

Uncovering the rules of microbial community invasions

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Understanding the ecological and evolutionary processes determining the outcome of biological invasions has been the subject of decades of research with most work focusing on macro-organisms. In the context of microbes, invasions remain poorly understood despite being increasingly recognized as important. To shed light on the factors affecting the success of microbial community invasions, we perform simulations using an individual-based nearly neutral model that combines ecological and evolutionary processes. Our simulations qualitatively recreate many empirical patterns and lead to a description of five general rules of invasion: (1) larger communities evolve better invaders and better defenders; (2) where invader and resident fitness difference is large, invasion success is essentially deterministic; (3) propagule pressure contributes to invasion success, if and only if, invaders and residents are competitively similar; (4) increasing the diversity of invaders has a similar effect to increasing the number of invaders; and (5) more diverse communities more successfully resist invasion.

The invasion of foreign species into uninhabited environments is a major threat to world biota and has been a focus of research in macro-organisms for decades^{1–3}. In contrast, despite relevance to bacterial pathogenesis^{4,5}, only recently has attention been paid to microbial invasion as an ecologically important process⁶. This is partly because a traditional view in microbial ecology that ‘everything is everywhere, but the environment selects’⁷ led to the assumption that natural microbial communities lack the biogeographic patterns necessary for invasion^{8–10}. High-throughput 16S ribosomal RNA sequencing of environmental samples has challenged this perspective by revealing substantial geographic variation in microbial community composition across similar environmental and ecological parameters^{8,11,12}. Microbial invasions are therefore expected to be ecologically important due to the widespread availability of environments in which the invaders can grow but are non-indigenous⁶. Like other invasive species¹³, once established, invasive microbes can have large effects on the composition and function of resident communities^{14–16}. These effects can in turn have implications for macro-organisms, for example through changes in the function of host-associated microbiomes^{17–19}.

It is imperative to understand the ecological and evolutionary processes that determine invasion outcome across ecosystems. Classical ecological theories related to invasion were mostly developed for macro-organisms^{20,21}. Microbes represent an emerging system in which to further our understanding of invasion⁶. For example, it is possible to test ideas about microbial invasion with high-throughput manipulative experiments that are impractical for macro-organisms²². Ecological theory developed for macro-organisms has often proved applicable in microbial systems²³—we suggest that the reverse is also true. Theories developed for microbes may be used as a basis for more general theories of invasion applicable to macro-organisms and microbes alike.

What factors influence the outcome of microbial invasions? A large tradition of microbial ecology involves studying pairwise competition, which is a special case of invasion where a monoculture of residents is challenged by introducing identical invaders^{24–26}.

The dynamics of pairwise competition are normally described by trait-based approaches. These could be either implicit, in terms of positive or negative interactions between genotypes^{27–29}, or explicit, driven by differential consumption and production of environmental resources^{25,29,30}. Several studies have sought to understand microbial invasions more generally by invading laboratory-assembled microbial communities (rather than mono-cultures) with non-native genotypes. Together, these studies have investigated the effect of resident community diversity^{31,32}, resource supply^{33,34} and number of invading individuals^{15,35}; some have also performed co-invasions (invasion by multiple genotypes, also referred to as community coalescence)^{16,36,37}.

The models that have been applied to microbial communities have mostly adopted a trait-based approach, with ecological dynamics modelled at the population level³⁸. For example, extensive use has been made of Lotka–Volterra^{39,40} and consumer-resource like models^{30,41,42}. These models have been invaluable but we suggest several reasons for exploring alternative theoretical approaches. First, to support experimental invasions in high-diversity communities, which would require many parameters to model with existing theory^{13–15}. Second, stochasticity is increasingly recognized as playing an important role in microbial communities, particularly during invasions where invaders are introduced in low numbers^{46,47}. Third, it is generally accepted that evolution occurs on ecological timescales^{48–50} and is relevant to invasion dynamics; especially for microbes, which have short generation times. These evolutionary processes should be incorporated into theoretical studies, especially those focused on microbes.

Here we develop an individual-based theory of microbial community invasion that incorporates provision for high diversity, community invasion, stochasticity, evolution and selection. We used ecological neutral theory as a starting point due to its ability to incorporate high diversity and stochasticity in the form of ecological drift^{51,52}. In contrast to neutral theory, which assumes that individuals from all species have equal fitness and competitive ability, we use an ecological nearly neutral model^{53,54} where species identity

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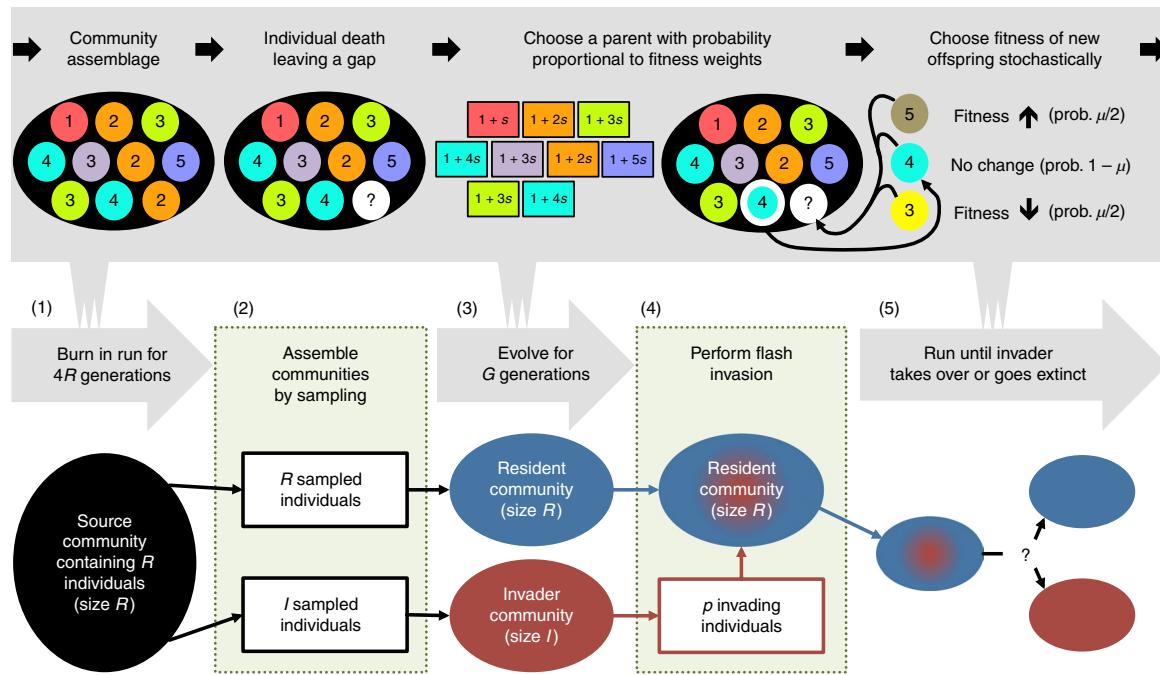


