Biodiversity in model ecosystems, I: coexistence conditions for competing species

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Abstract

This is the first of two papers where we discuss the limits imposed by competition to the biodiversity of species communities. In this first paper, we study the coexistence of competing species at the fixed point of population dynamic equations. For many simple models, this imposes a limit on the width of the productivity distribution, which is more severe the more diverse the ecosystem is (1994, Theor. Popul. Biol. 45, 227–276). Here we review and generalize this analysis, beyond the "mean-field"-like approximation of the competition matrix used in previous works, and extend it to structured food webs. In all cases analysed, we obtain qualitatively similar relations between biodiversity and competition: the narrower the productivity distribution is, the more species can stably coexist. We discuss how this result, considered together with environmental fluctuations, limits the maximal biodiversity that a trophic level can host.
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Keywords: Biodiversity; Lotka-Volterra equations; Species assembly; Competition matrix

1. Introduction

One of the most striking characteristics of living systems is their amazing diversity. Theoretical ecologists have devoted much of their effort to explain why Nature is diverse and to identify the mechanisms that enhance or limit species coexistence. While the observations show that rich and diverse ecosystems are the rule and not the exception, stable, highly diverse systems rarely arise in mathematical models.

In the early decades of theoretical ecology, emphasis has been placed on the *principle of competitive exclusion*. Stated qualitatively, this principle asserts that two or more species occupying the same ecological niche cannot stably coexist in the same ecosystem. The first attempt to transform this principle into a mathematical theorem is due to Volterra (1928). Generalizations of Volterra's theorem to an S species ecosystem have been provided by several authors (MacArthur and Levins, 1964; Rescigno and Richardson, 1965; Levin, 1970). It has been shown that S species cannot coexist at a fixed density if they are limited by less than S independent resources.

This approach, however, presents two kinds of shortcomings. The first one is of a mathematical nature. It has been shown that the theorem of competitive exclusion in the previous form does not hold if some conditions are relaxed. Most importantly, it no longer applies if the growth rates depend nonlinearly on the resources and if coexistence at a fixed point is replaced by the more general condition of persistence (Armstrong and McGehee, 1980; Koch, 1974; Kaplan and Yorke, 1977). Such nonlinear behavior is to be expected in

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natural ecosystems. Similarly, the theorem of competitive exclusion is violated when age structured populations are considered, when resource is not uniform in quality (May, 1974; Diamond, 1978) or when physical space is considered (Solé et al., 1992). The prolonged coexistence of a large number of competitive plankton species has been justified through barriers to mixing of species in an otherwise homogeneous environment (Bracco et al., 2000).

The second, more important difficulty is related to field observations, which can hardly ever claim to give a full account of all resources and the functional dependence of growth rates on them. Hence, the theorem of competitive exclusion has little actual predictive value. The simultaneous presence of similar species can always be ascribed to yet unknown resources or to unknown functional forms of growth rates.

Field research has shown that coexistence of competing species is far from rare in real ecosystems. As a result, the conditions favoring coexistence are receiving increasing attention from the ecological community (McCann et al., 1998; Chesson, 2000; Kokkoris et al., 2002; Roberts and Stone, 2004). These theoretical analysis and empirical observations suggest that the competitive exclusion principle could be replaced by a 'coexistence principle' (den Boer, 1986).

In the present suite of two papers, we analyse species coexistence for a class of models where competitive exclusion does not hold, since species growth is limited both by biotic resources (explicitly represented in the model) and by other limiting factors (implicitly considered), modeled as self-damping terms in the population dynamics equations. In the first paper we consider coexistence at the fixed point of population dynamics, and show how the combination of competition and environmental fluctuations limit the maximum amount of biodiversity that a trophic level can host. In the second paper we consider models of species assembly, kept away from the fixed point of population dynamics through the continuous arrival of new species due to immigration or speciation events. These models can reproduce species-area laws in good agreement with field observations. The coexistence condition presented in this paper can be generalized to that situation as well. We define therefore an effective model of biodiversity across a food web, based on an approximation to the population dynamics equations and on the condition of maximum biodiversity derived in this first paper. The effective model predicts that biodiversity as a function of the trophic level has a maximum at an intermediate level.

The present paper is organized as follows. After introducing the population dynamics equations that we use, we discuss in Section 3 coexistence in a single trophic layer, in the framework of a mean-field approximation of the competition matrix. The coexistence condition that we derive imposing that all equilibrium densities are positive is equivalent to the one demonstrated by Chesson through the criterion of invasibility (Chesson, 1994, 2000). Several different models yield the same coexistence condition, be competition represented either explicitly in the population dynamics equations or implicitly, through the effect that other species have on resources. This condition states that species coexistence depends crucially on the *distribution of rescaled net productivity*, i.e. productivity not taking into account the competition load and rescaled through the carrying capacity: the productivity distribution has to get narrower to allow the coexistence of a larger number of species. This result is also in agreement with theoretical studies stating that many species can coexist provided they are similar enough (Kokkoris et al., 2002).

The coexistence condition is then generalized to generic competition matrices, beyond the mean-field approximation. We show that the angle formed by the principal eigenvector of the competition matrix, which we name the competition load, and the rescaled productivity must be narrow to permit species coexistence. This result allows to generalize the coexistence condition from one trophic layer to structured food webs, as discussed in Section 5.

