



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 (nonrandom) communities and accounts for invasion-driven species extinctions. We derive analytical expressions relating invasion fitness to invader abundance, shifts in the community, and extinction conditions. These results can be understood through a 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.

ecological invasions | perturbation theory | eco-evolutionary dynamics | consumer–resource models | complex ecosystems

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 the presence of ecological feedbacks, i.e., the fact 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 (Fig. 1A). 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

Significance

How do ecosystems respond when new species invade? This question is central to ecology yet difficult to answer because invaders can drive resident species to extinction. Using tools from statistical physics, we demonstrate that invasion outcomes follow surprisingly simple patterns when viewed through the lens of “dressed invasion fitness”—a measure capturing how species interact both directly and indirectly through shared resources. Our framework successfully predicts experimental results across ecosystems and reveals an unexpected evolutionary pattern: New mutations often replace unrelated low-abundance species rather than their parent strains. This challenges conventional thinking and suggests that community structure strongly influences which species persist over time. These insights provide a foundation for managing invasive species, designing microbial communities, and understanding how ecosystems evolve.

The authors declare no competing interest.

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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 nonlinearities (32)]. Our theory also makes direct connection with experiments, highlighting its potential for connecting theoretical predictions with empirical observations.

1. 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. 1A, 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 sufficiently diverse (SI Appendix, Fig. S4) and at steady state, the introduction of invaders can be viewed as adding a small initial perturbation to the existing ecosystem. Our framework exploits this observation to predict invasion outcomes systematically using a linear-response theory for ecological invasions, which works even though invaders that start at low abundances can eventually grow to large abundances. Our assumption of linear response is justified whenever the effective ecological interactions in pre- and postinvasion communities are approximately similar (see SI Appendix, section 3 for precise definition). For many canonical ecological models (e.g., the Lotka–Volterra and MacArthur consumer resource models), we can show that this assumption is exactly true, not just approximate (SI Appendix, sections 3 and 5). For a wide variety of other models, we find that this assumption is often approximately valid (Fig. 2 and SI Appendix, Fig. S4). As a result, our framework can successfully predict invasion outcomes even in experimental data from low-diversity communities with <10% error (Section 5).

1.1. 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 steady state, but it need not be unique. Our framework works equally well for ecosystems with multiple stable steady states (SI Appendix, Fig. S2). 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 $\vec{X}_S^{\text{new}} = \vec{X}_S^{\text{old}} + \delta \vec{X}_S$ for $j \in \mathcal{S}$. Note that the quantity $\delta \vec{X}_S$ characterizes the shift in species abundances pre- and post-invasion.

To achieve our goal, we will write a set of 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,

$$A^{\text{old}} = \begin{pmatrix} A_{\mathcal{S}\mathcal{S}} & A_{\mathcal{S}\mathcal{E}} \\ A_{\mathcal{E}\mathcal{S}} & A_{\mathcal{E}\mathcal{E}} \end{pmatrix}. \quad [2]$$

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

$$g_{\mathcal{S}}(\vec{X}^{\text{new}}) = \vec{r}_S - A_{\mathcal{S}\mathcal{S}} \vec{X}_S^{\text{new}} - A_{\mathcal{S}0} X_0 = 0. \quad [3]$$

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

$$g_{\mathcal{E}}(\vec{X}^{\text{new}}) = \vec{r}_E - A_{\mathcal{E}\mathcal{S}} \vec{X}_S^{\text{new}} - A_{\mathcal{E}0} X_0 < 0. \quad [4]$$

Our key insight is to note that even though the abundances of extinct species X_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.

