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SFI WORKING PAPER: 2008-03-008

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Diversity emerging: From competitive exclusion to neutral coexistence in ecosystems

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In this communication we present a unifying framework to understand the emergence and maintenance of diversity in ecological systems, which combines R^* theory (exploitative competition for resources) in an adaptive dynamic framework. Our model shows that competitive exclusion and neutral coexistence represent different regimes of the same adaptive dynamics. We point out that biodiversity generation through mutation and maintenance through neutrality are a consequence of the finite nature of habitats and limitation by resources. We show that this framework provides the theoretical foundations to understand the emergence and maintenance of diversity in microbial ecosystems and the growth advantage in stationary phase (GASP) succession in particular.

I. INTRODUCTION

The process by which diversity is generated and maintained in ecosystems is at the core of ecological theory. And yet, it is striking that we do not have a simple and general quantitative theory of biodiversity generation and maintenance, notwithstanding several recent effort in this direction (Hubbell 1997, 2001, Huisman et al. 2001, Allen et al. 2002, Brown et al. 2004). One of the impediments for achieving a general theory is the fondness of ecologists (and physicists in ecology) 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. Volkov et al. 2007). In this context, it is not surprising that most theories, such as niche and resource based theories as well as neutral and stochastic theories (Caswell 1976, Tilman 1982, 1994, Chesson 2000, Tilman and Pacala 1993, Hubbell 1997, 2001) 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 understanding the processes underlying the emergence of diversity (Rainey et al. 2000, Seehausen 2007).

It is well-known that microbial cultures after inoculation with an isogenic strain gradually give raise to diversity, or genetic polymorphisms in the form of mutant strains, even in the absence of environmental heterogeneity (e.g., Zambrano et al. 1983, Rosenzweig et al. 1994,

Riley 2001, Maharjan et al. 2006). Typically, population takeovers by fitter mutants (i.e., periodic selection, Atwood et al. 1951) have been the rule in chemostat (Novick and Szilard 1950, Helling et al. 1987) and in serial transfer batch cultures (Lenski and Travisano 1994). Periodic selection is closely associated with competitive exclusion and thus with the winning and complete take over by the fittest mutant. Chemostats and sequential transfer experiments, however, may not adequately represent all potentially generated 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 stressful conditions associated to low resource levels and intense competition, that are common in natural microbial ecosystems (Morita 1988, 1997, Zinser and Kolter 2004, Finkel 2006), and the increased mutation rate that these stresses may trigger (Bjedov et al. 2003, Tenaillon et al. 2004) further affecting potential diversity. As any human being knows well, scientist in particular, stress is a powerful force, a source of innovation, and an essential part of life be this bacterial or human. To shed light upon the subject of bacterial evolution under stress conditions Kolter and co-workers (see Zambrano et al. 1993, Finkel and Kolter 1999, Zinser and Kolter 1999, 2000) set out a simple experiment of prolonged starvation using constant batch cultures of *Escherichia coli* to which no nutrients are added, or individuals removed, after initial inoculation. Interestingly this experiment resulted in the commonly observed periodic selection, which con-

fers mutants with a *growth advantage in stationary phase* (GASP), up to a point where mutants could not exclude each other (competitive equivalence) and coexistence and diversity increased. This system shows that competitive exclusion under certain conditions gives rise to neutrality and thus diversity. This model system was early recognized as holding important insights for understanding the mechanisms underlying the emergence of diversity in ecosystems (Finkel and Kolter 1999, see reviews in Zinser and Kolter 2004, Finkel 2006) but as yet, no theory has explained it.

In this paper, we present a unifying, yet simple, framework to understand the emergence and maintenance of diversity in ecological systems, which combines R^* theory (exploitative competition for resources, Hansen and Hubbell 1980, Tilman 1982) in an adaptive dynamic framework to give rise to neutral biodiversity dynamics. Our central tenet is that biodiversity and neutrality are driven by two density-dependent mechanisms: spatial constraints to individual packing and resource constraints to individual persistence and reproduction. The interaction between these two limiting factors underlie 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 and the *growth advantage in stationary phase* (GASP) succession in particular (Zambrano et al. 1993, Finkel and Kolter 1999, Zinser and Kolter 1999, 2000).

A. The GASP phenomenology

Suppose we infect an otherwise virgin, finite and isolated, habitat patch made of fresh *LB* (*Luria-Bertani*) medium with a wild type strain of *E. coli* bacterium. The first day of such batch culture consists of what microbiologists call the *log phase* of growth (Malthusian exponential expansion); the second day, a fully developed population has reached what is called *stationary phase* (patch saturation); the third day, habitat degradation prompts (local) population extinction (*death phase*).