The coexistence condition alone does not impose a limit on biodiversity if the productivity distribution can be arbitrarily narrow. However, in natural ecosystems, this distribution has a finite width due to unavoidable environmental fluctuations on time-scales much shorter than those of population dynamics. This limits the maximal biodiversity the system can host, and produces a typical shape of biodiversity versus trophic level (Lässig et al., 2001), as we discuss in the companion paper.

2. General framework

We study here models of multispecies communities. A key ingredient in the models is biodiversity, meaning the number of reproductively separated populations in the environment. Biodiversity arises from a balance between the assembly process involving speciation and immigration and the extinction process driven by population dynamics, in a spirit similar to MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson, 1967). Population dynamics is represented through generalized Lotka–Volterra equations of the form

$$\frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = \sum_{j \neq i} g_{ij}(\mathbf{N}) - \sum_{j=1}^{S} \beta_{ij} N_j(t) - \alpha_i, \qquad (1)$$

where the community is formed by S interacting species, N_i represents the biomass density of species i, and $\mathbf{N} = \{N_1, N_2, \ldots, N_S\}$.

The function $g_{ij}(\mathbf{N})$ models prey–predator relationships, and is called *predator functional response* (PFR). It is zero for pairs of species not connected by a predator–prey relationship. If species i is a predator and species j is its prey, g_{ij} is positive and represents the rate of prey consumption per unit of predator biomass. The sign is negative if species i is a prey and j is its predator. We assume in this case $g_{ij}(\mathbf{N})N_i = -g_{ji}(\mathbf{N})N_j/\eta$. The term $\eta \leqslant 1$ is the efficiency of conversion of prey biomass into predator biomass. In the present paper we set $\eta = 1$, in order to simplify formulae. In the companion paper the factor η will play a more important role, and it will be explicitly indicated.

Several different mathematical forms of the PFR have been proposed and discussed in the biological literature. We study here two cases: (i) prey dependent PFR linear in prey density, i.e. $g_{ij}(\mathbf{N}) = \gamma_{ij}N_j$; (ii) ratio dependent PFR, i.e. g_{ij} is a function of the ratio between prey and predator density (Arditi and Ginzburg, 1989).

The matrix β_{ij} models competition as a linear reduction in growth rates.[1] All its elements are nonnegative, and the diagonal elements β_{ii} are different from zero. These intraspecific competition terms play an essential role in allowing coexistence. Since competition for prey is already represented through the terms g_{ij} and the dynamics of prey species, the terms β_{ij} stand for competition for resources not explicitly included in the model. Such terms naturally arise from "integrating out" some trophic links in a community. The term $\alpha_i > 0$ accounts both for the death rate and for the energy consumption necessary for the activity of species i.

Eq. (1) are complemented with the condition that species below a critical density N_c get extinct. This condition takes into account that species are composed of discrete entities and also mimics the effect of demographic stochasticity.

We represent explicitly a single external resource, interpreted as abiotic and considered as an additional "species" $N_0(t)$ (Caldarelli et al., 1998; Bastolla et al., 2001). Its dynamics is chosen in such a way that species feeding on it feel an indirect competition effect. The qualitative behavior of the model does not depend on the detailed dynamics of the abiotic resource, as far as competition in the first trophic level is properly represented. The external resource introduces a new scale of density R. The dimensionless quantity $R/N_c \gg 1$ is an important control parameter in the system.

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[1] This linear model can be understood as the linearized version, around an equilibrium point, of a more general model, as far as equilibrium properties are captured in the linearized representation.

3. One-layer competition and productivity distribution

In this section, we reformulate results showing that the coexistence of several competing species tends to equalize their net productivity: the more coexisting species, the more similar their productivities should be (Chesson, 1994, 2000; Lässig et al., 2001; Kokkoris et al., 2002). This is done here imposing that the S competing species coexist at a fixed point of population dynamics, with all densities positive and larger than the threshold for extinction, N_c. We adopt a simple mean-field approximation of the competition matrix, which will be relaxed in the next section.

The condition derived in this way is qualitatively equivalent to a condition derived through the more general requirement of invasibility (Armstrong and McGehee, 1980; Chesson, 1994, 2000). Moreover, modeling competition through explicit interaction terms or implicitly, through the dynamics of the common resources, leads to the same condition.

3.1. Direct competition: mean-field approximation

Our study of competition starts from the simplest model

$$\frac{1}{N_i}\frac{dN_i}{dt} = P_i - \sum_j \beta_{ij}N_j. \tag{2}$$

The quantity P_i is assumed to be independent of species density, and represents the intrinsic growth rate of species i in the absence of competition.

We assume that the competition matrix β_{ij} is symmetric and all its elements are nonnegative. We further assume for convenience that the matrix is positive definite. It can be proven that these hypothesis hold if the competition terms arise in an effective way through the dynamics of underlying resources. The stability properties of the fixed point $N_i^* = \sum_k (\beta)_{ik}^{-1} P_k$ are governed by the community matrix (May, 1974), which in the present case is $A_{ij} = -N_i^* \beta_{ij}$. For positive definite competition matrices, positivity of all the N_i implies that the community matrix is negative definite, thus the system is locally stable. Furthermore, under these conditions, it is possible to construct a Ljapunov function (MacArthur and Levins, 1964; May, 1974), which guarantees that the equilibrium point is globally stable as well. Thus, we can ignore coexistence along periodic as well as chaotic orbits.

