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In this communication we present a unifying framework to understand the emergence and maintenance of diversity in ecological systems. We do this by developing a deterministic population model including density dependent limitation in resources and available space. Our model shows that competitive exclusion and neutral coexistence represent different regimes of the same adaptive dynamics suggesting that neutrality is the general result of an adaptive process in a finite habitat with limited energetic resources. Our model explains the emergence of biodiversity through mutation and its maintenance through neutrality. We show that this framework provides the theoretical foundations to understand the emergence and maintenance of diversity in microbial ecosystems.

Keywords emergence · diversity · adaptive dynamics · competition · neutrality

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1 Introduction

The processes by which diversity is generated and maintained in ecosystems are at the core of ecological inquiry. And yet, it is striking that we do not have a simple and general quantitative theory of biodiversity generation and maintenance, notwithstanding several recent efforts in this direction [1–5]. One of the impediments for achieving a general theory is the fondness of ecologists with complex ecological systems such tropical forests and coral reefs, as if a general theory of biodiversity should be easier to achieve under the inspiration of highly diverse ecosystems, e.g. [6]. In this context, it is not surprising that most theories, such as neutral and stochastic theories as well as niche and resource based ones [1, 2, 7–11] emphasize biodiversity maintenance but lack a formal treatment of biodiversity generation. In contrast, simple ecosystems represented by cultured bacteria populations, by virtue of their large population size, short generation time and easy of experimentation, have gradually taken a leading role in fostering our understanding of the processes underlying the emergence of diversity [12, 13].

It is well-known that cultures inoculated with an isogenic strain of bacteria gradually give raise to diversity, or genetic polymorphism in the form of mutant strains, even in the absence of environmental heterogeneity, e.g., [14–17]. Typically, population takeovers by fitter mutants (i.e., periodic selection, [18]) have been the rule in chemostat [19, 20] and in serial transfer batch cultures [21]. Periodic selection is closely associated with competitive exclusion and thus with the winning and complete takeover by the fittest mutant. Chemostats and sequential transfer experiments, however, may not adequately represent all extant diversity due to potential losses accrued by dilution (as in chemostats) or by transferring only a sample of the population to a fresh medium (as in sequential transfer lines). Further, the usual culturing conditions might not adequately represent the stress associated to low resource levels and intense competition, which are common in natural microbial ecosystems [22–25], and the increased mutation rate and diversity that these may trigger [26, 27]. In fact, experimental results on bacterial evolution under stress conditions (i.e. batch cultures with prolonged starvation, [14, 28–30]) resulted in the commonly observed periodic selection, but also in high levels of strain diversity (see Fig. 1). Interestingly, while it was early recognized that these result could hold important insights for understanding the mechanisms underlying the emergence of diversity in ecosystems [25, 28], see reviews in [31], no theory has explained them as yet.

In this paper, we present a general model to understanding the emergence and maintenance of diversity in ecological systems, which uses exploitative competition for resources [8, 32, 33], in an adaptive dynamics framework. Our central tenet is that diversity is driven by two density-dependent mechanisms: spatial constraints to individual packing and resource constraints to individual persistence and reproduction. Our model shows that the interaction between these two limiting factors underlies biodiversity generation through mutation (innovation) and maintenance through neutrality. Further, we show that this

framework provides the theoretical foundations for understanding the emergence and maintenance of diversity in microbial ecosystems.

2 The Model

Following [34], we consider a logistic Verhulst-type growth scenario

$$\frac{d}{dt}\phi = r\phi(1 - \phi), \quad (1)$$

where ϕ is the biomass of the bacterial strain. The logistic term in this equation represents the effect of the finiteness of the habitat wherein resources and biomass are contained, such that even if resources to provision further growth are present, this will not occur because of lack of space to put new biomass.