Drawing on these observations, in SI Appendix, section 1C we show the invader abundance can be expressed in terms of the quantities introduced above as

$$X_0 = \frac{r_0 - A_{0\mathcal{S}} \vec{X}_S^{\text{old}} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}\mathcal{E}} \vec{X}_E^{\text{old}}}{A_{00} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}0}}, \quad [5]$$

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

$$\delta \vec{X}_S = A_{\mathcal{S}\mathcal{S}}^{-1} (-A_{\mathcal{S}0} X_0 + A_{\mathcal{S}\mathcal{E}} \vec{X}_E^{\text{old}}). \quad [6]$$

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}_E^{old} that captures changes

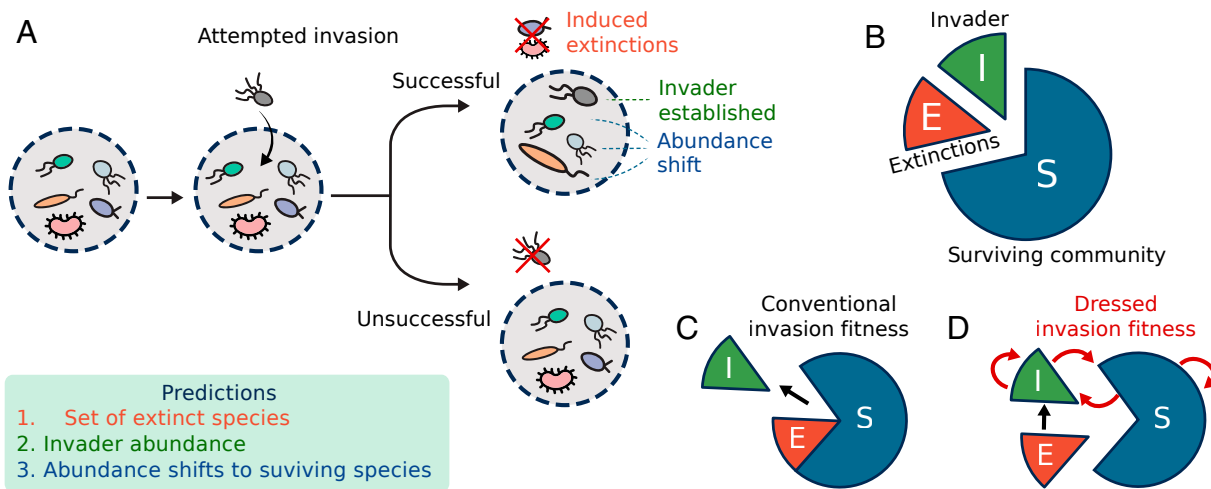


Fig. 1. Predicting invasion outcomes in diverse ecological communities. (A) Cartoon illustrating possible invasion outcomes. If an attempted invasion is unsuccessful, the community remains unchanged; if successful, the invader establishes, causing extinctions and abundance shifts among survivors. Our 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–D) We introduce “dressed invasion fitness” (Eq. 11), which incorporates ecological feedbacks and show it predicts invasion outcomes better than conventional invasion fitness, which only considers direct community interactions.

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_{SS}^{-1} . This is a global quantity that depends on the properties of all the surviving species S , highlighting that the outcomes of invasion depend intricately on the structure of all community members in an extremely complicated and nonlocal manner.

Note that we do not assume that invaders always cause a weak effect on a community: We explicitly include the strong effects of invaders on communities over the invasion process. Invaders exert a weak effect on the community initially, i.e., they invade at low abundance, as is common assumption across ecological literature (33). However, as invaders grow their effect becomes strong and can cause large changes to communities, such as extinctions of other resident species. These effects appear explicitly in Eqs. 5 and 6, as surviving species S behave differently from extinct ones E . To close this set of equations, we impose self-consistency. Namely, we require that surviving species S have positive abundances

$$\bar{X}_S^{\text{new}} = \delta \bar{X}_S + \bar{X}_S^{\text{old}} > 0, \quad [7]$$

and that the invasion fitness of the extinct species is 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. Fully solving these equations requires an exhaustive combinatorial scan that is computationally expensive. Instead, we use a simpler iterative approach (details in *SI Appendix, section 9 and Algorithm 1*) which is common in constrained optimization because of its efficiency and accuracy (~99% in our case). We will later show that these self-consistency equations have a 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.