We parameterize the competition matrix as

$$\beta_{ij} = \sqrt{\beta_{ii}\beta_{jj}}\,\rho_{ij}, \tag{3}$$

where $\rho_{ij} \in [0, 1]$ is a dimensionless quantity that we call *ecological overlap* (or niche overlap) and describes the similarity in the use of resources between species i and j. One has clearly $\rho_{ii} = 1$.

The parameters β_{ii} can be absorbed introducing the rescaled variables $n_i = (\beta_{ii})^{1/2}N_i$, $p_i = (\beta_{ii})^{-1/2}P_i$. The variables p_i^2 have dimensions of biomass per area per time, the same dimensions of productivity. By analogy, and as a shortening, we call the p_i productivities instead of rescaled growth rates, but they should not be mistaken for productivities measured in field studies. In terms of the new variables, the fixed point equations have the form

$$p_i = \sum_j \rho_{ij} n_j. \tag{4}$$

We start by considering a mean field approximation of the competition matrix, addressing the general case in the next section. The mean-field approximation consists in assuming that all non-diagonal elements are equal: $\rho_{ii} \equiv 1$, $\rho_{ij} \equiv \rho_0$ for $i \neq j$,[2] such that the solution of the fixed point equations reads

$$n_i^* = \frac{1}{(1-\rho_0)}\left(p_i - \frac{\langle p \rangle}{1 + (1-\rho_0)/\rho_0 S}\right), \tag{5}$$

where $\langle \rangle$ indicates the average over the S species in the community. All equilibrium densities are positive and above the threshold n_c if and only if

$$\frac{\langle p \rangle - p_i}{\langle p \rangle} \leqslant \frac{1 - n_c/\langle n \rangle}{1 + S\rho_0/(1-\rho_0)}. \tag{6}$$

For $n_c = 0$, this result is equivalent to the condition derived by Chesson (1994) imposing invasibility of the system.

The above condition only affects explicitly the p_i smaller than the average, but it is easy to see that it implies a condition on the variance of the productivity distribution. In fact, multiplying both sides by the quantity $(1 - (p_i - \langle p \rangle)/\langle p \rangle)$, which is always positive if the variance of the distribution is small enough, and averaging over all species, we find

$$\frac{\langle p^2 \rangle - \langle p \rangle^2}{\langle p \rangle^2} \leqslant \frac{(1-\rho_0)}{S\rho_0 + (1-\rho_0)}\left(1 - \frac{n_c}{\langle n \rangle}\right). \tag{7}$$

In other words, the coexistence condition requires that all p_i are very close to the average value when the number of species S is large. The maximal negative difference from the average is of order $1/S$ and the standard deviation is of order $1/\sqrt{S}$. Notice that, if the mean overlap ρ_0 equals unity, all p_i must be identical. This result corresponds to the formulation of the theorem of competitive exclusion in this framework.

For a resource rich system where the average reduced density $\langle n \rangle$ is well above the extinction threshold, the quantity $S_0 = (1-\rho_0)/\rho_0$ defines an intrinsic scale of biodiversity at which the productivity distribution gets

pretty narrow. For a much larger number of species S, the average reduced density $\langle n \rangle = \langle p \rangle/(1 + (S-1)\rho_0) \propto \langle p \rangle/(1 + S/S_0)$ is close to the extinction threshold, thus the r.h.s. of Eq. (6) becomes very small and the condition of coexistence becomes rather stringent. Therefore, the effect of positive n_c on biodiversity is only important for very diverse ecosystems.

3.2. Resource mediated competition, prey dependent PFR

We now consider S basal species feeding on a single external resource N_0 with a linear, prey dependent PFR: $g_{ij}(\{N_k\}) = \gamma_j N_j$. Competition is induced through the dynamics of the common resource N_0 and through the limiting factors not explicitly considered in the model. The population dynamics equations are

$$\frac{1}{N_i}\frac{dN_i}{dt} = \gamma_i N_0 - \sum_j \beta_{ij} N_j - \alpha_i,$$

$$\frac{1}{N_0}\frac{dN_0}{dt} = R\beta_0 - \beta_0 N_0 - \sum_{i=1}^{S} \gamma_i N_i. \tag{8}$$

Different equations for N_0 give qualitatively similar results, as far as N_0 is consumed by all the competing species. We consider the fixed point equations and substitute for N_0, finding

$$p_i - \sum_j \left(\frac{\gamma_i'\gamma_j'}{\beta_0} + \rho_{ij}\right)n_j = 0, \tag{9}$$

where we have defined the rescaled variables $\gamma_i' = \gamma_i/\sqrt{\beta_{ii}}$, $\alpha_i' = \alpha_i/\sqrt{\beta_{ii}}$, $p_i = \gamma_i' R - \alpha_i'$ and $n_i = N_i\sqrt{\beta_{ii}}$. The fixed point equations are thus equivalent to the equations obtained by considering direct competition, with an effective competition matrix that is symmetric and positive definite if β_{ij} is such.