Fig. 1 | Diagrammatic representation of the model and simulation experiments. The grey box shows a single model time step; each coloured circle represents a single individual with genotype indicated by the colour and fitness category of that genotype indicated by the number. The bottom half of the diagram shows a flow chart illustrating the simulations of invasion. The stochasticity of the model guarantees eventual extinction or fixation of invaders.

determines fitness in terms of reproduction probability. This allows invading individuals to have an inherent advantage or disadvantage over residents. Our model retains the ecological and evolutionary components of neutral theory, while relaxing the neutrality assumption to allow for adaptive evolution in the form of selection and competition. It is especially applicable to microbial communities due to their asexual reproduction, high diversity and rapid evolution; however, we believe it would also be applicable more generally. We use our model to conduct simulated invasion ‘experiments’ in which a potentially diverse collection of individuals from an ‘invading community’ enter a ‘resident community’ of ‘defender’ individuals. The concept of one community invading another, in some cases referred to as community coalescence^{36,37,55–57}, is a defining feature of many microbial invasions. This is in contrast to invasions of macro-organisms, where the focus is likely to be a single invading species. A thorough exploration of our model’s predictions reveals five general rules that determine the outcome of invasions. We find that: larger communities evolve better invaders and better defenders; where invader and resident fitness difference is large, invasion success is deterministic; propagule pressure (the number of invading individuals) contributes to invasion success if and only if invaders and residents are competitively similar; increasing the diversity of invaders has a similar effect to increasing the number of invaders; more diverse communities more successfully resist invasion. These general rules are consistent not only with our nearly neutral model but also with existing niche-based explanations for invasion and with numerous empirical studies.

Results

To simulate microbial community invasions, we first consider a source community, which is in turn used to seed an invader and a resident community. The invader and resident communities then separately undergo ecological and evolutionary dynamics for a given number of generations. Next, a number of individuals from the invader community are used to inoculate the resident community and their abundance is tracked to measure invasion success.

Throughout our simulations, the source, invader and resident communities are isolated from each other while being internally well mixed. All communities undergo their dynamics according to the same individual-based process, governed by two parameters: a mutation rate μ and selection strength s . Individuals in the community have a simple genotype, which encodes a fitness category c , describing how competitive they are in their environment. We assume a constant replenishing resource supply with each individual consuming an equal quantity of each resource per unit time, although resource supply is not explicit. The dynamics proceed as follows: in each time step, one randomly chosen individual in the community dies, leaving a proportion of unused resources, which are immediately exploited by new offspring of another individual reproducing asexually. All individuals are equally likely to die; however, the probability that any particular individual will reproduce is proportional to its fitness weight w , where $w = 1 + sc$. Thus, when $s = 0$ the model is neutral in that genotype and fitness category c no longer influence the fitness of an individual. Any new individual inherits the fitness category of its parent, unless it mutates with probability μ . If a mutation occurs, the new individual’s fitness category either increases or decreases by one, and it is considered to have a new genotype.

Our model follows from neutral models in the fields of population genetics^{58–60} and macroecology⁵¹. We also incorporate a component of selection in an ecological nearly neutral theory⁵⁴ overcoming one of the primary limitations of traditional neutral models, the absence of competitive differences. This is especially important in our study as fitness differences between the invading and resident communities form an essential part of a general understanding of invasion. There are further advantages to adopting a nearly neutral theory including the potential for a more realistic pace of community change^{53,54}. We use the language of genotypes rather than species because our focus is on asexually reproducing microbial communities where the distinction between species and genotypes is essentially an arbitrary threshold⁶¹. Some pre-existing studies have measured diversity at genotypic level³¹ and others at species level⁶²; we needed to choose one of these and be consistent.