1.2. 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 *SI Appendix, section 6*, 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 an effective interaction 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 four different classes of niche-based models in theoretical ecology: i) the Generalized Lotka–Volterra model, ii) the MacArthur consumer resource model with type I functional response; the iii) the Monod consumer resource model with type II functional response, and iv) the Microbial consumer resource model with cross-feeding (Fig. 2).

1.2.1. 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 *SI Appendix, section 11A* for details of parameters). After running the dynamics until steady state, on average 8 of the 10 original species survived in our simulations. 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 and C, the theory and simulations agree remarkably well.

1.2.2. MacArthur consumer resource models. Next, we applied our theoretical framework using the MacArthur consumer

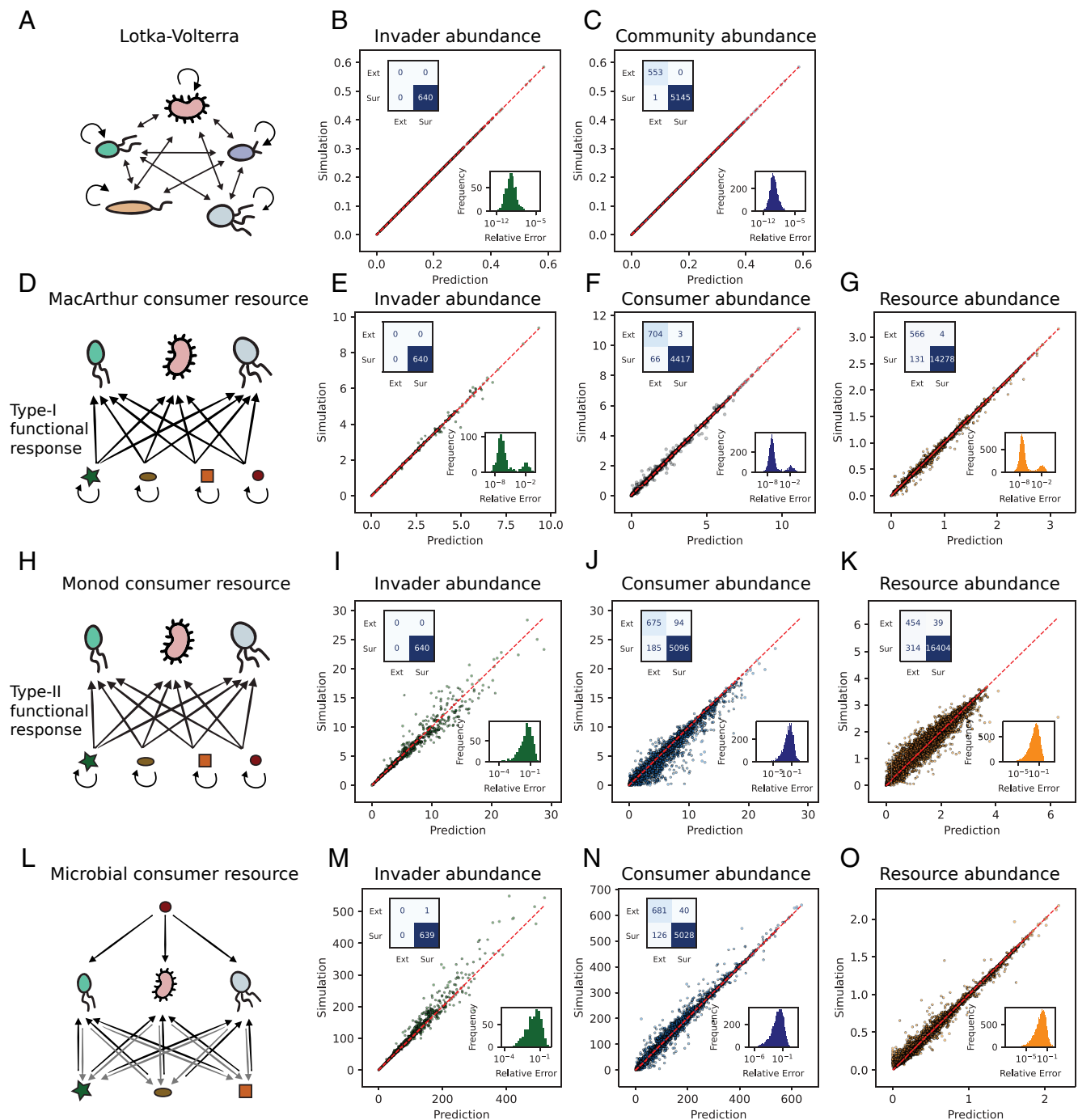


Fig. 2. Theory makes accurate predictions across diverse ecological models. Comparison between simulations theoretical predictions for (A–C) Lotka–Volterra models, (D–G) MacArthur consumer resource models with Type I functional response, (H–K) Monod consumer resource with Type II functional response (Monod dependence of growth rate on resource abundances), and (L–O) microbial consumer resource models with cross-feeding. Panels display simulated versus predicted abundances for invaders, community residents, and resources, respectively. Each data point indicates 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.

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

$$\begin{aligned} \frac{dN_i}{dt} &= N_i \left(\sum_{\alpha} C_{i\alpha} R_{\alpha} - m_i \right) \\ \frac{dR_{\alpha}}{dt} &= R_{\alpha} \left(K_{\alpha} - \sum_{\beta} Q_{\alpha\beta} R_{\beta} \right) - \sum_j C_{j\alpha} N_j R_{\alpha}, \quad [8] \end{aligned}$$

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. 2D presents a schematic representation of a typical MacArthur consumer–resource model.