We assume that the growth rate r depends on the quality of the habitat ω , $0 \leq \omega \leq 1$, which specifies the amount of local resources that can be turned into new biomass. Then

$$r(\omega) = f\omega - m, \quad (2)$$

with f and m being fecundity and mortality rates, respectively. Habitat-quality dynamics is modeled as

$$\frac{d}{dt}\omega = F - C, \quad (3)$$

where F and C are the supply and consumption rates of resources respectively. We model them using the following functional forms

$$F = \lambda(1 - \omega), \quad C = \epsilon\phi\omega f, \quad (4)$$

where λ is the supply rate of resources, while ϵ represents the amount of nutrients per unit biomass. This formulation comes from the resource-based model introduced by Roughgarden [35].

The scenario we are interested corresponds to a strain growing in a habitat that do not receive any external supply of resources after colonization, as in Kolter's bacterial batch culture, but where new resources become available from the inside as a result of biomass decomposition or as by-products of the metabolic activity of bacteria, through the process known as cross-feeding, e.g. [20]. Notice that, in our model, negative density dependence acts upon fecundity as well as mortality, such that when biomass saturates the habitat, reaching stationary-phase, both rates tend to zero. This is a well-known phenomena in bacterial cultures, where upon reaching stationary phase bacterial cells cease to grow and divide, entering metabolic arrest or a spore-like physiological state; surviving for long periods of time with minimal metabolic activity [36,37].

By using Eqs. 1, 3 we represent such ecology as

$$\frac{d}{dt}\phi = (f\omega - m)\phi(1 - \phi), \quad (5)$$

$$\frac{d}{dt}\omega = \lambda(1 - \omega) - \epsilon\phi\omega f. \quad (6)$$

This system has three possible long-term behaviors (indicated with supra indices):

- Extinction. In this scenario, biomass goes to zero $\hat{\phi}^0 = 0$. However, due to the resources supplied by the biomass through its metabolic activity, the habitat quality goes to its maximum $\hat{\omega}^0 = 1$ (i.e. the habitat is saturated with resources accumulated as a by-product of metabolism).
- Bottom-up regulated. Here we have that biomass in the long-term goes to $\hat{\phi}^{1/2} = \lambda(R - 1)/(f\epsilon)$, where $R = 1/\omega^*$ and $\omega^* = m/f$, while habitat quality goes to $\hat{\omega}^{1/2} = \omega^*$.
- Top-down regulated. Here biomass reach a maximum saturating the habitat, $\hat{\phi}^1 = 1$, while habitat quality goes to $\hat{\omega}^1 = H$, with $H = \lambda/(\lambda + \epsilon f)$.

If we normalize time as $1/f$ we arrive to the following simplified equations

$$\frac{d}{d\tau}\phi = (\omega - \omega^*)\phi(1 - \phi), \quad (7)$$

$$\frac{d}{d\tau}\omega = \frac{\lambda}{f}(1 - \omega) - \epsilon\phi\omega. \quad (8)$$

Here we assume that $\epsilon > 0$ and the resource recycling through cross-feeding $\lambda > 0$ are both fixed, and that the trait ω^* ($\omega^* = m/f$) is subject to an adaptive dynamics, whereby new mutant strategies characterized by slight changes in ω^* continuously arise in the population (see next section below).

As before there are three equilibrium points. The extinction equilibrium is stable when a strategy is characterized by $\omega^* > 1$ (i.e. mortality is higher than fecundity). The bottom-up regulated equilibrium is stable for strategies satisfying $H < \omega^* < 1$. As strategies with smaller ω^* are considered, the top-down regulated equilibrium will kick in. This last equilibrium, $\hat{\omega}^1 \equiv H$, is stable when $0 \leq \omega^* \leq H$ that is, when resources are no longer constraining biomass accumulation. At this point the finite nature of the habitat becomes a strong constraint upon new biomass, as there is no more free volume to put the new biomass that can be made. Here habitat quality is determined by the parameters λ and ϵ .

