix} \delta\vec{N} \\ \delta\vec{R} \end{pmatrix} = \begin{pmatrix} \delta\vec{m} \\ \delta\vec{k} \end{pmatrix} \tag{E14}$$

It can be solved with block matrix inversion

$$\begin{pmatrix} \delta\vec{N} \\ \delta\vec{R} \end{pmatrix} = \begin{pmatrix} (\mathcal{B}^N)^{-1}\mathcal{Q}^N & -(\mathcal{B}^N)^{-1}\mathcal{C} \\ (\mathcal{B}^{\mathcal{R}})^{-1}\mathcal{E} & (\mathcal{B}^{\mathcal{R}})^{-1}\mathcal{Q}^R \end{pmatrix}^{-1} \begin{pmatrix} \delta\vec{m} \\ \delta\vec{k} \end{pmatrix} \tag{E15}$$

For the generalized consumer resource model discussed previously, $(\mathcal{B}^N)^{-1} = -I$, $(\mathcal{B}^R)^{-1} = I$, $\mathcal{Q}^N = 0$, $\mathcal{Q}^R = Q$, $\mathcal{C} = C$, $\mathcal{E} = E$.

In general, if $\mathcal{Q}^N = 0$, we can retrieve the result for nonlinear consumer resource model by substitution

$$C \to -(\mathcal{B}^N)^{-1}\mathcal{C}, \tag{E16}$$

$$E \to (\mathcal{B}^R)^{-1}\mathcal{E}, \tag{E17}$$

$$Q^R \to (\mathcal{B}^{\mathcal{R}})^{-1}\mathcal{Q}^R. \tag{E18}$$

Appendix F: Linear response in the microbial consumer resource model

The Microbial consumer resource model (MiCRM) explicitly incorporates cross-feeding by modeling how metabolic byproducts from one species become resources for others. It describes the dynamics of microbial abundances N_i and resource concentrations R_α,

$$\frac{dN_i}{dt} = N_i(\sum_\alpha (1-l_\alpha) w_\alpha c_{i\alpha} R_\alpha - m_i) \tag{F1}$$

$$\frac{dR_\alpha}{dt} = K_\alpha - \omega R_\alpha - \sum_j c_{j\alpha} N_j R_\alpha + \sum_{j,\beta} l_\beta \frac{w_\alpha}{w_\beta} D_{\alpha\beta} c_{j\beta} R_\beta N_j, \tag{F2}$$

where l_α is the fraction of consumed resource secreted as byproducts, $D_{\alpha\beta}$ is the cross-feeding matrix describing conversion between resources, w_α are resource weights reflecting energetic values of resources, $c_{i\alpha}$ are resource preferences, and environmental factors are contained in resource supply K_α and decay ω. The steady state of this model, specifically the resource part, is not linear, thus requiring us to first linearize the model.

Defining effective depletion rate of resource α by species i:

$$\kappa_{i\alpha}^{\text{eff}} = -c_{i\alpha} R_\alpha + \sum_\beta l_\beta \frac{w_\alpha}{w_\beta} D_{\alpha\beta} c_{i\beta} R_\beta \tag{F3}$$

The steady state condition can be written as

$$0 = \sum_\alpha (1-l_\alpha) w_\alpha c_{i\alpha} R_\alpha - m_i \tag{F4}$$

$$0 = \frac{K_\alpha}{\omega} - R_\alpha + \sum_j \frac{\kappa_{i\alpha}^{\text{eff}}}{\omega} N_j \tag{F5}$$

Applying the formulation in the last section to linearize nonlinear consumer resource model, the self-consistency equations for microbial consumer resource model can be obtained by mapping it to the linear consumer resource model in the last section

$$C_{i\alpha} \to (1-l_\alpha) w_\alpha c_{i\alpha} \tag{F6}$$

$$E_{i\alpha} \to -\kappa_{i\alpha}^{\text{eff}}/\omega \tag{F7}$$

$$Q_{\alpha\beta} \to -\frac{\partial}{\partial R_\beta}(\frac{K_\alpha}{\omega} - R_\alpha + \sum_j \frac{\kappa_{i\alpha}^{\text{eff}}}{\omega} N_j) \tag{F8}$$

$$= \delta_{\alpha\beta}(1 + \frac{1}{\omega}\sum_j c_{j\alpha} N_j) - l_\beta \frac{w_\alpha}{w_\beta} D_{\alpha\beta} \sum_j c_{j\beta} N_j \tag{F9}$$