To test these theoretical predictions, we simulated 640 communities using Eq. 8, with parameters drawn randomly (see SI Appendix, section 11B 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 (Fig. 2 E–G). As in the Lotka–Volterra model, our theory for the MCRM recapitulates the simulation results. The error distributions for this model (Insets of Fig. 2 E–G) have two modes: The left peak ($\sim 10^{-6}\%$) is due to numerical errors, while the right peak ($\sim 1\%$) is due to occasional errors in our iterative approach to solve the self-consistency equations (a noniterative approach removes it; see SI Appendix, Fig. S6).

1.2.3. Monod model and Microbial consumer resource model with cross-feeding. Finally, to test our theory in more complex ecological settings, we applied our framework to two additional models: a consumer resource model with Monod or type II functional response and the Microbial consumer resource model (MiCRM) (31, 36). The Monod model extends the MacArthur model to include a nonlinear dependence of species' per capita growth rates on resource abundances (SI Appendix, section 6). 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 these extensions, the effective interaction matrix A^{eff} in these models depends on community state and is not fixed. In these cases, our theory assumes that the post-invasion A^{eff} is still approximately the same as the one pre-invasion. We can thus use the same steps as before to derive self-consistency equations for invader abundance and community abundance shifts (details of approximations and derivation for both models in SI Appendix, section 6). Fig. 2 I–O shows that despite approximations, there is remarkably good agreement between theoretical predictions and simulations (simulation details in SI Appendix, section 11C). These results suggest that our theory applies to a variety of ecological models and successfully predicts all key properties of invasion outcomes.

2. 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 invasion of 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

$$g_0^{\text{naive}} = r_0 - \sum_j A_{0j} x_j^{\text{old}}, \quad [9]$$

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

$$X_0 = g_0^{\text{dressed}} + \vec{c}_{\mathcal{E}} \cdot \vec{X}_{\mathcal{E}}^{\text{old}}, \quad [10]$$

where we have defined the “dressed invasion fitness”

$$g_0^{\text{dressed}} = \frac{g_0^{\text{naive}}}{A_{00} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}0}}, \quad [11]$$

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

$$\vec{c}_{\mathcal{E}} = \frac{A_{0\mathcal{E}} + A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}\mathcal{E}}}{A_{00} - A_{0\mathcal{S}} A_{\mathcal{S}\mathcal{S}}^{-1} A_{\mathcal{S}0}}. \quad [12]$$

