

## Biodiversity in model ecosystems, II: species assembly and food web structure

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### Abstract

This is the second of two papers dedicated to the relationship between population models of competition and biodiversity. Here, we consider species assembly models where the population dynamics is kept far from fixed points through the continuous introduction of new species, and generalize to such models the coexistence condition derived for systems at the fixed point. The ecological overlap between species and shared preys, that we define here, provides a quantitative measure of the effective interspecies competition and of the trophic network topology. We obtain distributions of the overlap from simulations of a new model based both on immigration and speciation, and show that they are in good agreement with those measured for three large natural food webs. As discussed in the first paper, rapid environmental fluctuations, interacting with the condition for coexistence of competing species, limit the maximal biodiversity that a trophic level can host. This horizontal limitation to biodiversity is here combined with either dissipation of energy or growth of fluctuations, which in our model limit the length of food webs in the vertical direction. These ingredients yield an effective model of food webs that produce a biodiversity profile with a maximum at an intermediate trophic level, in agreement with field studies.

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### 1. Introduction

In the first paper of this suite, we have considered coexistence at a fixed point of population dynamics. This is justified for some of the simplest population models, where it can be shown that the fixed point is both locally and globally stable, such that the asymptotic dynamics converge to it. However, the dynamics of more complex ecological models wander on periodic or chaotic attractors. Even when the trajectory would tend asymptotically to a fixed point, the time necessary to reach it may be very large, so that disturbances such as immigrations, speciations or environmental variations

can take place before the system effectively attains equilibrium.

In the present paper, we consider the coexistence of competing species in the framework of models of species assembly, in which the ecological community is continuously perturbed through immigration, speciation and extinction event that build up its biodiversity (MacArthur and Wilson, 1967). We argue that the relationship between the competition matrix and the productivity distribution derived for static ecosystems can be generalized in the slow assembly regime, in which new species arrive at the ecosystems over time-scales much larger than those of population dynamics.

In a previous work (Bastolla et al., 2001), we have modeled an insular ecosystem characterized by a constant immigration rate and by extinction produced

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by population dynamics. After a transient time, the model ecosystem reaches a statistically stationary state where the extinction rate and the immigration rate balance, as predicted by the equilibrium theory of island biogeography (MacArthur and Wilson, 1967).

We have shown that the model yields in a natural way to species area relationships in qualitative agreement with field observations. Despite the fact that space is not represented explicitly in our model, we represent the area  $A$  of the island as an effective parameter, influencing both the immigration rate  $I$  and the threshold density  $N_c$  at which extinction takes place. As pointed out by MacArthur and Wilson (1967), the immigration rate is expected to increase with the size of the island. We assume that  $I = I_0 + kA^{1/2}$ . The case  $I_0 = 0$  corresponds to an immigration rate proportional to the perimeter. We use it to model immigrations from a continent to an archipelago. The case  $k = 0$  in which the immigration rate does not depend on area is used to describe immigration coming from nearby islands in the same archipelago, since in this case, the immigration rate is expected to depend mainly on the distance from the closest island. The other parameter depending on area is the threshold density  $N_c$ . We assume that the number of individuals in the population is relevant for extinction, so the critical density is inversely proportional to the area, or  $N_c \propto 1/A$ .

Under the above assumptions, the model reproduces a broad range of observed Species Area Relationships. The logarithmic Species Area Law, observed for the central islands of the Solomon archipelago (Diamond and Mayr, 1976), is reproduced under the hypothesis that the immigration flux is independent of area,  $I = I_0$ . The power law  $S \propto A^{0.54}$ , observed by Adler (1992) for the number of bird species on archipelagos versus their area, is reproduced assuming that  $I \propto \sqrt{A}$ , a plausible assumption for archipelagos.

In this paper, we generalize our previous model considering speciation events beside immigrations. We show that simulations of the new model reproduce qualitatively the distributions of the ecological overlap measured for three large natural food webs, a quantity that we define here and that allows the characterization of the food web structure and of the interspecific competition.