The log and stationary phases can be understood as resulting from purely logistic considerations, acting through spatial limitation given by the *finite* character of habitats and by resource limitation, which is related to the amount and quality of the resources found within finite habitats. Batch cultured cells in stationary phase gradually begin to lose viability entering into a “death phase” where a number of ecological and evolutionary processes take place.

Considering this habitat phenomenology, the wild type is doomed to extinction unless new resources are added to the habitat patch. Interestingly, extinction does not happen. Indeed, the batch culture can be maintained for years without the addition of nutrients (only sterile distilled water to maintain osmolarity) giving rise to

a fifth phase in the bacterial cycle known as Long-term stationary phase where ever fitter mutants arise and take over (Zambrano et al. 1993) generating a succession of “waves of takeovers” (Zambrano et al. 1993, Finkel and Kolter 1999, Finkel et al. 2000) by mutants expressing the GASP phenotype. This GASP succession of mutants is characterized by two distinct regimes: competitive exclusion and stochastic coexistence.

a. The competitive exclusion regime is characterized by a low diversity community ($N \approx 2$). In this community, a mutant of order n , who originated by mutation from a previous mutant $n - 1$, outcompetes its parental type. As its resource space gets degraded, stress and mutation give rise to a new type of order $n + 1$ which repeats the cycle. This process has long been known from early chemostat studies (Novick and Szilard 1950) and been named “periodic selection” (Atwood et al. 1951)

b. Stochastic coexistence regime. The previous regime does not last for ever, at a certain point in a community’s ontogeny competitive replacements ceases and coexistence takes over. As a consequence, biodiversity unfolds and accumulates monotonically ($N \gg 2$).

II. THEORETICAL FRAMEWORK

We will elaborate a monomorphic case, for then to generalize it to a continuous strategy space by assessing the adaptive dynamics of the proposed model. The monomorphic case will allow us to study the possible dynamical behaviors of the system and the dynamic equilibria where it would likely settle. The adaptive dynamics, on the other hand, will allow us to assess the likely evolutionary responses and trajectories that different strategies (mutants) will follow in the adaptive fitness landscape specified by the model.

A. The monomorphic case

To investigate the possible ecological processes driving the phenomenology described above we follow Keymer et al. (2006) and develop a framework whose point of departure is the understanding of log and stationary growth phases. As we pointed out before, both phases can be understood if we consider a logistic Verhulst-type growth scenario

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

where ϕ represents the biomass, $0 \leq \phi \leq 1$, of the parental strain (or mutant of order 0 or wild type). Notice that, the logistic term in this equation represents the finiteness of the habitat wherein resources and biomass are contained. This reflects a geometric constraint, 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 a patch quality index ω , $0 \leq \omega_0 \leq 1$, which specify the amount of local resources that can be turned into new biomass. Following Roughgarden (1997) we represent such growth function as

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

Here f is fecundity and m mortality rates. Patch-quality dynamics is modeled as

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

where F represents patch supply and C habitat consumption. We use the following functional forms

$$F \equiv \lambda(1 - \omega),$$

$$C \equiv \epsilon\phi\omega f,$$

λ represents the supply of basal resource to the patch, while ϵ is the efficiency with which resources ω are converted in bacterial biomass ϕ .

1. Parental dynamics in a patch without resource renewal

The simplest scenario we can picture, corresponds to a parental type growing on a patch that do not receive any external supply of resources after colonization as in a bacterial batch culture.

By using Eqs. (1-3) we represent such ecology as

$$\frac{d}{dt}\phi = (f\omega - m)\phi(1 - \phi), \quad (4)$$

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

which in the long-term, biomass converges to extinction, $\hat{\phi} \equiv \phi(t \rightarrow \infty) = 0$, and habitat quality, $\hat{\omega} \equiv \omega(t \rightarrow \infty)$, is dependent on initial condition, see Fig. (1) for an illustrative example.

2. Parental dynamics in a patch with resource renewal

This case is the same as above but considering a not nil supply of resources. As Kolter's batch cultures (habitat patch) are not supplemented with resources (carbon sources) from the outside, these should come from the inside; derived from scavenging its own biomass (i.e. eating dead siblings, Zinzer and Kolter 1999) or in the form of by-products of the metabolic activity of bacteria (e.g., Helling et al. 1987). We refer to either case as "habitat modification" resulting from the activity of the bacteria inhabiting it which translate into a service (more properly an ecosystem service) provided for someone else. Mathematically this corresponds to changing Eq. (5) to

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

Now, the system has three possible long-term behaviors (denoted by the supra-indices 0, 1/2 and 1).