Eq. 10 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. 11). While the naive fitness only measures the invader's initial growth rate at small abundance, the dressed invasion fitness accounts for the invader's effect on the community as its abundance gets larger. As an invader grows, it starts to affect other community members, which affect it back. The dressed invasion fitness augments naive invasion fitness (numerator) with exactly this effect (denominator of Eq. 11). Fig. 3 C and 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. 3E 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 Monod model and MCRM (see SI Appendix, sections 5–8 and Fig. S3, omitted here for brevity). Once again

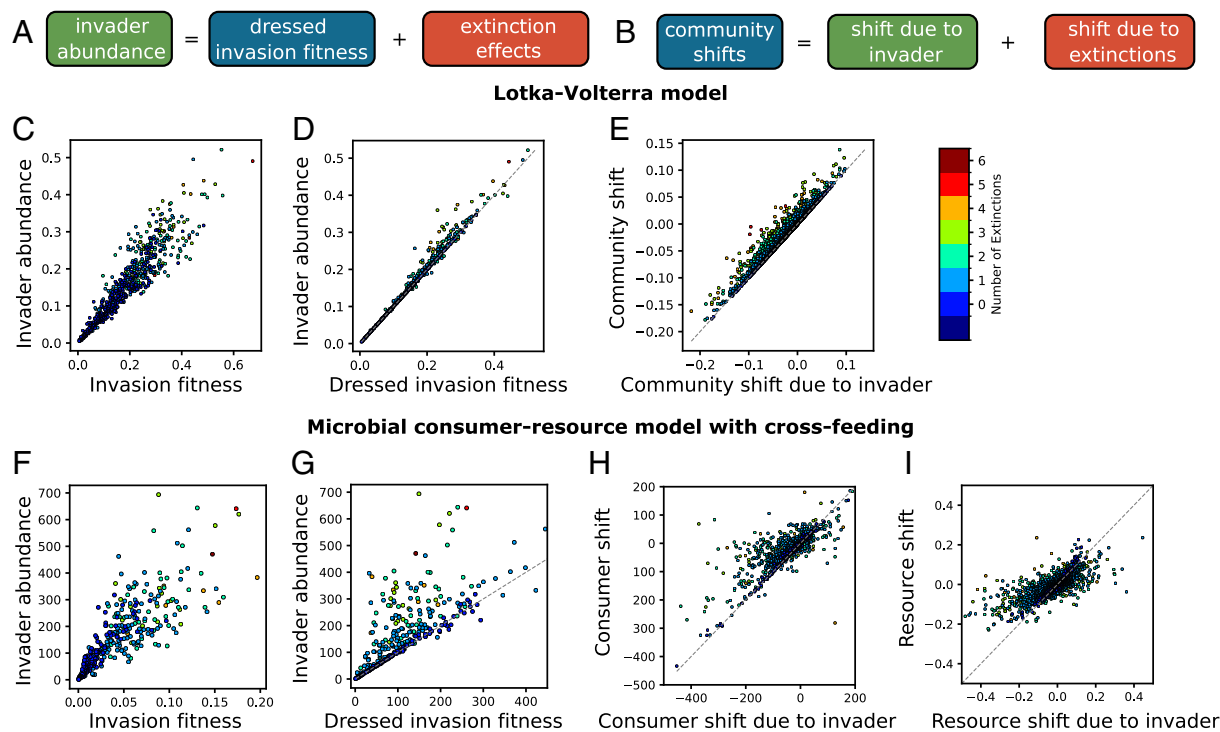


Fig. 3. Dressed invasion fitness and extinction-induced feedbacks govern invasion outcomes. Our theory shows that both (A) invader abundance and (B) shifts in community abundances can be decomposed into two parts: direct contribution from the invader—through the dressed invasion fitness—and an indirect contribution due to extinctions (Eq. 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). *SI Appendix, Fig. S3* shows analogous plots for the MacArthur and Monod consumer resource models.

all relevant quantities can be decomposed into a contribution due to the invader and a contribution due to extinctions. As can be seen in Fig. 3 F–I, these decompositions continue to hold in consumer resource models despite the presence of more complex dynamics.