We then define and study an effective model for the biodiversity profile in food webs. In the previous paper, we have shown that environmental fluctuations on time-scales much shorter than those of population dynamics, combined with a coexistence condition for competing species, limit the maximal biodiversity the system can host. This role of rapid environmental fluctuations complements the result that fluctuations on slower time-scales can promote biodiversity through mechanisms such as the storage effect and the nonlinearities in the environmental response (Chesson, 2000).

Our effective model of biodiversity consists of the condition on the maximum allowed biodiversity at each trophic level, combined with equations obtained from population dynamics for the across level variation of the competition overlap, the biomass density and the fluctuations in rescaled growth rates. This effective model produces a profile of biodiversity versus trophic level presenting a maximum at intermediate level, in qualitative agreement with field observations (Cohen et al., 1990). A mean field study of the model was preliminarily reported in Lässig et al. (2001).

## 2. Species assembly through immigration and speciation

Here, we generalize our previous species assembly model (Bastolla et al., 2001), including speciation events in it. Some features of this new model have been described in Bastolla et al. (2002). For a recent review of several models of food web structure, dynamics and assembly, see Drossel and McKane (2003).

In our model, biodiversity arises from a balance between species origination through immigration and speciation events, and extinction of species resulting from population dynamics. The ecosystem is continuously maintained far from the fixed point of population dynamics through species origination events that occur regularly, at time intervals equal to  $T_{mig}$ . Eventually, a state of statistical equilibrium is reached where the average properties do not vary with time.

As described in the companion paper, population dynamics equations have the form of generalized Lotka–Volterra equations,

$$\frac{1}{n_i^{(l)}} \frac{dn_i^{(l)}}{dt} = \eta \sum_j \tilde{\gamma}_{ij}^{(l)} n_j^{(l-1)} - \tilde{\alpha}_i^{(l)} - \sum_j \rho_{ij}^{(l)} n_j^{(l)} - \sum_j \tilde{\gamma}_{ij}^{(l+1)} n_j^{(l+1)}, \quad (1)$$

where the superindex stands for the level where the species belongs. The dynamical variables  $n_i$  are rescaled population densities,  $n_i = \sqrt{\beta_{ii}} N_i$ , where  $N_i$  is the population density and  $\beta_{ii}$ , defined in the first paper, is proportional to the inverse of the carrying capacity,  $\beta_{ii} = \alpha_i / N_i^*$ . The coefficient  $\eta < 1$  is the efficiency of conversion of prey biomass into predator biomass, and it is assumed to be independent of level. The coefficients of the Predator Functional Response,  $\tilde{\gamma}_{ij}^{(l)}$ , and the death rates  $\tilde{\alpha}_i^{(l)}$  have been rescaled dividing them by  $\sqrt{\beta_{ii}}$ .

Using rescaled variables, the competition overlaps  $\rho_{ij}$  are dimensionless parameters with  $\rho_{ii} \equiv 1$ . We assume that  $\rho_{ij}$  for  $i \neq j$  is proportional to the predation overlap  $q_{ij}$ ,  $\rho_{ij} = \lambda q_{ij}$ , where  $q_{ij}$  is defined as the fraction of common preys shared by species  $i$  and  $j$ . Introducing a predation matrix  $\pi_{ik}$ , such that  $\pi_{ik}$  equals one if  $k$  is a

prey for  $i$ , and zero otherwise, the predation overlap is formally defined as

$$q_{ij} = \frac{\sum_k \pi_{ik} \pi_{jk}}{\sqrt{\sum_k \pi_{ik} \sum_k \pi_{jk}}} \quad (2)$$

This definition guarantees that  $q_{ij}$  is one if and only if species  $i$  and  $j$  share exactly the same preys. Since competition for common preys is already implicitly represented through the prey dynamics, the coefficients  $\rho_{ij}$  model competition for resources not explicitly included in the ecosystem. The reason for the proportionality between the non-diagonal elements of the competition matrix  $\rho_{ij}$  and the predation overlap  $q_{ij}$  is that we expect that species sharing more prey are more closely related ecologically, so that their overall requirements are more similar.