In general, the important parameters for the stability of the system are ω^* , which measures the ratio between mortality and fecundity, and $\epsilon f/\lambda$, that appears in the threshold H . Figure 2 shows the stationary solutions for the equilibrium biomass $\hat{\phi}$ and their stability properties.

To understand the dynamic implications of this phenomenon, in an environment where new mutants may continually arise, we now turn to an adaptive dynamics framework (e.g. [38,39]).

2.1 Adaptive dynamics

An adaptive dynamics in a continuous trait space is particularly suited for uncovering the most likely course that evolution would follow under the conditions specified by our deterministic model [38,39].

Two of the fundamental ideas of adaptive dynamics are: (i) that a resident population, ϕ_r , can be assumed at equilibrium $\phi_r \equiv \hat{\phi}_r$ when new mutants, ϕ_μ , appear and that (ii) the fate of these mutants can be inferred from their growth rate when rare (i.e. at the beginning of the invasion) in the environment occupied by the resident, this per capita rate is defined below and it is known as the invasion exponent S or invasion fitness [40]. Finally we calculate the selection gradient S' which gives a local description of the fitness landscape experienced by an emerging (rare) mutant, indexed by μ , in the context of an equilibrium resident population, indexed by r , [39] under the ecological conditions described by Eqs. 7-8.

Notice that applying adaptive dynamics theory for this case is straightforward (see Online Resource 1), and we only need to consider the change in attractor stability when the evolving trait crosses a critical boundary, triggering a stability change in the fixed points for the resident population. In general, we need to perform an invasion analysis for each of the three regions of the parameters space, which correspond to attractors $\hat{\phi}^0$, $\hat{\phi}^{1/2}$, or $\hat{\phi}^1$.

Since in order to evolve, strategies must actually exist, we know that the relevant problem only involve strategies in the region $0 \leq \omega^* < 1$. So, only two cases must be considered as our equilibrium resident population $\hat{\phi}_r$: (a) bottom-up $\hat{\phi}_r^{1/2}$ scenario for strategies $H < \omega^* < 1$, and (b) a top-down $\hat{\phi}_r^1$ scenario for strategies $0 \leq \omega^* \leq H$.

In both cases we consider the fate (invasion exponent) of a rare strategy ω_μ^* , defined by

$$S \equiv S_{\omega_r^*}(\omega_\mu^*) \equiv \frac{1}{\phi_\mu} \frac{d}{d\tau} \phi_\mu = (\omega_r^* - \omega_\mu^*)(1 - \hat{\phi}_r), \quad (9)$$

within a background environment characterized by an equilibrium resident strategy ω_r^* resting at its (stable) equilibrium point $\hat{\phi}_r$ (see Online Resource 1).

The particular equilibrium point ($\hat{\phi}_r^{1/2}$ or $\hat{\phi}_r^1$) to consider for the resident equilibrium density $\hat{\phi}_r$, depends on what region of the strategy space is the resident trait ω_r^* at.

Case I, $H < \omega_r^* < 1$. Corresponds to the bottom-up regulated equilibrium. Thus, $\hat{\phi}_r^{1/2}$ ought to be considered. For this case the invasion exponent corresponds to:

$$S = (\omega_r^* - \omega_\mu^*)(1 - \hat{\phi}_r^{1/2}), \quad (10)$$

and the fitness gradient for the mutants looks like

$$S' \equiv \frac{d}{d\omega_\mu^*} S_{\omega_r^*} = \hat{\phi}_r^{1/2} - 1, \quad (11)$$

which is negative, $S' < 0$ since $\hat{\phi}_r^{1/2} < 1$. Thus, there is a directional evolution of the trait ω^* to the left (smaller values) in strategy space until it reaches strategies within the next region, to the left of $\omega_c^* \equiv H$.