We now adopt the mean-field approximation of the previous section, $\rho_{ii} \equiv 1$, $\rho_{ij} = \rho_0 < 1$ ($i \neq j$). The approximation is applied only to the matrix ρ_{ij}, since the other part of the competition matrix depends on the productivity vector, nevertheless the result turns out to be equivalent to the previous one. Substituting $\gamma_i' = (p_i + \alpha')/R$ in Eq. (9), we get

$$(1-\rho_0)n_i = p_i(1 - S\langle n \rangle a) - \alpha_i S\langle n \rangle a - \rho_0 S\langle n \rangle, \tag{10}$$

where $a = \langle \gamma' n \rangle/\langle n \rangle \beta_0 R$. We then neglect the dependence of a on $\langle n \rangle$ and solve for this variable. Rearranging the various terms, we find again that the coexistence of S species is only possible if the minimal productivity differs from the average at most in an amount $(1-\rho)/\rho S$:

$$\frac{p_i - \langle p \rangle}{\langle p \rangle} - \frac{a\langle \alpha' \rangle}{a\langle \alpha' \rangle + \rho_0 + (1-\rho_0)/S}\frac{\alpha_i' - \langle \alpha' \rangle}{\langle \alpha' \rangle}$$

$$\leqslant \frac{1 - n_c/\langle n \rangle}{1 + S\rho/(1-\rho)}, \tag{11}$$

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[2] In the context of May and MacArthur's theory of competition, this hypothesis is realized when the niche space has many dimensions (May and MacArthur, 1972).

where the effective competition overlap ρ is defined as

$$\rho = \frac{\rho_0 + a\langle\alpha'\rangle}{1 + a\langle\alpha'\rangle} \leqslant 1. \tag{12}$$

This coincides with Eq. (6) in the limit $a\langle\alpha'\rangle = \langle\alpha'\rangle\langle\gamma'n\rangle/\langle n\rangle\beta_0 R \to 0$, in which resources are not limiting. In the opposite limit the condition on minus the energy consumption rate $-\alpha_i'$ becomes more demanding than the condition on the p_is, and ρ tends to one. Notice that the competition overlap ρ is different from zero even if the explicit competition overlap ρ_0 vanishes.

3.3. Resource mediated competition, ratio dependent PFR

We now assume that the PFR depends on the ratio between the density of the prey and the density of its predators (Arditi and Ginzburg, 1989) as

$$g_{i0}(\mathbf{N}) = \frac{b_0 c_i N_0}{b_0 N_0 + \sum_{p \in P(0)} c_p N_p}. \tag{13}$$

(see also Schreiber and Gutierrez, 1998; Solé et al., 2000; Drossel et al., 2001). In this expression species "0" is the prey and the sum in the denominator runs over its predators, represented as the set $P(0)$. In the case of just one predator, Eq. (13) can be seen as a Holling type III PFR (Holling, 1959), where the prey density at which the functional response saturates is proportional to the predator's density. Notice that, unlike prey dependent PFR, the ratio dependent PFR does not contain any externally specified biomass scale. For this reason, it is in some sense simpler than prey dependent PFR (Bastolla et al., 2001). We do not aim at discussing which form of the PFR is most suitable to explain observational data (Abrams and Ginzburg, 2000), but just use it as a second example of population dynamics where, aside from ratio dependence, competition for preys is explicitly represented through the sum over predators in the denominator. Since competition is now explicitly represented, we do not need an additional equation for the external resource N_0 and we assume that it renews rapidly enough such that its density remains constant. The dynamical equations have now the form

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{bc_i N_0}{bN_0 + \sum_j c_j N_j} - \alpha_i - \sum_j \beta_{ij}N_j,$$

$$N_0(t) \equiv R. \tag{14}$$

To simplify formulae, we use the rescaled variables $c_i' = c_i/\sqrt{\beta_{ii}}$, $n_i = N_i\sqrt{\beta_{ii}}$ and apply the mean-field approximation to the matrix β_{ij}. The solution of the fixed point equations is then

$$n_i^* = \langle n\rangle + \frac{1}{(1-\rho_0)}\frac{c_i' - \langle c'\rangle}{1 + Sa\langle n\rangle}, \tag{15}$$

where now $a = \langle c'n\rangle/\langle n\rangle bR$. Further, we consider the case of a productive system where the variation in the α_is can be neglected. The condition that all species are viable yields

$$\frac{\langle c'\rangle - c_i'}{\langle c'\rangle} \leqslant \frac{1 - n_c/\langle n\rangle}{1 + S\rho/(1-\rho)}, \tag{16}$$

where

$$\rho = \frac{\rho_0 + \langle\alpha'\rangle/\beta S\langle n\rangle}{1 + \langle\alpha'\rangle/\beta S\langle n\rangle} \tag{17}$$

is the effective competition coefficient and the product $S\langle n\rangle$ can be obtained solving a second-order equation, whose root remains finite in the limit $S \to \infty$.

Eqs. (6), (11), and (16) are equivalent coexistence conditions for three different population dynamics models. They all show the quantitative dependence between the distribution of productivities and biodiversity. Qualitatively identical coexistence conditions were obtained through the invasibility criteria, i.e. imposing that an invading species (with very low density) has a positive growth rate (Chesson, 2000).

4. One layer competition without mean-field

In this section, we analyse the coexistence condition without relying on the mean field approximation of the competition matrix. Our starting point is the fixed point equations (4), where rescaled variables are used. To simplify the presentation, most calculations are reported in Appendix A. Here we only show and discuss the final results.