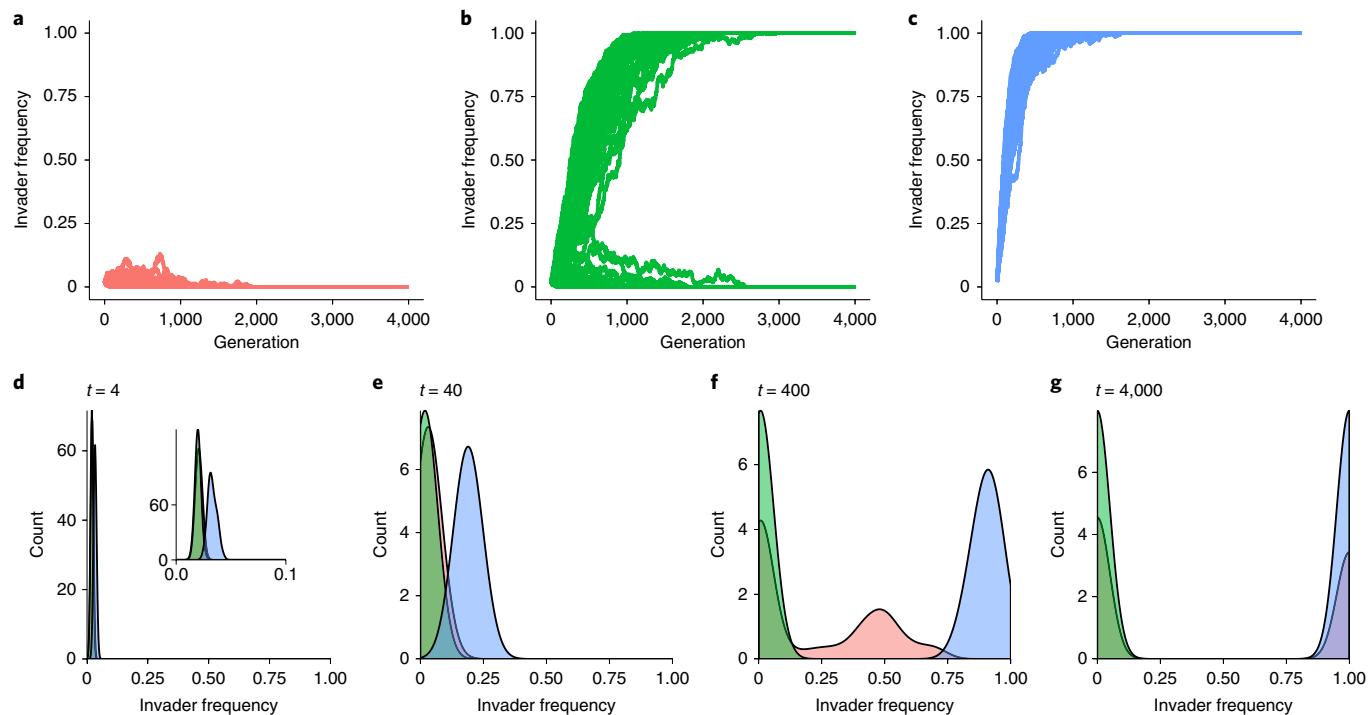


Fig. 2 | One hundred independent invasion experiments for each of three unique invader community sizes. The invader community sizes were: red, 1,000; green, 10,000; blue, 100,000. Other parameters were fixed at $s=0.001$, $\mu=0.0001$, $p=200$, $R=10,000$ and $G=600$. **a–c**, For any given community size, several outcomes can be observed: the invader always go extinct (**a**); the invader goes to either fixation or extinction stochastically (**b**); the invader always achieves fixation (**c**). **d–g**, For these three sets of invasion experiments, we show the distribution of invader frequencies at four time points: $t=4$ generations (**d**), $t=40$ generations (**e**), $t=400$ generations (**f**), $t=4,000$ generations (**g**). The inset of panel **d** shows the same data expanded along the x axis to aid visibility. At the end of invasion ($t=4,000$) invader frequency always converges to 0 or 1 (**g**), whereas at start of invasion (**a**) invader frequency is largely determined by other factors. At intermediate timescales invader frequency varies on a continuous scale (**e**, **f**) between 0 and 1.

Our simulated invasion experiments consist of five steps, illustrated in Fig. 1.

Step 1: We start with a uniform source community containing R individual organisms, which is simulated for a liberal burn-in period of $4R$ generations where a generation consists of $R/2$ discrete birth–death events. Much like classical neutral theory, the distribution of genotype abundances reaches a dynamic equilibrium where diversity is maintained as a balance between stochastic extinction (ecological drift) and mutation/speciation; $4R$ generations are sufficient to reach equilibrium (Supplementary methods) rendering the original initial conditions irrelevant to our results. Unlike genotype abundance, the distribution of fitness category abundances never reaches equilibrium but instead forms a peaked distribution that acts as travelling wave moving with fixed speed in the direction of increasing fitness⁶³, an evolutionary ‘arms race’ of increasing fitness. This appears consistent with the seemingly unbounded pool of potential adaptation seen in long-term microbial evolution experiments^{64,65}.

Step 2: A resident community containing R individuals (the same size as the source community) and an invader community containing I individuals are then seeded from this source community by random sampling of individuals (Supplementary methods).

Step 3: For G generations, pre-invasion community dynamics are simulated in which both the resident and invader communities can assemble and evolve independently for the same amount of time. The invader and resident communities are not necessarily at equilibrium after these G generations (Supplementary Fig. 1).

Step 4: A ‘flash’ invasion is carried out by replacing p individuals in the resident community with p randomly sampled individuals from the invader community. In microbial systems, this could reflect invaders displacing residents through direct competition (for

example, toxin production) or indirect competition (for example, resource depletion). In reality, invasions could occur both as large instantaneous events and as a continuous trickle, like the immigration rates used in models for island biogeography⁶⁶. We focus on the former scenario, where microbial invasions are rare but carry multiple individuals: this mimics typical laboratory studies.

Step 5: The resident community, including its invaders, is then simulated according to the same basic dynamics until invaders achieve fixation or go extinct; we track the invader frequency through time. If pre-invasion community dynamics are for a short period, some genotypes might appear in both the invader and the resident communities. In such cases, the invading individuals and their direct descendants are marked as distinct from the (otherwise identical) residents and these labelled invaders are still required to reach fixation or go extinct to determine the eventual invasion outcome. A conclusive outcome is guaranteed eventually because the model is stochastic and total fixation or extinction of invaders are absorbing states⁵¹.

Depending on the model parameters, several outcomes can be observed. For some regions of parameter space, invasion outcome always achieves fixation or extinction (Fig. 2a,c). In other regions of parameter space, invasion outcome varies (Fig. 2b). We experimented with measuring invasion success as the invader frequency at different points in time (ranging between 1 and 4,000 generations; Fig. 2d–g). We found that when measuring too soon after invasion, invader frequency is entirely determined by initial propagule pressure and resident community size (Fig. 2d). Conversely, when measuring invasion too late after inoculation, invader frequency converges to 0 or 1 and is less informative (Fig. 2g). We therefore chose to define success of a single invasion as the relative abundance of invader community members after 40 generations post-invasion