Case II, $0 \leq \omega_r^* \leq H$. Corresponds to strategies that saturate available space. For these strategies, the equilibrium point to consider corresponds to the top-down regulated one $\hat{\phi}_r \equiv \hat{\phi}_r^1 = 1$. In this case the invasion exponent of any new mutant vanishes, since

$$S = (\omega_r^* - \omega_\mu^*)(1 - \hat{\phi}_r^1) = 0. \quad (12)$$

A plot of the selection gradient, S' , associated to the bottom-up equilibrium is negative, implying a steep fitness landscape where new mutant strategies carry a selective advantage over the resident one, and thus can invade the population (Fig. 3). However, as soon as the bottom-up regulated equilibrium is reached the invasion exponent of any new mutant vanishes and as a consequence the fitness gradient becomes flat and a neutral ecology emerges, where any possible mutant that arises is ecologically equivalent.

3 Discussion

Ever since the struggle for existence and the competitive exclusion principle, diversity, and more generally coexistence, has been a vexing problem in ecology and evolutionary biology [41].

Spontaneous beneficial mutations are the fundamental source for adaptation, innovation and diversity. In asexual populations, however, mutants better endowed with fitness will tend to replace other mutants through periodic selection or clonal interference [42, 43] putting a ceiling to diversity at its lowest value. Several hypothesis and models based on resource partitioning, cross-feeding, demographic trade-offs and frequency dependent selection have envisioned realistic scenarios for fitness equalization and thus coexistence and microbial diversity [15, 20, 44–48] with the recently proposed neutral theory [2] representing an extreme explanation, which assumes that individuals live in a flat fitness landscape, such that diversity is driven by mutation, dispersal and ecological drift [2].

Our model builds on resource-based competition, which when taking place in a finite habitat gives way to neutrality as a result. It unifies both approaches by assuming that species, in addition of being limited by resources (our bottom-up regulation) also face the geometric constraints imposed by the finiteness of their habitats (our top-down constraint), when packing biomass into individuals. The combined action of these density-dependent effects gives raise to an adaptive dynamics characterized by a transition from fitness mediated competitive exclusion to neutrality. The later arises when the habitat patch is saturated with biomass, such that any new favorable mutation, let say for using a different amino acid as a source of carbon, is not better endowed than any other one. This result is equivalent to the biotic saturation or zero-sum assumption in first-generation neutral models [2]. In this regard, what our model shows is that space limitation is sufficient to put the dynamics of species diversity, as driven by competition and speciation, into a

flat fitness landscape or neutral regime. In this sense space limitation provides a hard boundary that equalizes fitness by not allowing room for new and better adapted varieties. Recent neutral models have relaxed the zero-sum assumption but have retained the neutrality or symmetry assumption that all individuals behave the same under the same intraspecific circumstances [49, 50] in order to derive observables such as abundance distributions. Our model is fundamentally different in this regard, as we do not assume neutrality but arrive to it through an adaptive dynamics driven by food and space limitation. In this sense it is similar to recent models where neutrality is the result of ecological equivalence driven by mechanisms that equalize fitness (e.g. life-history tradeoffs and dispersal limitation) and therefore allows for the coexistence of different types in competitive communities [51–54]. It differs from them, however, in that the main forces driving diversity and coexistence are limitation for energy resources and space, while not assuming species specific tradeoffs in competitive abilities or dispersal. It remains to be explored how the neutral dynamics resulting from our model compares with predictions derived from neutral models, such as species abundance distributions and other observables [55].

Our model captures the essential features of the long-term starvation experiments that inspired its development [28], that is, waves of successive takeovers or periodic selection followed by coexistence of multiple mutants. The mechanisms underlying the emergence of progressively fitter mutants that get a growth advantage in stationary phase (i.e. that possess the GASP phenotype), with a competitive advantage to mutants of order $n + 1$ over those of lower order (i.e. that emerged earlier in the population), is related to several GASP mutations [14, 24, 29, 30] which, among other things, result in an increased ability to catabolize one or more amino acids as a source of carbon and energy.