We will use the spectral representation of the matrix ρ_{ij}, which we assume to be symmetric and positive definite. Therefore, all of its eigenvalues λ_α are real and positive, and its S eigenvectors $\mathbf{u}^\alpha$ form an orthonormal system. In graph theory (Bollobás, 1998) the matrix ρ_{ij} is called the adjacency matrix. Its maximal eigenvalue is defined by the property $\lambda_1\sum_i v_i^2 \geqslant \sum_{ij}\rho_{ij}v_iv_j$ for every vector $\mathbf{v}$. The equality holds if and only if $\mathbf{v}$ is proportional to the principal eigenvector $\mathbf{u}^1$. It holds that $\lambda_1 \geqslant \sum_{ij}\rho_{ij}/S$, so that the main eigenvalue is expected to be proportional to the number of species S. Moreover, all components of the principal eigenvector either have the same sign (we can choose it arbitrarily to be the positive sign) or are zero. We will assume that the graph cannot be separated in disconnected components. If this is not the case, the analysis can be applied separately to each disconnected component. This hypothesis implies that all components of the principal eigenvector are strictly positive: $u_i^1 > 0$. We call the principal eigenvector of the competition matrix the *competition load*.

It is useful to define the average of the $S-1$ eigenvalues excluding the principal one, which we will

denote with the symbol $1 - \rho_0$:

$$1 - \rho_0 \equiv \frac{1}{S-1} \sum_{\alpha=2}^{S} \lambda_\alpha. \tag{18}$$

It follows from the condition on the trace of the matrix ρ_{ij} that $\sum_\alpha \lambda_\alpha = S$, so the principal eigenvalue λ_1 can be expressed as

$$\lambda_1 = S\rho_0 + (1 - \rho_0). \tag{19}$$

We now use for simplicity the notation $v^\alpha \equiv \sum_j v_j u_j^\alpha$ for the projection of a vector $\mathbf{v}$ along the αth eigenvector, $\mathbf{u}^\alpha$. We show in Appendix A that the coexistence condition (6) can be written, for a general competition matrix, as

$$\frac{\sum_i p_i^2 - (p^1)^2}{(p^1)^2} \leqslant \frac{\lambda_2}{S\rho_0 + (1 - \rho_0)} \left(1 - \frac{n_c}{\langle n \rangle}\right), \tag{20}$$

where λ_2 is the second largest eigenvalue, which is of order one.

If the matrix ρ_{ij} has the mean field form, Eq. (20) is identical to Eq. (7). In fact, in the mean field case, it holds that $\lambda_\alpha = (1 - \rho_0)$ for $\alpha \geqslant 2$. Moreover, in this symmetric system the principal eigenvector is uniform, $u_i^1 \equiv 1/\sqrt{S}$, so that $p^1 = \sqrt{S}\langle p \rangle$, yielding Eq. (7).

Eq. (20) tells us that the productivity vector, $\mathbf{p}$, has to be almost parallel to the competition vector $\mathbf{u}^1$ in order to allow coexistence of all species: species with larger competition component u_i^1 need a comparatively larger productivity to survive. The angle between the productivity vector and the competition vector has to become narrower as competition becomes stronger, until only a perfect coincidence guarantees the survival of all species. The strength of competition increases with the overlap parameter $1 - \lambda_2$, with the ratio $n_c/\langle n \rangle$, and with the largest eigenvalue $\lambda_1 \approx S\rho_0$. Therefore, competition becomes more severe as the number of species increases, unless the competition matrix is sparse. Since the resources on which the S species feed are finite, we expect on ecological grounds that the strength of the competition increases as more species are packed in the ecosystem. This can be shown in some mechanistic models of competition, in which the matrix ρ_{ij} is derived from the underlying dynamics of the resources.

5. Competitive coexistence in a food web

We now turn to the more general case of an L-levels food web. After integrating the upper and lower levels, the effective equation for the fixed point density of species at a given level has the familiar form of a competition equation, and displays the same qualitative behavior discussed for the case of the single level.

As in our previous work (Lässig et al., 2001), we assume a hierarchical trophic organization, so that species at level l feed only on species at level $l - 1$ and compete only with species at their same level. Species at level L are top predators. Level zero can be interpreted either as basal species or as abiotic resources described by an effective equation. The dynamical equations, using linear, prey dependent PFR, read

$$\frac{1}{N_i^{(l)}} \frac{\mathrm{d}N_i^{(l)}}{\mathrm{d}t} = \sum_j \gamma_{ij}^{(l)} N_j^{(l-1)} - \alpha_i^{(l)}$$
$$- \sum_j \beta_{ij}^{(l)} N_j^{(l)} - \sum_j \gamma_{ij}^{(l+1)} N_j^{(l+1)}, \tag{21}$$

where the superindex stands for the level where the species belongs. The matrix $\gamma_{ij}^{(l)}$ represents predation from level l to level $l - 1$. It vanishes identically for $l = 0$ and $l = L + 1$. The parameters $\alpha_i^{(l)}$ stand for energy consumption and death rates of species at level l for $l \geqslant 1$, whereas $-\alpha_i^{(0)}$ is the fictitious growth rate of the resource at level zero. The direct competition for species at level l is represented through the matrix $\beta_{ij}^{(l)}$. As above, we assume that it is symmetric and positive definite.