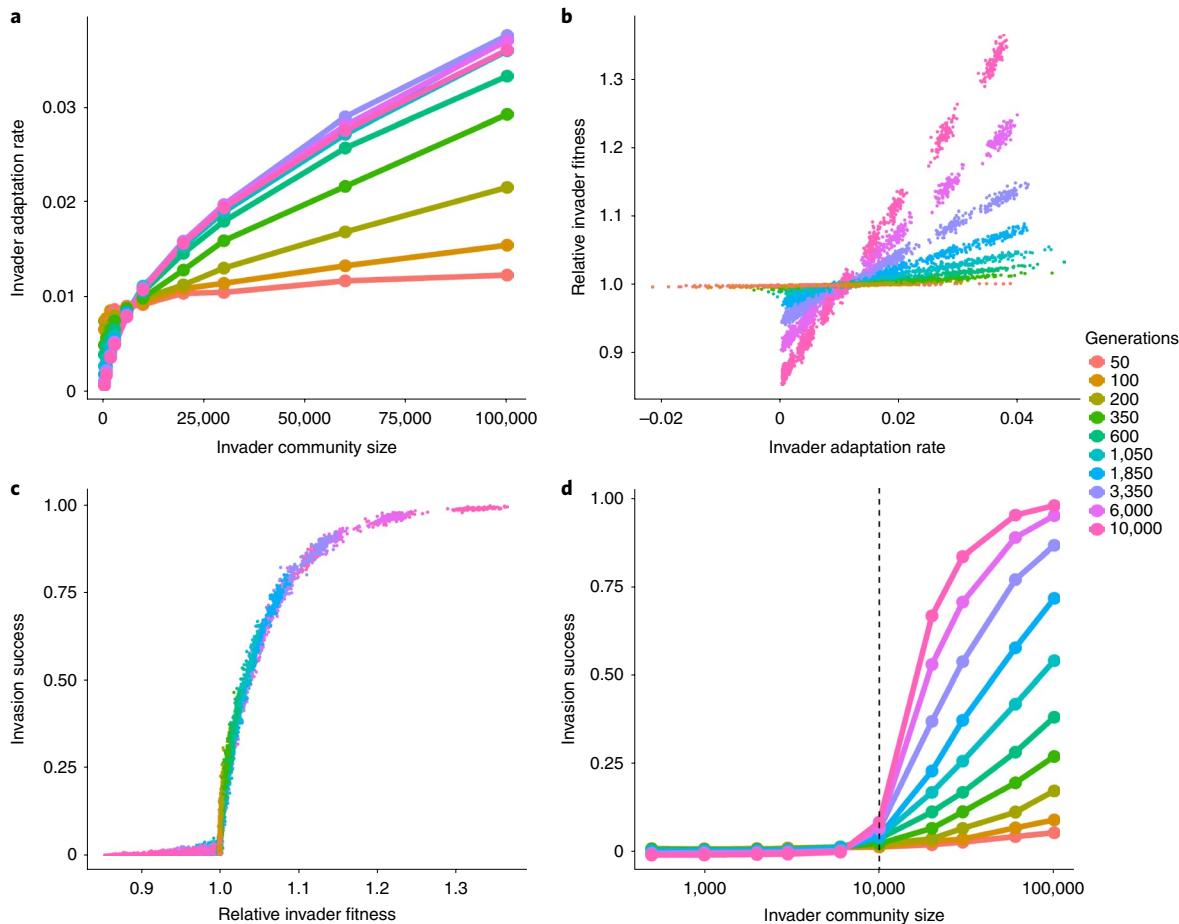


Fig. 3 | Adaptive divergence of resident and invader community determines invasion success. **a**, Larger communities experience a faster rate of adaptation, here measured as the mean fitness category increase per generation in invader community. **b**, Invader communities with a faster rate of adaptation than resident communities will produce invaders that are fitter compared with residents. **c**, When the invader fitness is greater than the fitness of resident community members, invasion success increases rapidly. **d**, Overall, these factors lead to a positive relationship between size of the invader community and invasion outcome. Adaptation rate is measured as the mean change in fitness category per generation. Relative invader fitness is given as the mean fitness category of invaders divided by the mean fitness category of resident community members. In all panels, the colours correspond to the numbers of generations during which the invader and resident communities undergo evolution before the invasion (parameter G in Fig. 1). Invader community size varied ($I = 500, 1,000, 2,000, 3,000, 6,000, 10,000, 20,000, 30,000, 60,000$ and $10,0000$) and all other parameters were fixed at $s = 0.01$, $\mu = 0.0001$, $p = 200$ and $R = 10,000$. The discernable clusters of points in **b** and **c** correspond to different simulated parameter values for invader community size (I).

(Fig. 2e). This balances the need for timescale to not be too long or too short, reflects the timescales of a typical laboratory invasion experiment (for example, Jousset et al.)³¹ and provides a simple and continuous measure of invasion success.

To explore the factors that will affect microbial invasion, we performed simulations across a broad range of the parameter space in a factorial study consisting of 45,000 unique parameter combinations, each simulated 100 times (see Supplementary Table 1). We consider how these parameters affect both invasion outcome and emergent properties of the community such as genotypic richness and mean fitness category.

Across our simulations, invasion success is mainly determined by an interplay between community size and time allowed for evolution to take place in both communities before invasion. Larger communities evolve at a faster rate (Fig. 3a) although this relationship shows diminishing returns in very large communities, probably due to clonal interference^{67–69}. Communities that evolve more rapidly tend to produce invaders with a higher mean fitness category relative to the resident community (Fig. 3b), with the effect of adaptation rate more readily observed after a longer period of

pre-invasion adaptation. When invaders have evolved too slowly and are therefore competitively inferior to defenders (relative fitness <1), invasion almost always fails. In contrast, longer periods of rapid evolution allow the possibility for invaders to increase in fitness relative to resident community and invasion success increases until invasion asymptotically converges to an upper bound of one (fixation of invaders after 40 generations in all replicates). Consequently, large communities evolve fitter invaders that have higher invasion success. This overall relationship displays a sigmoidal curve (Fig. 3d).

When invader competitive ability is much higher or much lower than that of residents, invasion outcome is essentially deterministic and repeat invasion always results in the same outcome (Fig. 2a). Under such conditions, propagule pressure and number of invading genotypes have little effect on invasion outcome (Fig. 4). For example, even the least fit member of the invading community arriving as singleton still has such a large competitive advantage that it will almost certainly achieve fixation. However, when invaders and residents have evolved similar competitive abilities, repeat invasion experiments can have different outcomes (Fig. 2b).