The population dynamics equations are complemented by a threshold density  $n_c = \sqrt{\beta_{ii} N_c}$  below which a species is considered extinct and is eliminated from the system. The community is maintained by a number of external resources, which are represented as extra populations  $N_i$  with intrinsic growth rate  $\gamma_{i0} R$  and predators only. The dimensionless parameter  $R/N_c$ , ratio between the carrying capacity determined by the external resources and the density threshold for extinction, plays an important role in controlling the biodiversity in the model.

The introduction of new species is modeled as follows. First, we choose at random one of the species present  $i$  which acts as “mother species” for the new one, with label  $i' = i + 1$  (old species with  $j > i$  are renumbered accordingly). Three parameters define the similarity between  $i$  and  $i'$  regarding their preys and predators. Each link of the mother is (i) either deleted from the daughter species with probability  $p_{delete}$ , (ii) or copied with probability  $p_{copy}$ , (iii) or redirected to another species with the complementary probability  $1 - p_{delete} - p_{copy}$ . After this is done, with probability  $p_{new}$  a new link is added, such that  $i'$  gets a new prey or a new predator.

The links that are copied mutate their strength with respect to that of the mother species according to the stochastic rule  $\gamma_{i'j} = (\gamma_{ij} + \delta \gamma_{max} \xi) / (1 + \delta)$ , where  $\xi \in [1, -1]$  is a randomly chosen number,  $\gamma_{max}$  is the maximal allowed value of the connection strengths, and  $\delta = 0.05$ . For newly extracted links, the connection strength is chosen uniformly in the interval  $[0, \gamma_{max}]$ . New preys are extracted only in the set of species with  $j < i'$ , while new predators are extracted in the set of species with  $j > i'$ . This condition is imposed in analogy with the cascade model (Cohen et al., 1990), and prevents the formation of feeding loops.

In the limit  $p_{copy} \rightarrow 0$ , the introduction of new species proceeds through pure immigration, as in our earlier model (Bastolla et al., 2001). When  $p_{copy} \rightarrow 1$  the

daughter species are most similar to their mothers, apart from deletions and additions of links and small mutations in the link strength. This mimics a system where biodiversity is maintained by speciation rather than immigration events.

### 3. Productivity distribution in species assembly models

In our simulations, population dynamics never reaches a fixed point between two immigration events: the system contains species with a positive growth rate as well as species with a negative growth rate, which are slowly driven towards extinction. These can be either unsuccessful immigrants or resident species outcompeted by newly arrived ones. As in our earlier model (Bastolla et al., 2001), the system reaches a stationary state where the average biodiversity does not vary with time. This stationary biodiversity increases as a power law of the immigration rate  $1/T_{mig}$  and as the logarithm of the external resources  $R/N_c$ .

To get analytical insight on this species assembly model, we note that in the stationary state the typical time required for the extinction of one species must coincide with the time between arrivals of new species,  $T_{mig}$ . Species that get extinct more rapidly than this do not contribute to the stationary biodiversity. This implies the following condition for species that belong to the instantaneous transient community:

$$\frac{1}{n_i} \frac{dn_i}{dt} \geq - \frac{1}{T_{mig}} \quad (3)$$

This equation generalizes the fixed point equations that we studied in the first paper, which correspond to the limit  $T_{mig} \rightarrow \infty$ . We can apply this condition to one-layer communities or structured food webs, as we already did in the case of fixed point coexistence. Applying a mean field approximation to the effective competition matrix, the condition of coexistence in transient communities can be generalized to

$$\frac{\langle p \rangle - p_i}{\langle p \rangle} \leq \frac{1 - n_c / \langle n \rangle}{1 + S\rho / (1 - \rho)} + \frac{1}{\langle p \rangle T_{mig}} \quad (4)$$

where  $p_i$  is the effective rescaled growth rate arising both from preys and predators of species  $i$ , after eliminating the effective competition with species with shared preys (see the companion paper). Here and elsewhere, angular brackets denote averaging over species at the same trophic level.

If the quantity  $\langle p \rangle T_{mig}$  is large, i.e. for slow immigration rates, the system can get close to the fixed point, and the above equation modifies only slightly the result for static systems ( $T_{mig} \rightarrow \infty$ ) presented in the previous paper, which is equivalent to a previous result by Chesson (1994). Therefore, in the slow immigration

regime the variance of the distribution of the  $p_i$  decreases as  $1/S$ , as for systems at the fixed point.