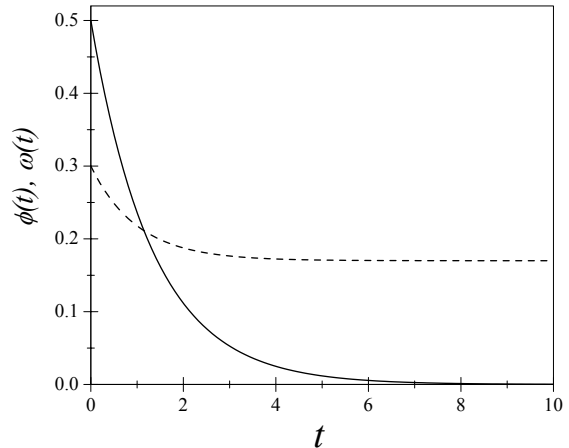


FIG. 1: Evolution for parental dynamics in a patch without resource renewal. This case evolve to the extinction of the biomass. Continuous line and dash line represent biomass and patch-quality.

a. Extinction. In this scenario, as before biomass goes extinct $\hat{\phi} = 0 \equiv \hat{\phi}^0$. However, due to the ecosystem services supplied by the wild type biomass, the patch quality goes to its maximum $\hat{\omega}^0 = 1$ (i.e. the patch is saturated with resources in the form of the carbon sources storage in dead biomass or accumulated as a by-product of metabolism).

b. Bottom-up regulated. The patch is not fully saturated due to its lack of quality (i.e. resources). 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 $\hat{\omega}^{1/2} = \omega^*$.

c. Top-down regulated. Correspond to a totally saturated patch that can sustain a maximum amount of biomass, $\hat{\phi}^1 = 1$, while keeping quality to $\hat{\omega}^1 = H$, with $H = \lambda/(\lambda + \epsilon f)$. Notice that this equation corresponds to an scenario where through the habitat modification accrued by the parental or wild type, new resources become available. So the wild (mutant of order n), through its modification of the environment provides resources that can be used by another type (mutant of order $n + 1$), which in turn will do the same creating a nutrient cycle. For the sake of simplicity we model the general phenomenon of biomass change in a finite habitat with resource renewal.

III. ADAPTIVE DYNAMICS AND DIVERSITY SYMMETRY BREAKING

The most important feature that we are interested in is the transition between periodic selection to neutrality and coexistence, which in the context of Kolter's experiments translates into the transition from an early GASP

period of competitive replacements to a later one in which biodiversity accumulates. An adaptive dynamics is a stochastic process in a continuous trait space, which is particularly suited for uncovering the most likely course that evolution would follow if driven by resource stress and habitat geometric constraints. To model the adaptive dynamics we will proceed to consider the minimal model that includes these ingredients.

A. The minimal case

If we normalize time as $1/f$ we can see that the minimal system under resource renewal (Eqs. 4,6) for a fully serviced patch being

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

$$\frac{d}{d\tau}\omega = \frac{\lambda}{f}(1 - \omega) - \epsilon_0\phi\omega. \quad (8)$$

Here we assume that $\epsilon > 0$ and the ecosystem service $\lambda > 0$ are both fixed, and that the trait ω^* ($\omega^* = m/f$) is subject to an adaptive dynamics.

1. Stability of the equilibrium points

As we discussed for the general monomorphic ecology, there are three equilibrium points.

a. Extinction equilibrium correspond to the trivial solution, $\hat{\phi}^0$. This equilibrium is stable when a strategy is unsustainable $\omega^* > 1$. Since consumption disappears, ecosystem services (i.e. resource renewal processes) set corresponding long-term patch quality to its best possible value $\hat{\omega}^0 \equiv 1$.

b. Bottom-up regulated when the system is limited on the –ecosystem service– supply side, the patch’s quality is set (as in R^* -theory) by a strategy or consumer phenotype $\hat{\omega}^{1/2} \equiv \omega^*$. This equilibrium is stable for strategies satisfying: $H < \omega^* < 1$. As strategies with smaller ω^* are considered, the equilibrium below will kick in.

c. Top-down regulated occurs, when the only limitation comes from the top-down, meaning that resources (i.e. patch quality) are no longer constraining biomass accumulation. The easy interpretation is that at this point the finite nature of habitats put a strong constraint upon new biomass as there is no more free volume (vacancy) to put the new biomass that can be made. Here the patch quality is no longer determined by the strategy phenotype but by the parameters λ and ϵ . Thus, $\hat{\omega}^1 \equiv H$. This is the stable equilibrium when: $0 \leq \omega^* \leq H$.