3. 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 (Fig. 4A). 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 coexist in the ecosystem. An example of this is shown in Fig. 4B 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 (*Materials and Methods*). Remarkably, after just 40 successful mutations, the consumer preference matrices of the evolved and assembled communities looked qualitatively distinct (Fig. 4B). Quantifying these differences revealed two key distinctions. First, species in evolved communities exhibit much higher trait correlations, with the interspecies correlation histogram showing a second peak near 0.8 (Fig. 4E). This is reflected in a generic block-like structure in evolved consumer–resource interactions (Fig. 4B) (38). Second, evolved communities contain fewer low-abundance species (Fig. 4D). This pattern emerges because low-abundance species disproportionately go extinct following successful mutations (Fig. 4C), 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 (*SI Appendix, section 11D*). We then used our theory to predict whether 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-

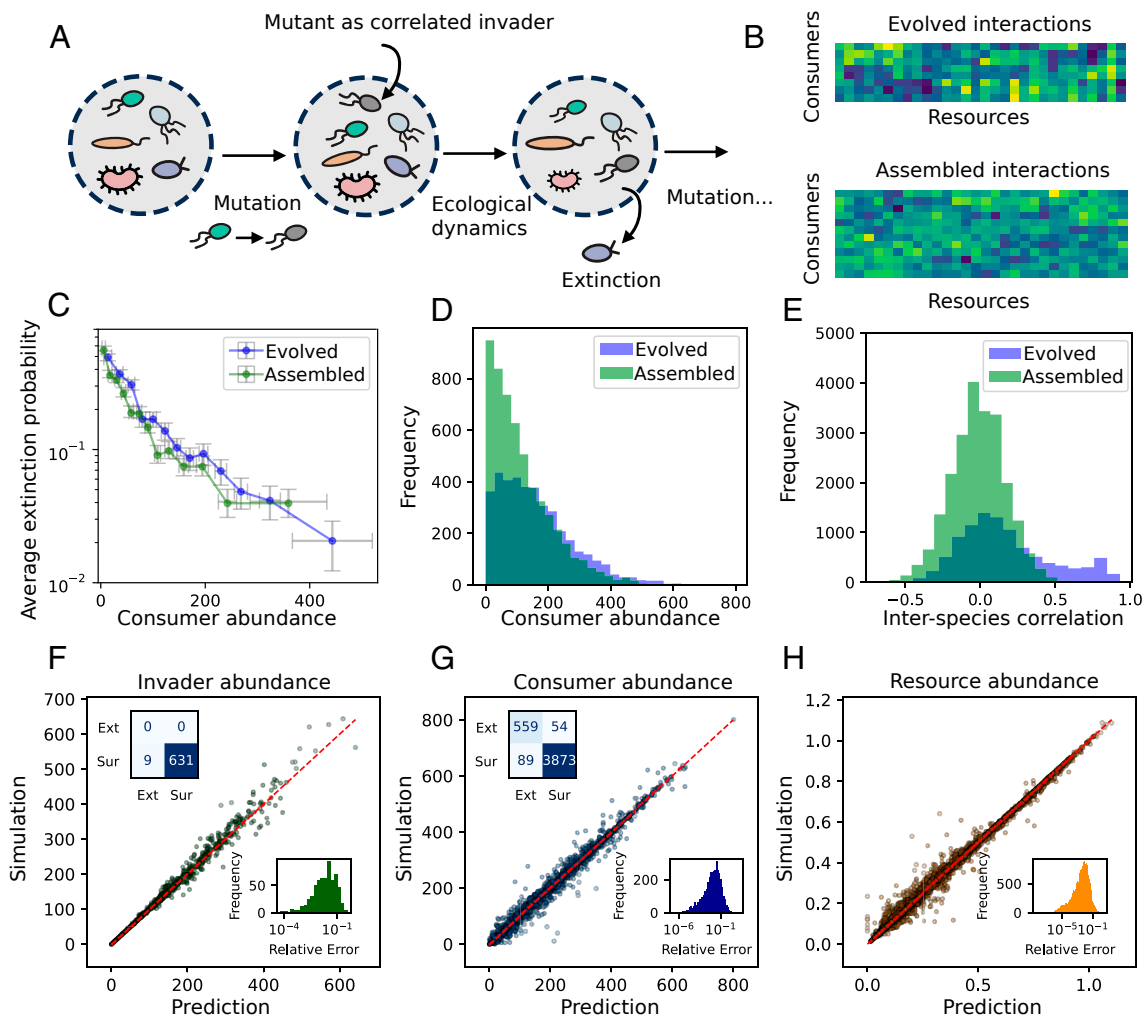


Fig. 4. Evolved communities are markedly different from assembled communities, yet predictable. (A) Schematic showing one step of community evolution; starting with a steady-state community, we invade communities with mutants—highly correlated with a randomly chosen parent in consumer preferences—one 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 SE. (D) Histogram of species abundances and (E) interspecies 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.

parent correlations, and community diversity—as long as one incorporates ecological feedbacks.

4. Validation Using Experimental Data

To test whether our framework could successfully predict invasion outcomes in *stable* experimental communities, we analyzed six datasets spanning diverse ecological systems (three shown in Fig. 5; remaining in *SI Appendix, Fig. S7*). Each dataset included species abundance measurements collected under consistent environmental conditions, with different combinations of species seeded in the ecosystem. Each ecosystem contained 4 and 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 view-

ing 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 for each ecosystem, done separately by fitting a GLV model to the data (42, 43). In some datasets, the presence of experimental replicates allow us to estimate error bars. These experiments provide the information needed to implement our framework, and comprise an appropriate test of our theory.

Applying our theoretical framework to all 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 *Materials and Methods* in *SI Appendix, section 9*). Fig. 5 shows results for three datasets: a) plant communities from the southeastern United States [data from Kuebbing et al. (39)]; b) herbivore-algae communities [data from Rakowski and Cardinale (40)]; and c) ciliated protist communities grown across a range of temperatures [15 °C to 25 °C; data from Pennekamp et al (41)]. *SI Appendix, Fig. S7*