For more frequent immigration (smaller  $\langle p \rangle T_{mig}$ ), the variance of the productivity distribution increases. Thus it becomes easier to pack a larger number of species in the ecosystem, in agreement with the results of our simulations, where the stationary biodiversity increases as a power law of the immigration rate  $1/T_{mig}$  (Bastolla et al., 2001), and consistently with the predictions of the theory of island biogeography (MacArthur and Wilson, 1967).

We show in Fig. 1 the productivity distribution for the first trophic level of the simulated ecosystem. As expected, the distribution is narrow, and its variance decreases with the number of species  $S_1$  (see Inset), the inverse of the variance being well fitted with a linear function of  $S_1$ , as predicted by Eq. (4).

In addition to the dependence of biodiversity on the immigration rate, the number of species at the stationary state also increases as the fraction of speciation events gets larger (growing  $p_{copy}$ ). Also this behavior is easy to rationalize through Eq. (4). In fact, new species originated through speciation have a higher probability of remaining in the ecosystem, since all of their ecological parameters are similar to those of their mother species, which have been already selected through the ecological dynamics. Thus, a larger fraction of speciation events implies a higher effective rate of appearance of new species.

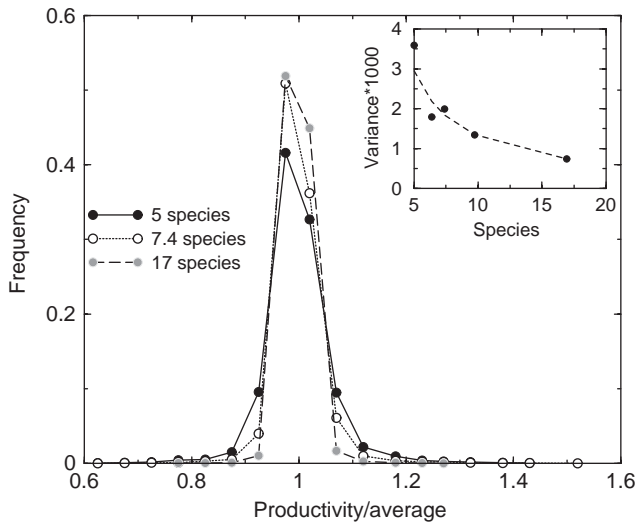


Fig. 1. Distribution of the normalized productivity  $p_i / \langle p \rangle$  at the first trophic level. Inset: variance of the productivity distribution versus the number of species. The dashed line is the best fit of the variance with  $V \simeq (a + S/S_0)^{-1}$ . In this simulation, the ecological parameters have values  $\alpha_i = 1$ , for all  $i$ ,  $\beta = 1$ ,  $\gamma_{max} = 2$ ,  $R = 10^3$ ,  $N_c = 1$  for the three curves. The parameters for the speciation process differ in each case: for  $S_1 = 5$  we used  $p_{copy} = 0$ ,  $p_{delete} = 0.2$ , and  $p_{new} = 0.2$ ; for  $S_1 = 7.4$  parameters are  $p_{copy} = 0.4$ ,  $p_{delete} = 0.6$ , and  $p_{new} = 0.2$ ; finally, for  $S_1 = 17$  we had  $p_{copy} = 0.8$ ,  $p_{delete} = 0$ , and  $p_{new} = 0.2$ .

#### 4. Ecological overlap in real and model ecosystems

To characterize the structure of food webs, we have studied the distribution of the ecological overlap, defined in Eq. (2). The overlap distribution is a property that bears the fingerprint of the topology of the species network. In the framework of species assembly models, this distribution is influenced both by the process of species origination, either through immigration or through speciation, and by the extinctions driven by population dynamics. Furthermore, the overlap distribution can be measured in real food webs for which sufficiently detailed information is available, and in this way it allows to compare the results of our model with empirical observations.