The important parameters for the stability of the system are ω^* , that measures the ratio between mortality and fecundity, and $\epsilon f/\lambda$, that appears in the threshold H . Figure 2 shows the branches of stationary solutions for ϕ and its stability properties.

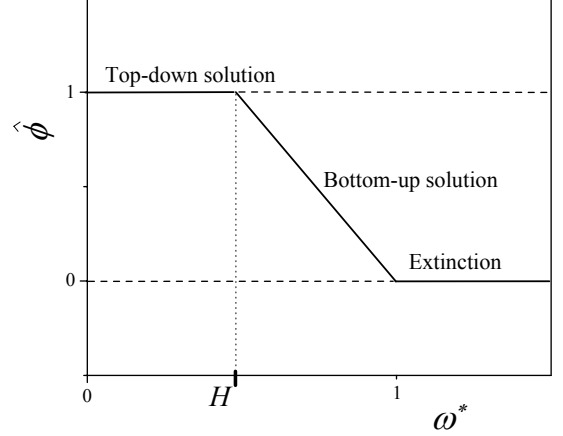


FIG. 2: Equilibrium states for the dynamics of biomass in a patch with resource renewal. Continuous and dash lines represent stable or unstable equilibria.

2. Adaptive dynamics in strategy space

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 those mutants can be inferred from their original growth rate when rare in the environment consisting on the resident. Notice that such landscape, changes each time a successful invasion takes place.

The rest –of our task– is to describe the invasion exponent S , defined below, and the selection gradient S' which gives a local description of the fitness landscape experience by an emerging (rare) mutant, indexed by μ , in the context of an equilibrium resident population, indexed by r , ecological condition described by Eqs. (7-8).

Notice that applying adaptive dynamics theory for this case is straight forward, and we only need to consider in the analysis the change in attractor stability when the evolving trait crosses the critical boundary, triggering a change in the stability 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 such: $0 \leq \omega^* < 1$. So, only two cases must be considered as our equilibrium resident population $\hat{\phi}_r$ are: (a) bottom-up $\hat{\phi}_r^{1/2}$ scenario for parental strategies such $H < \omega^* < 1$, and (b) a top-down $\hat{\phi}_r^1$ scenario for parental strategies such $0 \leq \omega^* \leq H$.

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 $\hat{\phi}_r$.

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 which region of strategy space is the parental trait ω_r^* .

a. Case I, $H < \omega_r^ < 1$.* Corresponds to the case when the stable equilibrium point of the ecology is bottom-up regulated. Thus, $\hat{\phi}_r^{1/2}$ ought to be considered. Therefore the invasion exponent correspond to:

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

and therefore following the fitness gradient for the mutants (assumed similar to its parent) looks like

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

thus is negative, $S' < 0$ since $\hat{\phi}_r^{1/2} < 1$. Then, there is a directional evolution of the trait to the left (smaller values) in strategy space. This at least until we reach strategies to the left of critical strategy $\omega_c^* \equiv H$.

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

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

As a consequence, the fitness gradient is not defined (i.e. it becomes a flat fitness landscape) and a neutral stochastic ecology emerges, where any possible mutant that arises is equivalent, such that the state of the system is driven by random birth, dead and mutation process.

Notice that in the case where there is no saturation of biomass, the solution $\hat{\phi}_r^{1/2}$ is the only stable one, and a simple adaptive dynamics analysis shows that the selection gradient is always negative with constant unity value. This processes is completely different from the one discussed above, where the stress situation generated by finite space is of relevant importance.

IV. DISCUSSION

Ever since the struggle for existence and the competitive exclusion principle, diversity and coexistence in general, and in asexual organisms in particular, has been a vexing problem in ecology and evolutionary biology (Muller 1932). Spontaneous beneficial mutations are the fundamental source for adaptation, innovation and diversity. In asexual population, however, mutants better endowed with fitness will tend to replace other mutants through periodic selection or clonal interference (Gerrish and Lenski 1998) putting a ceiling to diversity at its lowest value. The evolutionary mechanisms underlying clonal interference, and in particular how favorable