Appendix G: Algorithm to solve the self-consistency formula

Here we present a simple algorithm to solve the self-consistency formula iteratively. The code can be found at https://github.com/Emergent-Behaviors-in-Biology/invasion-theory

Algorithm 1 Iterative solver for self-consistency equations

Input: Pre-invasion system interaction matrix A, species abundances $\vec{X}$, growth rates $\vec{r}$, invader interaction matrices A_{II}, A_{IS}, A_{SI}, and invader growth rates u_I, maximum number of iterations `max_num_iters`.
Initialize: Set extinction boolean *Ebool* to `False` for all species (i.e., assume no species are extinct)
for $i = 1$ to `max_num_iters` **do**
  According to *Ebool*, extract submatrices and vectors for surviving, extinct, and invader species as described in Eq. (A14)
  Solve invader abundances using Eq. (5)
  Compute abundance shifts for the surviving community using Eq. (6)
  Update extinction boolean *Ebool*:
  - Set *Ebool* = `True` for species with negative abundance
  - Set *Ebool* = `False` for species with positive invasion fitness

  if convergence condition met then
    Break loop
  end if
end for
return Final predicted invader abundances, community shift, and extinction boolean

Appendix H: Numerical details for simulations

1. Lotka-Volterra Model

In Fig. 2. (b)-(c), and Fig. 4(c)-(e), we simulated an ensemble of 640 Lotka-Volterra models. We assembled each system's pre-invasion community with $n = 10$ species, which resulted in an average of 8 surviving species. The interaction matrices followed statistics

$$\langle A_{ij} \rangle = \mu_A/n + \delta_{ij}, \langle A_{ij} A_{kl} \rangle = \delta_{ij}\delta_{kl}\frac{\sigma_A^2}{n} + \delta_{il}\delta_{jk}\frac{\rho\sigma_A^2}{n}. \tag{H1}$$

And the environmental parameters similarly were independent and had mean μ_r/n and variance σ_r^2/n. In this figure we chose $\mu_A = 2$, $\sigma_A = 0.2$, $\rho = 1$ for a symmetric model, and $\mu_r = 2$, $\sigma_r = 0.1$. We chose the threshold for extinction as 10^{-5}. Invaders were uncorrelated to the system but shared the same statistics of interaction matrix and environmental parameters. We performed simulations with numerical ODE simulator 'LSODA', with hyperparameters atol=1e-12, rtol=1e-12, and checked convergence by ensuring the maximum derivative was less than 1e-12.

2. MacArthur Consumer Resource model

In Fig. 2(e)-(g), we simulated an ensemble of 640 generalized MacArthur consumer resource models. We assembled each system's pre-invasion community with 60 consumers and $n = 30$ resources, which resulted in an average of 7 surviving consumers and 22 surviving resources. In this model, we set consumer extinction threshold at 10^{-3} and resource extinction threshold at 10^{-9}. The consumer preference matrix followed statistics:

$$\langle C_{i\alpha} \rangle = \frac{\mu_C}{n}, \langle C_{i\alpha} C_{j\beta} \rangle = \delta_{i\alpha}\delta_{j\beta}\frac{\sigma_C^2}{n}$$

In the figure we used $\mu_C = 60$, $\sigma_C = 0.5$. For demonstration purpose of the generality, the resource had a self-interaction matrix Q with statistics,

$$\langle Q_{ij} \rangle = \mu_Q/n + \delta_{ij}$$

$$\langle Q_{ij} Q_{kl} \rangle = \delta_{ij}\delta_{kl}\frac{\sigma_Q^2}{n} + \delta_{il}\delta_{jk}\frac{\rho_Q\sigma_Q^2}{n},$$

where we used $\mu_Q = 0.1, \sigma_Q = 0.1, \rho_Q = 0.1$.

For environmental parameters, we had mean and variance of consumer mortality rate, μ_m/n, σ_m^2/n, with $\mu_m = 1$, $\sigma_m = 0.1$. And mean and variance of carrying capacity were, μ_k/n, σ_k^2/n, with $\mu_k = 2$, $\sigma_k = 0.1$. Again, the invader parameters were uncorrelated with the system and followed the same statistics. We used a constraint optimization algorithm instead of numerical ODE for simulation. The algorithm was similar to the one used in community simulator [cite].