We now consider the fixed point equations. For every level l, we solve for the densities of species at different levels $l' \neq l$ and substitute, thus getting fixed point equations for species at level l with the form of effective competition equations with a symmetric competition matrix:

$$\sum_j C_{ij}^{(l)} N_j^{(l)} = P_i^{(l)}. \tag{22}$$

Three different integration schemes yield different equations of the same form (22). In the scheme described in Appendix B, densities at levels $l' < l$ are recursively solved starting from level zero, and densities at levels $l' > l$ are recursively solved starting from the maximum level L. Levels above and below l (predators and preys) contribute both to the competition matrix and to the productivity vector. Therefore, as is known, competition can be induced not only through common preys, but also through common predators.

In a second possible scheme, levels above l only contribute to $\mathbf{P}^{(l)}$ as an effective energy consumption term, whereas levels below l contribute both to the competition matrix and to the productivity vector as a growth term. Finally, in the third scheme, levels above l contribute both to the effective competition and to the productivity vector, whereas species at levels below l only contribute to the productivity. In all three cases, the effective equations for species at level l have the form (2) of effective competition equations, where the competition matrix and the productivity vector depend on the properties of species at the other levels.

The result of the previous section implies that also for a structured food web the effective productivity vector

at level l must form a narrow angle with the principal eigenvector of the effective competition matrix.

6. Environmental variability and biodiversity

The coexistence conditions derived above yield a natural scale for assessing the degree of biodiversity of an ecosystem.[3] Ecosystems with $S \ll (1 - \rho)/\rho$ are *loosely packed*. They impose mild conditions on the productivity distribution, and can easily incorporate new species. Ecosystems with $S \gg (1 - \rho)/\rho$ are *tightly packed*. There, the productivity distribution is subject to strict constraints and incorporation of new species is very difficult. Which ecological mechanisms distinguish between the two kinds of situations? On the one hand, as we will discuss in a next paper, the immigration and speciation rates play a key role in smoothing the effects of condition (6) and allowing a large number of species into the system. On the other hand, an important role in determining biodiversity is played by environmental fluctuations (Hutchinson, 1961; Chesson, 2003a).

The growth rates considered in the previous models are subject in real systems to environmental fluctuations, such as for instance, variation in rain levels, temperature and daily light, or forest fires for plant communities, natural obstacles to the movement of animal species, or fluctuations in the number of interacting populations also affected by the environmental noise. Some of these variables fluctuate over time-scales much shorter than the characteristic time-scales of population dynamics. We thus interpret the growth rates p_is as time averaged quantities with superimposed fast fluctuations due to environmental variability. These preclude that the productivities take identical values, even for populations with identical ecological properties.

To take into account these fast environmental fluctuations, we assume that they tend to broaden the productivity distribution so that there is a minimum width given by the equation

$$\frac{\langle p \rangle - p_{\min}}{\langle p \rangle} \geqslant \Delta \left(1 - \frac{1}{S} \right). \tag{23}$$

The factor $1 - 1/S$ ensures that the condition (23) is satisfied for $S = 1$, when $p_{\min}$ and $\langle p \rangle$ coincide. The term $0 < \Delta \leqslant 1$ is an effective measure of environmental variability. For $\Delta = 0$ the condition (23) is always satisfied, while for $\Delta = 1$ it imposes a very small $p_{\min}$ (recall the p_i are positive quantities). Values of $\Delta > 1$ cannot be realized in the large S limit.

[3]This scale is relevant in ecosystems where $\langle N \rangle \gg N_c$, otherwise biodiversity is controlled by the threshold density. We are assuming here that our ecosystem is large enough so that the condition $\langle N \rangle \gg N_c$ holds where the number of species is of the order $(1 - \rho)/\rho$ at which competition effects are important.

Combining Eq. (23) with the coexistence condition (6), we get a limit to the maximal biodiversity that the ecosystem can host. In fact, Eq. (6) requires that the productivity distribution gets narrower as biodiversity increases, but at some point the largest difference tolerated becomes of the order of the minimal difference compatible with the actual environmental variability. The maximal biodiversity is a function of the competition overlap ρ, of the environmental variability Δ, and of the ratio between the average biomass and the threshold for extinction, $n_c/\langle n \rangle$, and is given by the inequality

$$\frac{1 - n_c/\langle n \rangle}{1 + S\rho/(1 - \rho)} \geqslant \Delta \left(1 - \frac{1}{S} \right), \tag{24}$$

leading to a second-order inequality that can be simplified for large S as

$$S \leqslant 1 + \left(\frac{1 - \rho}{\rho} \right) \left(\frac{1 - \Delta - n_c/\langle n \rangle}{\Delta} \right). \tag{25}$$

For large competitive overlap ρ close to unity or large variability $\Delta \simeq 1$, only one species can survive in the long run. If both the overlap and the variability are small, on the other hand, the maximal number of species can be rather large. Only in case of small variability the ecosystem can be tightly packed.

7. Discussion

In this work, we have considered simple models of competition, either represented as explicit terms in the population dynamics equations or effectively introduced through the dynamics of common prey and predator species. We have focused our attention on the fixed points of population dynamics, imposing the condition that all species at equilibrium have positive densities. For the simplest model of competition, this condition ensures that the fixed point is both locally and globally stable, but for more complex situations this represents an oversimplification. We will consider in the companion paper systems far from equilibrium, and argue that a suitable modification of the coexistence condition derived at the fixed point remains generally valid.