The ecological scenario of a batch cultured population of *E. coli* entering GASP (around 10 day after initial inoculation) is characterized by the nearly exhaustion of carbon sources from where to extract energy, unless new mutations allow for the use of the only carbon sources available; organic compounds derived from metabolic activity and those trapped in bacterial biomass. Once a GASP mutant arises it will take over the population only to be replaced by mutants more efficient in using other available sources of carbon, scavenging for the carbon retained in the debris of dead bacterial cells or both. Indeed, in [29] it is shown that GASP mutations act additively, conferring faster growth on mixtures of amino acids. During the neutral phase all resources have been transformed to bacterial biomass, which becomes the resource itself. During this stage, it is possible to hypothesize that fitness will no longer increase after all the mutations required to use available amino acids have occurred, putting the dynamics onto a flat fitness landscape where bacterial biomass becomes the consumer and the resource. In this sense our density dependent constraint linked to habitat size somehow impose a limit to adaptation. It is also possible that successive strains are engaged in niche construction dynamics [56] such that although they may exclude each other, the winner always change the selective environment to favor a new variety until no further construction

is possible. The functioning of this neutral ecosystem will slowly degrade in time as a consequence of energy dissipation, causing biomass to decrease. So far, long-term starvation experiments of bacteria have lasted for more than 5 years, and although there is evidence of a biomass decrease, see Fig. 1 in [25], further analyses are necessary.

Finally, it is important to point out that resource and geometric constraints due to habitat finiteness are simple but fundamental ubiquitous characteristics of life, present since its emergence on earth. The model proposed herein derives how under these constraints competitive exclusion, diversity and neutrality can arise. Further, our model suggests that neutrality may not only be an assumption for mathematical tractability or a null model for ecological understanding [2, 7, 57] but the general results of an adaptive process in a finite habitat with limited resources.

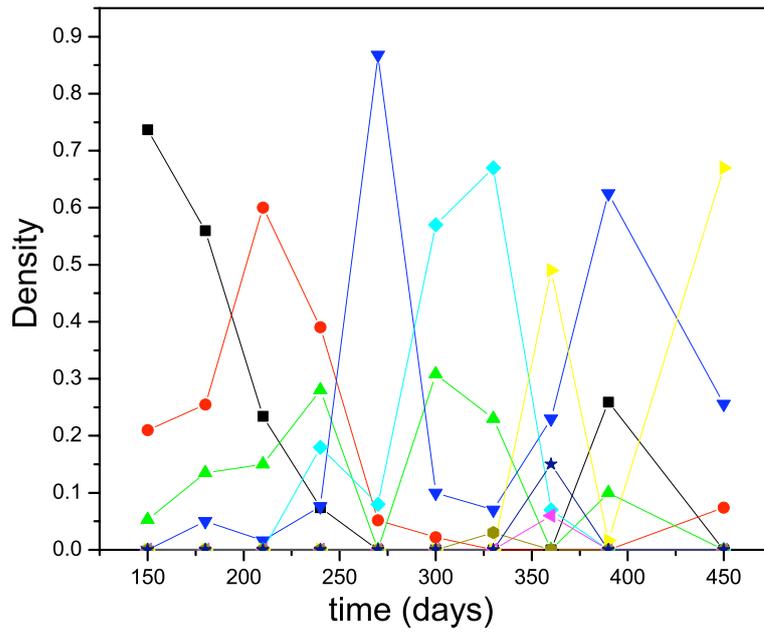


Fig. 1 Coexistence of different colony morphotypes, indicated by colors, during long-term incubation of an initially isogenic strain of *E. coli*. From data in Figure 4 of [28].