3. Microbial consumer resource model

In Fig. 2 (i)-(k), Fig. 4 (b)-(e) with legend "Assembled", and Fig. 3 (f)-(i), we simulated an ensemble of 640 microbial consumer resource models (MiCRM). We assembled each system's pre-invasion community with 60 consumers and $n = 30$ resources, which resulted in an average of 8 surviving consumers, while resources were abiotic and did not go extinct. It had a cross-feeding structure where we supplied one of the resources at a high rate $k = 1000$, while others were by-products. Similar to before, the consumer preference matrix was

$$\langle c_{i\alpha} \rangle = \frac{\mu_c}{n}, \langle c_{i\alpha} c_{j\beta} \rangle = \delta_{i\alpha}\delta_{j\beta}\frac{\sigma_c^2}{n}$$

with $\mu_c = 10$, $\sigma_c = 3$, the leakage rate was a constant $l = 0.8$ across consumers. We chose the sparsity parameter for cross-feeding matrix to be 0.2. We fixed extinction threshold abundance for consumers at 0.1. We performed the simulation with community simulator, which used an Expectation-Maximization algorithm that utilized a constraint optimization algorithm to find the ecological steady states.

4. Eco-evolutionary dynamics of MiCRM

In Fig. 4 (b)-(h), we performed a series of simulations for eco-evolutionary dynamics for 40 successful invasions on an ensemble of 640 microbial consumer resource models. We first initialized the communities with parameters whose statistics were identical to communities from the previous section on the microbial consumer resource model (MiCRM); we removed all extinct species at an ecological steady state. Then, at each iteration, we randomly selected a parent from the surviving consumers, and sampled a mutant as an invader with consumer preference vector $\vec{c}_{\text{mutant}}$ correlated with a randomly selected parent $\vec{c}_{\text{parent}}$ according to the equation

$$\vec{c}_{\text{mutant}} = \mu_c + \rho(\vec{c}_{\text{parent}} - \mu_c) + \sqrt{1-\rho^2}\vec{z}_c \tag{H2}$$

where ρ is the correlation between mutant and parent traits, and z_c is a random vector composed of uncorrelated standard normal variables. For our analysis, we used $\mu_c = 10$ and $\rho = 0.8$. After we sampled the invader and added it to the community, we solved for the new ecological steady-state using the iterative optimization algorithm common to all MiCRM simulations. We removed extinct species if they were below a threshold abundance of 0.1 (chosen arbitrarily). We repeated this iterative eco-evolution until we observed 40 successful invasions in each community.

In figure 3(b), we applied hierarchical clustering to the consumer preference matrix to group consumers and resources based on their pairwise correlations. We computed Pearson correlation coefficients for rows (consumers) and columns (resources) separately, and performed clustering using the average linkage method. We reordered the matrix based on the resulting dendrograms to highlight correlation of similar consumers and resources. We visualized the reordered matrix as a heatmap with interaction strengths represented by color intensity.

In Figure 3(c), we calculated the average extinction probability versus consumer abundance by grouping the consumers into bins according to their pre-invasion abundance and computing the average extinction probability for consumers within each bin. The bins are grouped with approximately the same number of samples per bin. Number of bins in this plot is chosen to be 13, with around 350 samples per bin for the evolved systems, and around 460 for the assembled systems. The error bars represent the standard error for both axes, calculated for each bin.

Appendix I: Methods for Data Analysis and Visualization

In Fig. 5, we used species abundance data obtained from three different experimental works from Kuebbing et al.[38], Rakowski and Cardinal [39], and Pennekamp et al. [40]. In addition, we used the Lotka-Volterra interaction matrix fitted for these datasets in a previous work [47].

We repeated the same set of procedures for these 3 different datasets as follows: (1) we first took the median abundance of each species in the largest ecosystem (containing all species) as the true values corresponding to new community abundance X_S^{new} and invader abundance X_0, plotted on the y-axis; (2) then we considered the abundance of smaller ecosystems with one fewer species than the largest system and treated the missing species as an invader to those smaller systems as X_S^{old}; (3) Using our framework described by Eq. (2)-(7), we predicted X_S^{new} and X_0. Since for each dataset, researchers repeated the same experiment with the same community composition 5 to 10 times, we had a prediction for each of these replicas. In Fig. 5, we plotted the median values on x-axis, and used the 25th and 75th percentiles as error bars.