We first analysed coexistence at the fixed point, adopting a mean-field approximation of the competition matrix. This approximation is expected to hold when there is a main nutrient on which all species are dependent, or when the niche space has many dimensions.

Within the mean-field approximation, coexistence of S species competing with each other implies a condition on the distribution of their rescaled growth rates, $p_i = P_i/\sqrt{\beta_{ii}}$, where β_{ii} is the inverse of the carrying capacity: the width of the distribution has to shrink with increasing number of species S, competition overlap ρ or ratio $N_c/\langle N \rangle$ of the minimal viable density to the

average density. Notice that, if the carrying capacities vary from one species to another, for instance depending on body size, this conclusion does not apply to growth rates prior to rescaling.

This coexistence condition is equivalent to the one obtained by Chesson (1994, 2000) by imposing the requirement of invasibility, which demonstrates its robustness. We found formally identical coexistence conditions in models with explicit competition terms and in models where competition is induced by the dynamics of shared resources, within a single trophic layer and within a whole structured food web.

The mean-field approximation is not appropriate to describe more complex competition matrices, for instance when there is a continuum of resources distributed along one dimension (May and MacArthur, 1972), or when species can be grouped according to their ecological similarity. We have therefore generalized the coexistence condition beyond mean-field competition matrices. In the general case, an important role is played by the principal eigenvector of the competition matrix, which we named the competition load. The angle between the vector of competition loads and the vector of rescaled growth rates has to be narrower for stronger competition, i.e. for increasing average competition overlap and number of species. This generalizes the condition on the variance of the distribution of rescaled growth rates to the case of a generic matrix.

The coexistence condition Eq. (7), stating that the variance of the rescaled growth rates must decrease as $1/S$ due to competition, is reminiscent of May's theorem, according to which the coexistence of S species randomly interacting requires that the variance of their interactions vanishes as $1/S$ (May, 1974). In fact, May's theorem was derived imposing local stability of the fixed point of population dynamics and, for the simplest models of competition, the condition that all densities are positive at the fixed point also implies local stability. The condition for the coexistence of species whose rescaled growth rate lies below the average is stricter: they must differ from the average at most by an amount of the order of $1/S$, which is smaller than that imposed by the condition on the variance. This appears more demanding than the condition in May's theorem, probably because here all species are in competition with each other instead of being randomly interacting.

The coexistence condition that we described does not limit biodiversity, as long as the angle between rescaled growth rates and competition loads can be made arbitrarily small. However, environmental fluctuations, due to biological or abiotic processes with time-scales shorter than those of population dynamics, necessarily limit the possibility to fine tune ecological parameters in order to accommodate a larger biodiversity. We include environmental variations in our competition model in an effective way, as a force broadening the distribution of rescaled growth rates. Considering this new ingredient sets a limit on the maximal biodiversity that a system of competing species can host. In the companion paper, we will combine this limitation to "horizontal" biodiversity imposed by competition, with either dissipation of energy or growth of perturbations in the "vertical" direction along the food chain.

Environmental changes characterized by longer time scales, as seasonal changes or the storage effect, have not been included in our analysis, although they certainly affect coexistence conditions. Interestingly, in some cases the adaptive responses of species to these environmental fluctuations with time scale comparable to that of population dynamics are predicted to enhance species coexistence (Chesson, 2003a,b). This contrasts with the prediction presented here that a fast fluctuating environment would set a limit on biodiversity. It would be therefore quite desirable to set up a general theory of how environmental noise on different time-scales modulates biodiversity.

Acknowledgements

Appendix A. Coexistence condition for a generic matrix

Our starting point is Eq. (4), $p_i = \sum_j \rho_{ij} n_j$, and we want to demonstrate the coexistence condition (20) using the spectral properties of the competition matrix ρ_{ij}. For simplicity of notation we shall indicate with a superscript α the component of a vector in the direction of the αth eigenvector of the matrix ρ_{ij}, $n^\alpha = \sum_j n_j u_j^\alpha$. λ_α denotes the corresponding eigenvalue. Using this notation, Eq. (4) can be written in the eigenvector basis as $p^\alpha = \lambda_\alpha n^\alpha$, from where we get the equilibrium biomasses

$$n_i = \sum_{\alpha=1}^{S} \frac{p^\alpha u_i^\alpha}{\lambda_\alpha} \geq n_c. \qquad (26)$$

We now bring to the r.h.s. the contribution of the principal eigenvector u_i^1 and multiply both sides times the quantity $[(p_i - p^1 u_i^1)/p^1 - u_i^1]$, which, as we will demonstrate at the end, is always negative if the system

size is large enough. We get

$$\sum_{\alpha=2}^{S} \frac{p^{\alpha} u_i^{\alpha}}{\lambda_{\alpha}} \left(\frac{p_i - p^1 u_i^1}{p^1 u_i^1} - 1 \right)$$
$$\leqslant \left(n_c - \frac{p^1 u_i^1}{\lambda_1} \right) \left(\frac{p_i - p^1 u_i^1}{p^1 u_i^1} - 1 \right). \quad (27)$$