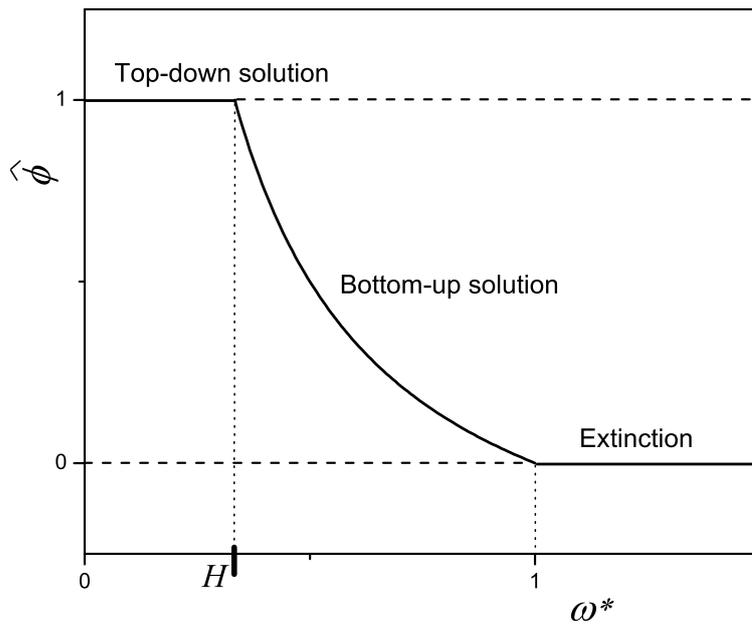


Fig. 2 Equilibrium states for the dynamics of biomass in a patch with resource renewal. Continuous and dashed lines represent stable and unstable equilibria respectively.

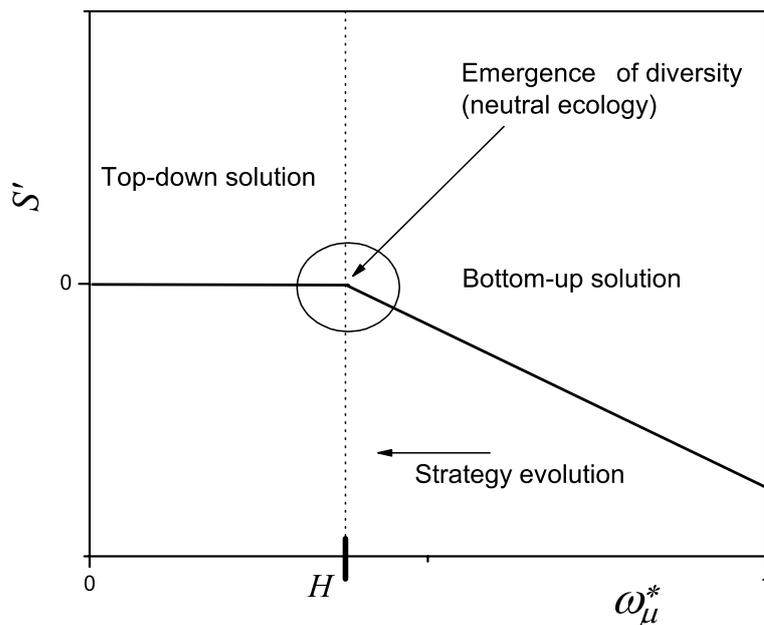


Fig. 3 Selection gradient as a function of ω^* . The threshold value H , is where the top-down solution becomes stable. This is the boundary at which a neutral ecology emerges.

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ONLINE RESOURCE 1

Article Title: Diversity emerging: From competitive exclusion to neutral coexistence in ecosystems

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In this online resource we provide a detailed explanation of how to carry out the invasion analysis and adaptive dynamics shown in our article.

We begin by defining the relevant equations (see eqs. 7-8 in the main text):

$$\frac{d}{d\tau}\phi = \phi(1 - \phi)(\omega - \omega^*) \quad (1)$$

$$\frac{d}{d\tau}\omega = \lambda'(1 - \omega) - \epsilon\phi\omega \quad (2)$$

where $\lambda' = \lambda/f$.

Eq. 1 correspond to the population dynamics of a single type in the ecological time-scale, while eq. 2, corresponds to the dynamics of habitat quality ω .