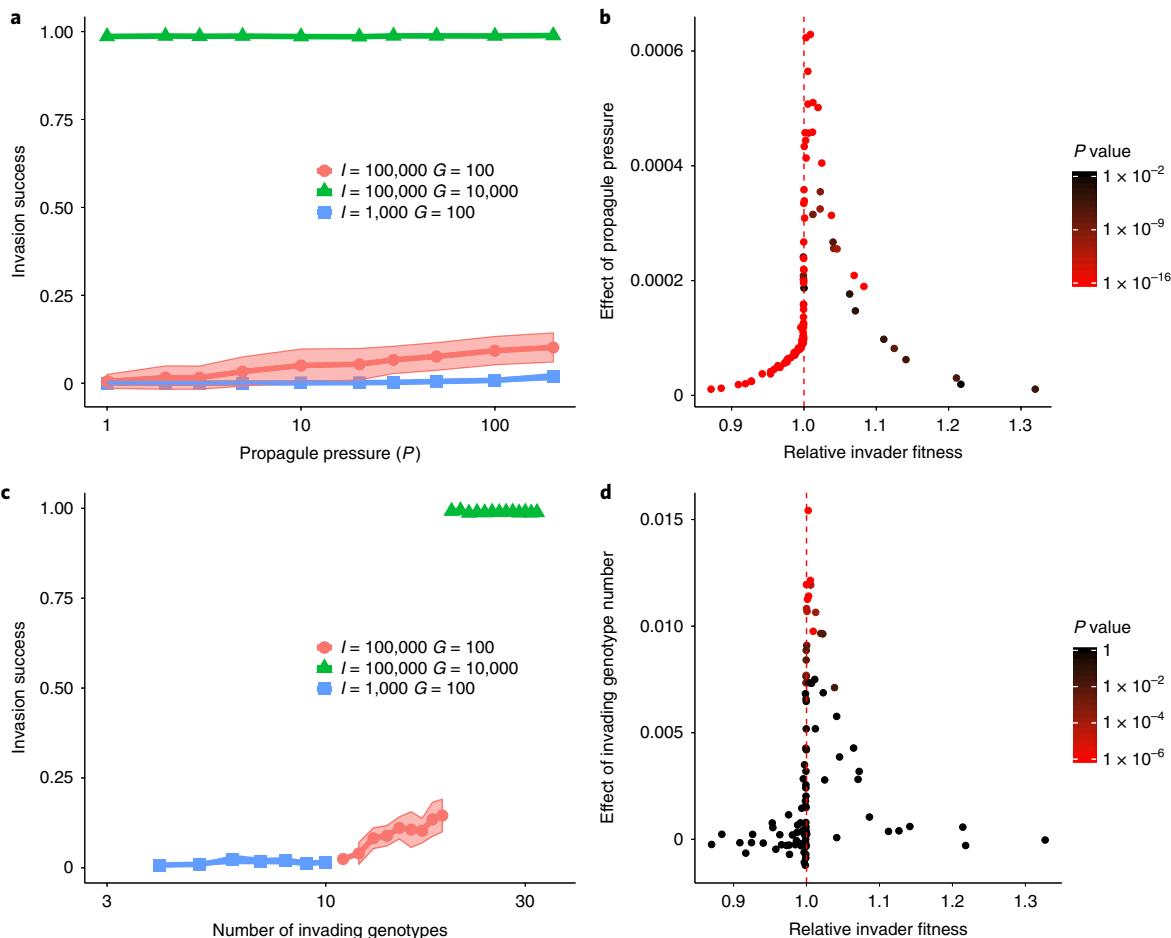


Fig. 4 | Propagule pressure and invader genotype richness can increase invasion success. **a,c**, General relationships for representative example parameter values shown in different colours. Each point gives the mean invasion success and the shaded regions give one standard deviation from that mean. **b,d**, The same results as shown in **a** and **c** but more generally across a broad set of parameter combinations ($s=0.01$, $\mu=0.0001$, $R=10,000$, G ranging between 50 and 10,000 and I ranging between 500 and 100,000; Supplementary Table 1). In panels **b** and **d**, each point corresponds to the slope of a linear regression fitted to the invasion success outcomes of many simulations. **b**, The simulation data used for each point runs across a range of different propagule pressure (p) values so that propagule pressure is the explanatory variable of the regression (see Supplementary Fig. 2a). **d**, The simulation data used for each point comes from a set of simulations where propagule pressure $p=200$ and all other parameters are also kept constant. Genotype number, an emergent property of the simulations, naturally varies and was used as the explanatory variable of the regressions in **d** (see Supplementary Fig. 2b). For each point in **b,d**, the colour shows the P value associated with the regression slope (Bonferroni corrected for multiple comparisons).

In these circumstances, probability of success or failure is affected by both propagule pressure and the genotypic diversity of the invaders. Large propagule pressure reduces the probability of stochastic invader extinction, leading to increased mean invasion success (Fig. 4a,b and Supplementary Fig. 2a). High genotypic diversity increases the probability that at least one invader is substantially fitter than any member of the resident community, thus also increasing the chance of invasion success (Fig. 4c,d, Supplementary Fig. 2b and Supplementary Fig. 3).

When resident community size (in terms of number of individual organisms) varies, we find a strong negative relationship between community diversity and invasion success as more diverse communities tend to be larger and are thus also more resistant to invasion. Even in the absence of selection (a neutral model with $s=0$), larger communities are more resistant to invasion for stochastic reasons (Fig. 5a). When selection is incorporated (a nearly neutral model with $s>0$), this effect is stronger because larger communities also evolve more rapidly (Figs. 3 and 5b). When comparing communities of identical size, those that are more diverse are still harder to invade for those simulations incorporating selection (Fig. 5c and Supplementary Fig. 4).

In addition to our exploration of parameter space, we also compared our model simulations with two published microbial experiments. The first of these performed invasions of *Serratia liquefaciens* into 95 different communities of *Pseudomonas fluorescens* covering a gradient of genotypic richness, measuring invasion success as relative invader abundance after 30–40 generations³¹. For a qualitative comparison with this study, we compared invasions into communities of varying richness and measured relative invader abundance 40 generations post-invasion. To mirror the order of magnitude difference in community size that was seen empirically by Jousset et al.³¹ ($\sim 3 \times 10^6$ to $\sim 3 \times 10^7$ bacteria ml⁻¹ for a fixed volume), our simulations were conducted using three different resident community sizes ($R=1,000, 5,000$ and $10,000$). The second study by Acosta et al. to which we compare our results introduced the golden alga, *Prymnesium parvum* into microbial assemblages collected from lake water with different propagule pressures, and tracked invader frequency over 2 weeks¹⁵. For a qualitative comparison we compared invasions into communities of constant size at three different propagule pressures ($p=1, 10$ and 100).

When comparing our simulations to empirical data we find qualitatively similar results. In particular, we found a weak relationship