We show in Fig. 2 the overlap distribution obtained from simulations of our model for non-basal species above the first trophic level. To better compare different ecosystems, the delta function at overlap equal to zero is eliminated and the continuous part of the distribution is normalized to one. The peaks that one sees arise from the discreteness of the system: the number of prey per species is a small integer number. Peaks at high overlap are produced by speciation events, while peaks at small overlap are due to distantly related species.

In the inset of Fig. 2, we notice that the fraction of species with overlap equal to zero increases with the number of possible preys at trophic level one,  $S_1$ . This is expected on the ground of the following simple calculation, based on a mean-field argument. We assume that all species at level two have  $k < S_1$  preys at level one, and that these preys are chosen at random. Neglecting terms of higher order in  $1/S_1$ , we can

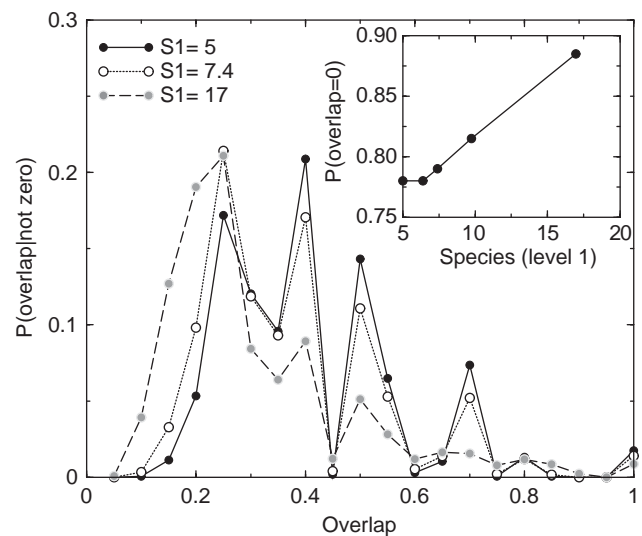


Fig. 2. Overlap distribution for species at level larger than one in the model ecosystem. A delta function in zero has been removed. Inset: the probability that the overlap is exactly zero increases with the number of possible preys at level one. All parameters are as in Fig. 1.

compute the average predation overlap as  $\bar{q} = k/S_1$ . Under these assumptions, the distribution of the overlap is expected to be Poissonian, so that the expected fraction of pairs with zero overlap is given by  $P\{q = 0\} = \exp(-k/S_1)$ , which is an increasing function of  $S_1$ .

We have considered three of the largest food webs analysed in field studies: a freshwater marine interface (Ythan estuary, see Huxham et al., 1996), a lake (Little Rock, see Martinez, 1991), and a community associated to a single plant (Silwood Park, see Memmott et al., 2000). They have been studied in enough detail to allow a statistical characterization of their network structure (Montoya and Solé, 2002). For these three large food webs, we have calculated the overlap between all pairs of predators as defined in Eq. (2), and we have obtained the overlap distribution and the average overlap,  $\bar{q}$ .

The Ythan estuary food web, described in Huxham et al. (1996), is formed by  $S = 134$  species and contains 592 links from predators to preys. Of these species, 42 are metazoan parasites contributing to a total of 52 top species. Only 5 species are basal. The average number of preys per predator is 6.4 and the number of predators per prey 4.6. The average overlap for this food web is  $\bar{q} = 0.102$ .

Silwood park network is constituted by trophic interactions between herbivores, parasitoids, predators, and pathogens associated with a single plant, the broom *Cytisus scoparius* (Memmott et al., 2000). This web is formed by 154 species, of which 66 are parasitoids, and 60 predators. There are 117 top species and a total of 370 links: the average number of preys per predator is 2.4, the number of predators per prey is 10, and the average overlap between predators is  $\bar{q} = 0.134$ .

Finally, the study of Little Rock lake (Martinez, 1991) reports a total of 182 consumer, producer, and decomposer taxa. This is a highly lumped food web: in Little Rock, 63% of “species” correspond to genera-level nodes. This lack of resolution is probably responsible for systematic statistical deviations, as the fact that some “species” have a very large number of predators or preys. The network has 2430 links from predators to preys, 63 basal species and a single top species. The average number of preys per predator is 20.4, and the number of predators per prey is 13.4. The average overlap between predators is  $\bar{q} = 0.195$ .