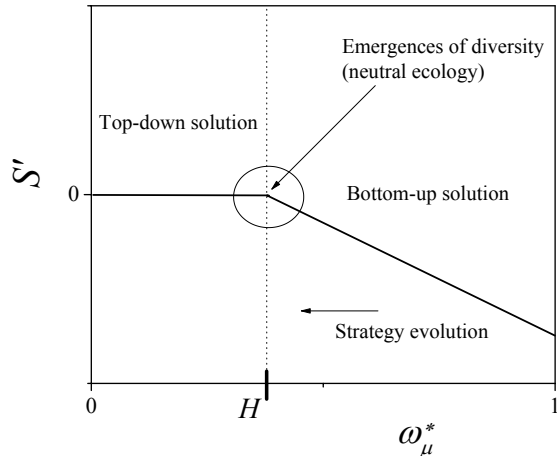


FIG. 3: Selection gradient as a function of ω^* . The parameter H , where the top-down solution begins, is the boundary at which a neutral ecology emerges.

mutations can become fixed in asexual organisms are relatively well-known (Gerrish and Lenski 1998, Hegreness et al. 2006). The ecology of the process can also be understood in the context of resource-based competition models, as shown by Hansen and Hubbell (1980) for bacterial strains competing on a single nutrient. For this case, the winning strain will always be that with the smallest subsistence requirements or whose Zeroth Net Growth Isocline is more to the left (Tilman 1982). Several hypothesis and models based on resource partitioning, cross-feeding, demographic trade-offs and frequency dependent selection have portrait realistic scenarios for fitness equalization and thus coexistence and microbial diversity (Helling 1987, Rosenzweig et al. 1994, Turner et al. 1996, Rozen and Lenski 2000, Czaran et al. 2002, Kerr et al. 2002, Friesen et al. 2004) with the recently proposed neutral theory (Hubbell 2001) representing an extreme explanation which assumes that individuals live in a flat fitness landscape to start with, such that diversity and coexistence is a stochastic process guided by mutation, dispersal and ecological drift (Hubbell 2001). Our model builds on resource-based competition as well as in neutral theory to propose a model that unifies both approaches by assuming that species, in addition of being limited by resources (our bottom-up regulation) also face the geometric constraints given by the finiteness of habitats (our top-down constraint). The combined action of this two density-dependent effect gives raise to an adaptive dynamics characterized by a transition from fitness mediated competitive exclusion to neutrality. Neutrality arise in our model when the habitat patch is saturated with biomass, such that any mutant that arise and carries a favorable mutation, let say for using aminoacids as a source of carbon, is not better endowed than any other one. This result is equivalent to the biotic saturation

assumption in first-generation neutral models (Hubbell 2001).

Our model provides a way to understand the emergence of neutrality through diversity and saturation. The basic idea is that resources are contained in finite habitats such that the ability of species to harvest resources, while dominant under no-saturation, is no longer the driver of the dynamics when the amount of resource-free space becomes critical. This regime shift, break symmetry, thus allowing for diversity and coexistence. This process is expressed in that eventhough the dynamics started with an isogenic strain, at the end there is coexistence of many different strains. The threshold for this shift depends on ϵ or the efficiency with which resources are converted into bacterial biomass.

Also, it captures the essential features of the long-term starvation experiments, that inspired its development (Finkel and Kolter 1999), that is, waves of successive takeovers or periodic selection followed by coexistence of multiple mutants. The mechanisms underlying the emergence of the GASP phenotype, which confers 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 (Zambrano et al. 1993, Zinser and Kolter 1999, 2000, 2004) which, among other things, result in an increased ability to catabolize one or more aminoacids 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; aminoacids trapped in bacterial biomass. Once a GASP mutant arise it will take over the population only to be replaced by mutants more efficient in scavenging for the carbon retained in the debris of dead bacterial cells. Indeed, Zinser and Kolter

(1999) showed that GASP mutations act additively, conferring faster growth on mixtures of aminoacids. During the neutral phase all resources have been transformed to bacterial biomass, such that the bacterial biomass 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 aminoacids 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 represents the limits of adaptation. The functioning of these 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 Finkel 2006) further analyses are necessary.

Finally, it is important to point out that resource and geometric constraints due to habitat finiteness are simple and fundamental characteristics of life, present since its emergence of earth. The model herein proposed derives how under these constraints competitive exclusion diversity and neutrality can arise. Further, our model suggest that neutrality may not only be an assumption for mathematical tractability or a null model for ecological understanding (Caswell 1976, Hubbell 2001, Alonso et al. 2006) but the general results of an adaptive process in a finite habitat with limited resources, something pretty much like earth.

Acknowledgements. We thank David Krakauer, Sander van Doorn, Elhanan Borenstein and Geoffrey West for constructive insight and criticisms. PAM acknowledges support from a John Simon Guggenheim Fellowship and grants FONDAP-FONDECYT 1501-0001 and ICM P05-02.

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