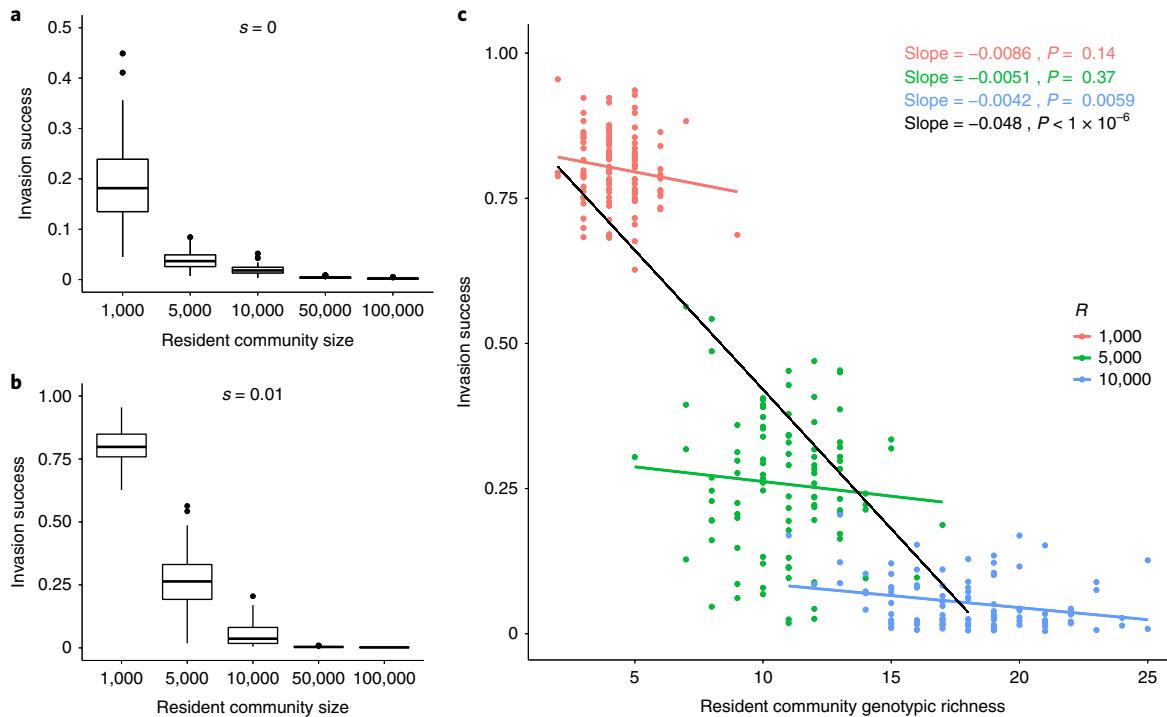


Fig. 5 | Larger and/or more diverse communities better resist invasions. **a,b**, Tukey boxplot of invasion success for simulations conducted with different resident community sizes under a neutral (**a**) and nearly neutral model (**b**). Even in a purely neutral model ($s=0$) larger communities are more resistant to invasion (**a**). The effect of community size is more marked under a nearly neutral model ($s=0.01$) as larger communities evolve more rapidly (Fig. 3) and so have a competitive advantage (**b**). **c**, Linear regression of invasion success against the number of genotypes in the resident community under the nearly neutral model ($s=0.01$). Independently of community size (R) more diverse communities are weakly more resistant to invasion; see the three coloured collections of points and corresponding coloured lines in **c**. The effect is stronger if community size is not corrected for: that is by considering communities of multiple sizes together, rather than separately—see the black line in **c**, which is fitted to all the points. For all data shown $\mu=0.0001$, $I=10,000$, $G=1,050$ and $p=200$. These qualitative results hold true for other choices of parameters (Supplementary Fig. 4).

between diversity and invasion success and this shows the least diverse communities are the easiest to invade, consistent with empirical data from Jousset et al. (Fig. 6a,b)³¹. We also find that propagule pressure can improve invasion success and this is reflected in empirical time series data replotted from Acosta et al. (Fig. 6c,d)¹⁵.

Discussion

Using an individual-based nearly neutral model, we simulated microbial community invasion to understand the mechanisms driving invasion outcomes. We sought to mechanistically model invasion dynamics in a microbial and eco-evolutionary context. Our model applies the rules laid out by the unified theory of ecology and macroevolution (UTEM)⁵⁴ to govern, birth, death and mutation of individual organisms. UTEM was first introduced as a single community model with no dispersal limitation; here we build on this with two isolated communities and bespoke scenarios in which one community invades the other through dispersal. UTEM was devised on the basis of ecological neutral theory⁵¹, which assumes that an individual organism's demographic rates are independent of species identity. However, UTEM, and by extension our model, relax this assumption to incorporate selection. In particular, individuals may have a reproductive advantage arising from their species identity, and can mutate in ways that are beneficial or detrimental to fitness. By incorporating some effects of selection, we address why classic neutral theory has attracted criticism in ecology and embrace the idea that neutral models serve as a starting point on which to build more complex processes⁷⁰.

Unconventionally for studies of microbial community ecology, we did not focus on differences between species, or species interactions.

Instead, we simulated the simplest possible scenario: a constant supply of a single resource shared equally between asexually reproducing individuals with no explicit niche construction. In this model, community level evolution is simply an arms race of increasing fitness. Our model also differs from invasion models in macroecology, which typically focus on species distribution models for individual invasive species^{71–73}. We expect our results to have several uses: (1) as a model of a single environmental niche containing high diversity; (2) as a parsimonious investigation of processes other than niches, such as stochasticity and evolution; (3) as a starting point for more complex future work including explicit niches; and (4) as a way to test whether explicit niches are required to explain observed patterns of community invasions.

Our simulations led us to propose five eco-evolutionary rules of microbial invasions that we suggest also apply more generally. Many of the rules depend on eco-evolutionary divergence between communities before invasion, mediated by community size. Larger communities evolve faster because they generate more variation for selection to act on (consistent with results at the population genetics level^{50,74}). The faster an invader or resident community evolves before invasion, and the longer it has to evolve, the higher the fitness of community members. Greater fitness elevates the chance of persisting after invasion (leading to rule 1). We found that these evolved fitness differences between communities determine the impact of chance, invader propagule pressure and invader diversity on invasion outcome. If the invaders have evolved a strong competitive advantage against residents then they will sweep through the community deterministically. Conversely, if the invaders are poor competitors, it is almost impossible for them to survive (rule 2).