In Fig. 3 we represent the distributions of overlaps  $P(q_{ij})$  for the three natural food webs described above. For the sake of comparison, we also show a distribution obtained in our simulations, with the parameters shown in the figure caption. The comparison shows that our model is able to reproduce overlap distributions in good agreement with field observations, at least in some range of its space of parameters. The probability that the overlap is zero is also in reasonable agreement with field data: its value is 0.7 in the Ythan and Little Rock food webs, and 0.8 in the Silwood food web. These values are

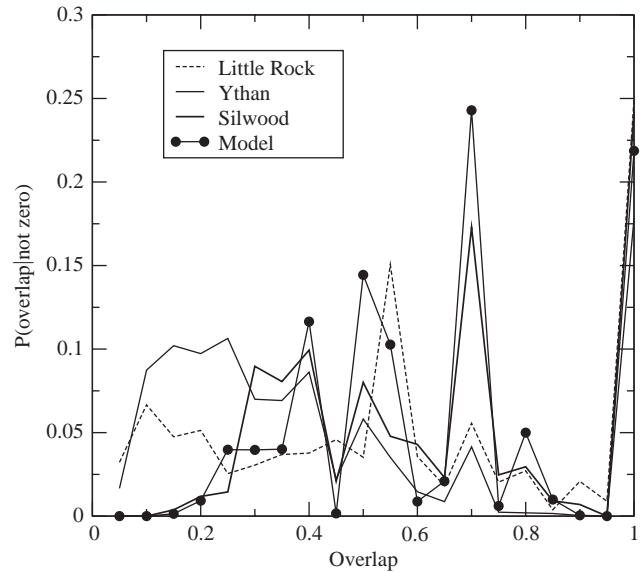


Fig. 3. Overlap distribution for natural ecosystems. We have calculated the overlap distribution for the three large food webs cited in the text. The dashed line was obtained from a simulation of the model ecosystem with parameters  $p_{copy} = 0.72$ ,  $p_{delete} = 0.2$ , and  $p_{add} = 0.3$ . The other model parameters are as in Figs. 1 and 2.

quite comparable with those shown in the inset of Fig. 2 for the model ecosystems.

### 5. Environmental fluctuations and biodiversity profiles in food webs

We have shown in the companion paper that the combination of a general condition for coexistence of  $S_l$  species competing at trophic level  $l$  and an effective model of short time-scale environmental fluctuations yields the following limit on biodiversity:

$$S_l \leq 1 + \left( \frac{1 - \rho_l}{\rho_l} \right) \left( \frac{1 - \Delta_l - n_c / \langle n_l \rangle}{\Delta_l} \right), \quad (5)$$

where  $\rho_l$  is the typical competition overlap between a pair of distinct species at level  $l$ ,  $\langle n_l \rangle$  is the average rescaled density of the  $S_l$  competing species,  $n_c$  is the threshold density below which extinction takes place, and  $\Delta_l$  represents the minimal width of the productivity distribution at level  $l$  compatible with environmental fluctuations. The variability  $\Delta_l$  is considered level dependent, since fluctuations in productivity propagate along the trophic chain and are expected to increase at higher levels (see below). This is important for characterizing the variation of biodiversity with trophic levels and the length of food webs.

In Lässig et al. (2001) we have used Eq. (5), with level-independent  $\Delta_l \equiv \Delta$ , in order to get an analytical insight on the biodiversity of a hierarchical trophic web. We assumed that the biodiversity at level  $l$  is the maximal

one allowed by Eq. (5). The validity of this assumption depends on the species assembly process, and we think that it is plausible for mature food webs, where there was enough time for filling all ecological niches.

Using the above assumption, we can define an effective model for the biodiversity profile across the trophic levels of hierarchical food webs. Being extremely simplified, this model presents the advantage that it can be solved analytically through some further approximation, and that the main processes responsible for the biodiversity profile can be individuated rather clearly. The model predicts under general conditions that biodiversity has a maximum at an intermediate trophic level, as observed in real food webs.