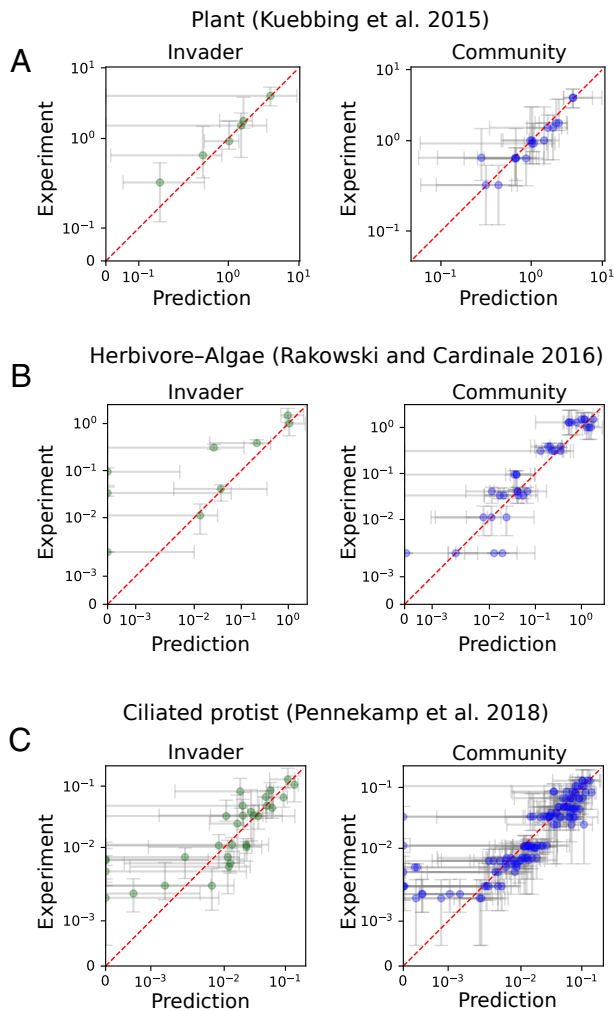


Fig. 5. Theory accurately predicts invasion outcomes across diverse experimental ecosystems. Scatter plots comparing experimentally measured abundances with theoretical predictions for three datasets assembling diverse ecological communities. We considered pairs of communities which differed from each other by the introduction of exactly one species, which we call the invader (*Materials and 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 nonzero data point. The datasets span (A) plant communities (39), (B) herbivore-algae communities (40), and (C) ciliated protist communities (41).

shows three additional plant datasets from a series of distinct biodiversity-ecosystem functioning (BEF) experiments (44–46). 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, suggesting that experimental noise in the datasets was the dominant source of error. Errors were smallest for the plant community dataset (Fig. 5A), which had the largest number of replicates (10); and highest for herbivore-algae communities (Fig. 5B) with the lowest number of replicates (5). The additional datasets (*SI Appendix, Fig. S7*) had no replicates, so we could not estimate error bars for them. 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: primarily measurement errors and biological variability, alongside uncertainty in fitted interaction strengths, as well as GLV dynamics being an approximation of the true dynamics. By inferring invasion fitness using GLV models fitted for these datasets (*Materials and Methods*), we also confirmed that dressed invasion fitness is a much better predictor of invader abundance than naive invasion fitness (*SI Appendix, Figs. S9 and S10*). Taken together, these results demonstrate that our framework can not only predict but also provide insight into invasion outcomes for diverse ecosystems spanning a range of environments, size scales, and trophic levels.

5. 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 predictions 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 and 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, 47) 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. Similar feedbacks appear in the cavity method for models of ecosystems, but these approaches are completely different in scope. Our framework uses known interactions to make predictions for specific invasions in specific communities, while the cavity method uses random parameters and can only describe statistical properties of an ensemble of invasions.

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). While parents and mutants do compete more strongly among themselves than with other community members, the cumulative effect of weaker interactions across a sufficiently diverse community may ultimately also affect the fate of a mutant. In our work, this occurs because mutants and parents interact not only directly

with each other but also through global feedbacks mediated by the entire community structure. This contrasting perspective motivates further empirical tests as well as theoretical work on population genetics in complex ecological communities. After successful invasion, the extinction probabilities of other residents decay exponentially with their pre-invasion abundance, effectively shielding abundant species while rendering rare species vulnerable regardless of their relatedness to the invader. These patterns are consistent with observations from natural communities which show a decreasing pattern of coexistence with phenotypic similarity (43, 48). Our results augment these observations: Despite the decrease, in a diverse community, phenotypically similar species are still reasonably likely (~40%) to coexist (*SI Appendix*, Fig. S11). This observation also highlights how ecological feedbacks fundamentally reshape evolutionary trajectories in ways that cannot be captured by traditional models that ignore invader-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 (49, 50). 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 (51–53). 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.

6. Materials and Methods

Please see *SI Appendix* Appendices for detailed Materials and Methods. Briefly, we developed a general theoretical framework for ecological invasions by treating invasions as perturbations to steady-state ecosystems and deriving self-consistency equations relating invader abundance, community shifts, and extinction probabilities (Eqs. 4–7). Our framework uses linear response theory augmented with the ability to account for invasion-induced extinctions. This requires solving mixed equality and inequality constraints, which we do using an iterative algorithm. We validated our theoretical predictions through numerical simulations across four ecological model classes: Lotka–Volterra, MacArthur consumer–resource, Monod consumer–resource, and microbial consumer–resource models with cross-feeding. We also validated our theory using eco-evolutionary dynamics by modeling community evolution as a sequence of invasions by mutants that were highly correlated with existing parent species. We then tested our framework against six experimental datasets spanning plant, herbivore–algae, and protist communities by fitting interaction matrices and comparing predicted versus observed invasion outcomes.

Data, Materials, and Software Availability. There are no data underlying this work.

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