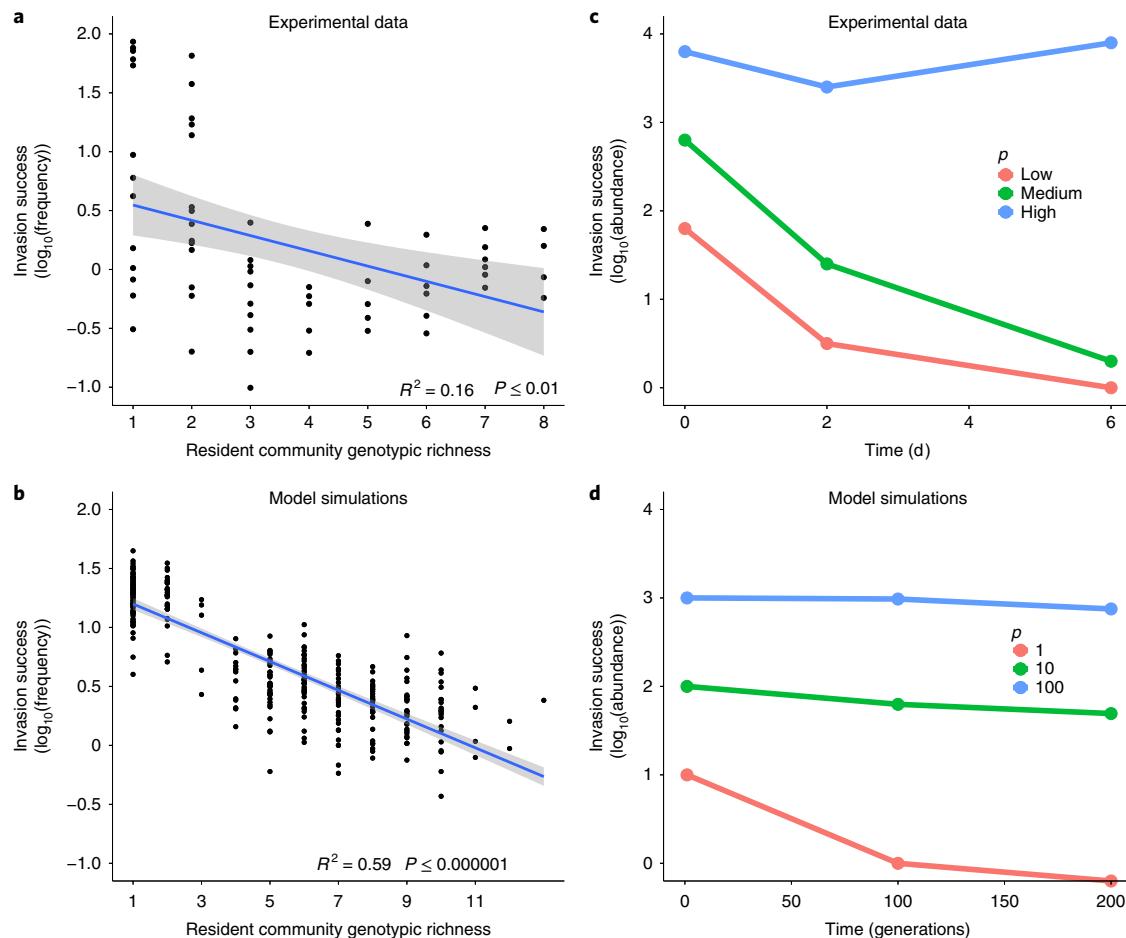


Fig. 6 | Model simulations are consistent with published experimental results. **a-d**, Qualitative comparison between empirical data (**a,c**) and simulation results under a neutral model ($s=0$) (**b,d**). Simulations of invasion with constant propagule pressure ($p=200$) into resident communities of varying size ($R=1,000, 5,000$ and $10,000$) reveal a significant negative relationship between community genotypic richness and invasion outcome (**b**) consistent with the relationship found by Jousset et al.³¹ (replotted in **a**). In **a** and **b**, the line is from an ordinary least-squares regression and the shaded region gives the 95% confident intervals. Simulation of invasions at three different propagule pressures ($p=1, 10$ and 100) into a community of constant size ($R=10,000$) reveal that invaders are more likely to persist when introduced in high number (**d**), consistent with results found in Acosta et al.¹⁵ (replotted in **c**). In **c** and **d**, each point is the mean invader abundance after 40 generations. In **b**, the other parameters chosen were $\mu=0.0001, l=10,000$ and $G=50$. In **d**, the other parameters chosen were $\mu=0.0001, l=6,000$ and $G=600$.

In between these two extremes exists a neutral zone where propagule pressure can tip the balance between success and failure as high propagule pressure reduces the chance of stochastic extinction early during the invasion process (rule 3). Neutral processes therefore play a key role in invasion outcome in a neutral zone determined by evolved competitive differences of invaders and invaded. In the same neutral zone, co-invasion also increases invasion success independently of propagule pressure because the chance of drawing some individuals that are slightly more competitive is higher when drawing from a mixed and diverse pool of invaders (rule 4).

Rule 5 proposes that more diverse communities are more successful in resisting invasion, a result that is often observed in low-diversity systems⁷⁵. A common ecological explanation for this emerges from stochastic niche theory which proposes that more diverse communities have stronger resource competition due to increased partitioning of resources and consequently are harder to invade^{76,77}. Our simulations suggest several alternative explanations. First, even when comparing equally sized communities, more diverse communities show wider variance in competitive ability, and are thus more likely to contain at least one superior genotype that can out-compete the invaders (Supplementary Fig. 3). This is

analogous to ‘selection effects’ wherein broader species sampling in more diverse communities increases the probability of containing a single species with disproportionate influence on community function such as invasion resistance⁷⁸. Second, there is a natural correlation between diversity and community size; as such, more diverse communities evolve better defenders due to their increased size (rule 1). Third, even in the absence of evolution, large communities dilute the ratio of invaders to defenders and so sometimes allow defenders to win through sheer weight of numbers. Thus, even in a neutral model, where no genotype has a competitive advantage, a weak diversity resistance relationship is expected (Fig. 5c). These three mechanisms combine to produce a strong positive relationship between diversity and resistance giving us our rule 5.

The rules of invasion that we propose are consistent with a range of invasion experiments using both microbes and macro-organisms. For example, Rivett et al.¹⁶ showed that increasing the genotypic richness of invaders increased the total persistence of invaders as predicted by our rule 4. Furthermore, several studies have shown that increasing propagule pressure can increase invasion success. We have highlighted one such study by Acosta et al.¹⁵ in Fig. 6, although others have found similar results^{79–81}. However,

other studies find no effect of propagule pressure⁸². This apparent inconsistency may be explained by our rules 2 and 3, which suggest propagule pressure only matters in a neutral zone where competitive differences between invaders and residents are negligible. More recent experimental studies show that propagule pressure only has an impact when genotypes from invader and resident communities are closely related^{35,47}. We propose that this genotypic similarity indicates similarity in competitive ability and occupancy of the neutral zone where an effect of propagule pressure is predicted by our rules.

A large body of work has shown that more diverse communities are more resistant to invasion^{31,62,83,84}, as predicted by rule 5. In Fig. 6, we highlight results from Jousset et al.³¹, which show that an increase in genotypic richness decreases invasibility. We find that even a purely neutral model can qualitatively recreate this pattern. Our findings do not imply that competitive and cooperative interactions are unimportant, rather they suggest that such interactions do not automatically follow from the observation. Our model cannot recreate the weak decrease in invasion resistance at very high genotypic richness that is sometimes seen. Experiments by Jousset et al.³¹ suggest that this pattern is due to lower production of invader-inhibiting toxins in high-diversity communities, a phenomenon that could be captured by a more complex extension of our model. A positive relationship between resident diversity and invasion success was also reported by Jiang and Morin⁸⁵. They showed this along a productivity gradient when measuring invasion success in terms of total invader abundance. Our model can reproduce this result, in a limited context. The mechanism is that larger (more productive) resident communities are more diverse and better able to support a higher absolute abundance of invaders, even if the relative abundance of invaders may be declining (Supplementary Fig. 5).