Summing over i, exploiting the orthonormality of the eigenvectors, and rearranging the factors, we obtain

$$\sum_{\alpha=2}^{S} \frac{(p^{\alpha})^2}{\lambda_{\alpha}} \leqslant \frac{(p^1)^2}{\lambda_1} - n_c(2p^1 \langle u^1 \rangle - \langle p \rangle). \quad (28)$$

Here brackets denote average over the S species. It holds $\langle p \rangle = \sum_{\alpha} p^{\alpha} \langle u^{\alpha} \rangle$. Neglecting, just for the sake of simplifying the final formula, the contribution of the eigenvectors with $\alpha \geqslant 2$ to the mean productivity, which is small since the components p^{α} and the mean eigenvectors $\langle u^{\alpha} \rangle$ are much smaller than the corresponding quantities for the principal eigenvector, we get

$$\frac{\sum_{\alpha=2}^{S} (p^{\alpha})^2 / \lambda_{\alpha}}{(p^1)^2} \leqslant \frac{1}{\lambda_1} \left(1 - \frac{n_c}{\langle n \rangle} \right). \quad (29)$$

Noticing that λ_2 is the largest of all eigenvalues with $\alpha \geqslant 2$, and that $\sum_{\alpha=2}^{S} (p^{\alpha})^2 = \sum_{i=1}^{S} p_i^2 - (p^1)^2$, and substituting the expression for λ_1, we finally get Eq. (20):

$$\frac{\sum_i p_i^2 - (p^1)^2}{(p^1)^2} \leqslant \frac{\lambda_2}{S\rho_0 + (1 - \rho_0)} \left(1 - \frac{n_c}{\langle n \rangle} \right). \quad (30)$$

This expression demonstrates our previous statement that the quantity $(p_i - p^1 u_i^1)/p^1 u^1$ is always smaller than one if system size is large enough, which is the property that we have used for deducing the above formulae.

Appendix B. Effective competition in a food web

Starting from the food web equations (21), we want to obtain effective fixed point equations for level l in the form (22). First, we write the fixed point equations in matrix notation:

$$(\gamma^{(l)})\mathbf{N}^{(l-1)} - \alpha^{(l)} - (\beta^{(l)})\mathbf{N}^{(l)} - (\gamma^{(l+1)})^T \mathbf{N}^{(l+1)} = 0. \quad (31)$$

Bold face symbols represent column vectors, while the other symbols represent matrices. An upper T indicates transposition of a matrix. The boundary conditions are $\gamma^{(L+1)} = 0$ (the top level L has no predators) and a formally identical equation with constant growth rate for the renewable abiotic resources at level 0:

$$\gamma^{(0)} R - (\gamma^{(1)})^T \mathbf{N}^{(1)} = \beta^{(0)} N^{(0)}. \quad (32)$$

We now focus on an intermediate level l. Species below level l can be integrated out solving for their equilibrium densities starting from level 0 upwards. Species above level l can be integrated out similarly, starting from the maximum level L. Both kinds of

species contribute to the effective competition matrix $C^{(l)}$ and effective productivity vector $\mathbf{P}^{(l)}$ of Eq. (22). The recursive equations to obtain these quantities are

$$C^{(l)} = (\gamma^{(l)})(M^{(l-1)})^{-1}(\gamma^{(l)})^T + \beta^{(l)}$$
$$+ (\gamma^{(l+1)})^T (\tilde{M}^{(l+1)})^{-1}(\gamma^{(l+1)}), \quad (33)$$

$$\mathbf{P}^{(l)} = (\gamma^{(l)})(M^{(l-1)})^{-1}\mathbf{Q}^{(l-1)} - \alpha^{(l)}$$
$$+ (\gamma^{(l+1)})^T (\tilde{M}^{(l+1)})^{-1}\tilde{\mathbf{Q}}^{(l+1)}. \quad (34)$$

Quantities with the tilde are recursively obtained from the upper levels, starting from level L:

$$\tilde{M}^{(l)} = \beta^{(l)} + (\gamma^{(l+1)})^T (\tilde{M}^{(l+1)})^{-1}(\gamma^{(l+1)}), \quad (35)$$

$$\tilde{\mathbf{Q}}^{(l)} = -\alpha^{(l)} + (\gamma^{(l+1)})^T (\tilde{M}^{(l+1)})^{-1}\tilde{\mathbf{Q}}^{(l+1)}. \quad (36)$$

The boundary condition is $(\tilde{M}^{(L)}) = \beta^{(L)}$, $\tilde{\mathbf{Q}}^{(L)} = -\alpha^{(L)}$. Quantities without the tilde are similarly obtained starting the recursion from level zero:

$$M^{(l)} = (\gamma^{(l)})(M^{(l-1)})^{-1}(\gamma^{(l)})^T + \beta^{(l)}, \quad (37)$$

$$\mathbf{Q}^{(l)} = (\gamma^{(l)})(M^{(l-1)})^{-1}\mathbf{Q}^{(l-1)} - \alpha^{(l)}. \quad (38)$$

The boundary conditions are in this case $(M^{(0)}) = \beta^{(0)}$ and $\mathbf{Q}^{(0)} = \gamma^{(0)} R$.

The effective competition matrix $C_{ij}^{(l)}$ is positive defined if all of the β and γ matrices are so.

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