To carry out the adaptive dynamics and invasibility analysis entails considering the population dynamics for two types (a mutant ϕ_μ and a resident or parent strain ϕ_r). In this case total biomass ϕ_T corresponds to the sum of both types present $\phi_T = \phi_\mu + \phi_r$. The equations for the two strategy dynamics then become:

$$\frac{d}{d\tau}\phi_\mu = \phi_\mu(1 - \phi_T)(\omega - \omega_\mu^*) \quad (3)$$

$$\frac{d}{d\tau}\phi_r = \phi_r(1 - \phi_T)(\omega - \omega_r^*) \quad (4)$$

$$\frac{d}{d\tau}\omega = \lambda'(1 - \omega) - \epsilon\phi_T\omega. \quad (5)$$

The key to understand adaptive dynamics is the realization that a mutant strain emerges at a larger evolutionary time scale where the ecological time scale is at equilibrium (asymptotic densities). Thus, we can think on the initial mutant density ($\phi_\mu(\tau = 0)$), as being very small ($\phi_\mu \rightarrow 0$) but non-zero ($\phi_\mu \neq 0$). Under the same arguments, the initial resident density ($\phi_r(\tau = 0)$) is to be considered as it were determined by the ecological conditions **before** the emergence of the mutant (which emerges at $\tau = 0$). This means that $\phi_T = \phi_\mu + \phi_r \rightarrow \hat{\phi}_r$ when the mutant just appeared (at a density which can be neglected in comparison with the resident abundance but which is nevertheless a non-zero density). Thus, the resident asymptotic density is determined by its monoculture ecology,

$$\frac{d}{d\tau}\phi_r = \phi_r(1 - \phi_r)(\omega - \omega_r^*) \quad (6)$$

$$\frac{d}{d\tau}\omega = \lambda'(1 - \omega) - \epsilon\phi_r\omega. \quad (7)$$

Once this monoculture has converged to its equilibrium for biomass $\hat{\phi}_r$ and resources $\hat{\omega}_r$, the fate of a rare mutant is given by its per capita growth

rate as rare and surrounded by a resident, which is at its previous equilibrium before the disturbance of "mutant emergence". The mutant can invade if it can grow in these conditions (which is captured by the fitness S). This per capita growth rate of a rare mutant in a pre-mutant equilibrium resident background is derived from:

$$\frac{1}{\phi_\mu} \frac{d}{d\tau} \phi_\mu = (1 - \phi_T)(\omega - \omega_\mu^*), \quad (8)$$

Notice that the expression above correspond to

$$\frac{1}{\phi_\mu} \frac{d}{d\tau} \phi_\mu = (1 - \phi_r - \phi_\mu)(\omega - \omega_\mu^*). \quad (9)$$

1 Rare mutant invasion to a resident in equilibrium

By considering that the mutant density is almost zero but not zero and that the resident density correspond to its monoculture equilibrium we substitute the equilibrium for the resident and take the limits for mutant rarity:

$$\frac{1}{\phi_\mu} \frac{d}{d\tau} \phi_\mu = (1 - \underbrace{\phi_r}_{=\hat{\phi}_r} - \underbrace{\phi_\mu}_{\rightarrow 0}) (\underbrace{\omega}_{\hat{\omega}_r} - \omega_\mu^*). \quad (10)$$

Thus we get,

$$S \equiv S_{\omega_r^*}(\omega_\mu^*) \equiv \frac{1}{\phi_\mu} \frac{d}{d\tau} \Big|_{\phi_r=\hat{\phi}_r; \phi_\mu \rightarrow 0} \phi_\mu = (\omega_r^* - \omega_\mu^*)(1 - \hat{\phi}_r). \quad (11)$$

This expression corresponds to the fitness S (or invasion exponent see eq. 9 in the main text) of a rare mutant μ with trait ω_μ^* when appearing as rare within the resident population of its parent, which has already reached equilibrium before the mutant's emergence.