Existing empirical work has mostly been unable to disentangle the effects of species' traits, stochasticity and evolution. Most of the rules that we propose (rules 2–5) could emerge from niche-dependent mechanisms as well as from the nearly neutral mechanism our model explores. Under a niche-based approach, invaders may show positive density dependence⁸⁶ and so be more likely to successfully invade when arriving in large number (rule 3). Similarly, under a niche-based approach, co-invaders can facilitate each other's invasion and so co-invasions would be more likely to succeed^{16,57} (rule 4). This illustrates the potential generality of our rules; however, a deterministic model cannot capture rule 2. The only rule that does not fit the classic niche-based view is rule 1 because it covers evolutionary dynamics not usually considered by this approach.

While the formulation of our model was with microbes in mind, we expect that many of our findings will translate directly to macro-organism invasions⁸⁷. Rapid evolution before and during invasions is pervasive in microbes and probably has a profound effect on invasion outcomes^{50,88,89}. Evolution will probably still be relevant to macro-organism invasions but be weaker or at least harder to observe. Despite this, many of our rules of microbial invasion have implications for macro-organisms. Our rule 1 suggests that smaller and more isolated communities will be easier to invade; this is consistent with the catastrophic effects of invasion on oceanic islands^{20,90,91}. Our rules 2 and 3, suggesting a restricted neutral zone inside which invasion success is stochastic and influenced by propagule pressure, may also hold true in macro-organisms. Finding empirical evidence would be challenging due to the difficulty of measuring propagule pressure and of determining successful or unsuccessful invasion^{87,92}. Invasions of macro-organisms will predominantly be invasions of single species into larger communities. Most experimental microbial invasions also fall into this category⁶. We expect that our conclusions will directly translate to the special case of a single species invasion. Such scenarios represent a biased sample from the invading community, instead of an unbiased sample consisting of multiple genotypes. We have shown with

our simulations that sampling effects (such as drawing more individuals or a higher diversity of individuals) typically only influence invasion outcome in the neutral zone where invaders and defenders are well matched. Consequently, we expect a biased sample of one genotype (or species) would do likewise; in the neutral zone the outcome will continue to be stochastic while otherwise outcomes would depend on the fitness of the single invading genotype. There cannot, however, be any effects of invader richness in single genotype invasions; our rule 4 would probably not be relevant for most macro-organisms.

We envisage numerous possibilities for future work. First, gradual invasion events could be studied rather than flash invasion events⁹³. This would mean that extinction of the invaders is no longer a stable state of the model, as the same invading community will have the opportunity to make further attempts. Second, the theory could be applied to macro-organisms with a minimal change in terminology from mutation and genotype to speciation and species. This will have consequences for the model details; in particular, use of protracted speciation⁹⁴ would be more consistent with a species definition of diversity rather than the genotype view of our study. Third, niches could be incorporated by considering multiple environments and assigning species a different fitness in each environment, with the possibility of trade-off mutations that increase fitness in one environment at the expense of fitness in the other environment. Such an addition of traits to the model would make it possible to incorporate trait-dependent ecological interactions, both antagonistic and cooperative^{27,95,96}. A more advanced model could explicitly capture environmentally mediated interactions, such as facilitation and toxin mediated antagonism, that have been shown to promote and suppress invasion across a wide range of systems and can result in high-order and intransitive interactions^{97–100}. Finally, our model was spatially implicit with invader and resident communities each being well-mixed individually and with invasion being modelled as a single event. The same dynamics could be simulated on a network of patches or a fully spatially explicit grid of locations. This would enable the more subtle relationship between community size and spatial structure to be incorporated and may have more general implications for microbial biogeography. For example, small bacterial communities may be only transient and easily swept away by rapid adaptation in larger communities. Evolution may homogenize community composition leading to the weak biogeographic gradients observed⁸.

In conclusion, we have developed and applied an eco-evolutionary modelling approach to microbial invasions. This has revealed five general rules describing invasion outcome under different circumstances. The rules are consistent with existing experimental observations, with intuition, and with a range of existing theory. Our model focuses on different mechanisms compared to previous thinking: in particular, it does not require explicit niches and instead points to eco-evolutionary processes as being critical. Stochasticity and propagule pressure also play an important role but only in a neutral zone when conditions are right for this. That either niche or neutral processes could result in many of our rules, highlights their generality but suggests the need for additional work to disentangle pattern from process. We hope that this research will invite experimental comparison and help frame future studies of invasion, at both micro and macro scales, in the context of a broader range of possible mechanisms.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data presented in this paper has been deposited in a public repository and can be accessed at <https://github.com/vilacelest/vilaetal2019>.

Code availability

All code presented in this paper has been deposited in a public repository and can be accessed at <https://github.com/vilacelestin/vilaetal2019>.

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Author contributions

All authors contributed to designing the study. J.C.C.V. performed the analyses with input from J.R. and with reference to code written by M.P. J.C.C.V. and J.R. wrote the paper. All authors revised the paper. J.C.C.V. and M.P. were postgraduate students in the research group of J.R. M.L.J. was a PhD student in the group of T.B.

Competing interests

The authors declare no competing interests.

Additional information

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Software and code

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| Data collection | Simulations where conducted using custom code written in C++ and are available: https://github.com/vilacelestin/Vilaetal2019 |
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| Research sample | The majority of our results were produced by simulation. A small number of results were reproduced from existing publications which are cited in the main text. Acosta, Francisco, Richard M. Zamor, Fares Z. Najar, Bruce A. Roe, and K. David Hambricht. 2015. "Dynamics of an Experimental Microbial Invasion." <i>Proceedings of the National Academy of Sciences of the United States of America</i> 112 (37): 11594–99. Jousset, Alexandre, Wiebke Schulz, Stefan Scheu, and Nico Eisenhauer. 2011. "Intraspecific Genotypic Richness and Relatedness Predict the Invasibility of Microbial Communities." <i>The ISME Journal</i> 5 (7): 1108–14. |
| Sampling strategy | Given that results were generated by simulation we choose a very large but arbitrary replication size bearing in mind efficient usage of high performance computational resources |
| Data collection | Data was collected by simulation or from existing literature as cited |
| Timing and spatial scale | Not Applicable |
| Data exclusions | No data was excluded from the analyses |
| Reproducibility | Our code is available at https://github.com/vilacelestin/Vilaetal2019 . re-running the simulation and analysis codes will reproduce our results. |
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