For fixed biodiversities  $S_l$ , we can calculate the average rescaled densities  $\langle n^{(l)} \rangle$  through a mean field approximation of the generalized Lotka–Volterra equations describing the population dynamics on the trophic web:

$$\langle n^{(l)} \rangle \approx \frac{c\eta\tilde{\gamma}^{(l)}\langle n^{(l-1)} \rangle - c\frac{S_{l+1}}{S_l}\tilde{\gamma}^{(l+1)}\langle n^{(l+1)} \rangle - \tilde{\alpha}^{(l)}}{1 - \rho_l + S_l\rho_l}, \quad (6)$$

where  $c \geq 1$  is the average number of preys per predator, which is assumed to be independent of level,  $cS_{l+1}/S_l$  is the resulting average number of predators per prey,  $\eta < 1$  is the efficiency of conversion of prey biomass into predator biomass, also assumed to be independent of level,  $\tilde{\gamma}^{(l)}$  is the average rescaled rate at which preys at level  $l - 1$  are consumed for unit of predator at level  $l$ , and  $\tilde{\alpha}^{(l)}$  is the average death rate or energy consumption rate of species at level  $l$ . In the calculations, for simplicity, the two last quantities were assumed to be independent of  $l$ .

Inserting the densities  $\langle n^{(l)} \rangle$  in Eq. (5), we obtain the maximum allowed biodiversities  $\{S_l\}$ . This procedure is applied iteratively, until convergence to a stable profile  $\langle n^{(l)} \rangle$  and  $\{S_l\}$  that solves simultaneously the maximum coexistence condition and the mean-field equations for the densities.

For all parameters sets we studied, the resulting  $\langle n^{(l)} \rangle$  decreases approximately as a negative exponential of  $l$ , as a result of metabolic energy dissipation along the food chain. In order to improve the analytical understanding of the model, we adopt in the following this phenomenological relationship, assuming that

$$\langle n^{(l)} \rangle \approx R \exp(-l/l_0). \quad (7)$$

Apart from the decrease across levels of the rescaled biomass density, the other effect that limits the length of the food web in this model is the propagation of the fluctuations along the chain, which determine an increase of the width of the productivity distribution as

$$\Delta_l \approx \Delta_0 \exp(l/l_\Delta). \quad (8)$$

A justification of this ansatz is provided in the next section.

To fully define the model, we still need an effective model for the variation of the overlap  $\rho_l$  across the level. For this purpose, we assume that each of the  $S_l$  species at level  $l$  is coupled to  $c$  species at the level below, provided there are more than  $c$  species at that level; otherwise it is coupled to all species:  $c_l = \min(c, S_{l-1})$ . We consider two different ways in which these connections are drawn, leading to two different models for the overlap:

1. The connections are drawn at random. In this case, the fraction of common links between two species at level  $l$  is  $q_l = c_l/S_{l-1}$ . We further assume that the competitive overlap  $\rho_l$  is proportional to the link overlap  $q_l$ :  $\rho_l = \lambda q_l$ , with  $\lambda \leq 1$ . We interpret  $\lambda$  as the fraction of limiting factors that are represented by the species at the level  $l - 1$ . We thus have

$$\rho_l = \lambda c_l/S_{l-1},$$

$$S_l = 1 + \left( \frac{S_{l-1}}{\lambda c_l} - 1 \right) \left( \frac{1 - \Delta_l - (N_c/R)e^{l/l_0}}{\Delta_l} \right). \quad (9)$$

2. In the second case, we consider that the  $S_l$  species are divided into  $S_l/\sigma_l$  clusters of size  $\sigma_l$ . Species in different clusters are not in competition. Species in the same cluster compete with the maximal possible overlap  $\rho = \lambda$ . We get

$$\sigma_l = 1 + \left( \frac{1}{\lambda} - 1 \right) \left( \frac{1 - \Delta_l - (N_c/R)e^{l/l_0}}{\Delta_l} \right),$$

$$S_l = S_{l-1}/c_l\sigma_l. \quad (10)$$

In both cases, at small  $l$  and for a broad range of parameters, biodiversity increases at low levels:  $S_2 > S_1$ .

At high levels, the second term in brackets on the r.h.s. of Eq. (10) becomes small and the biodiversity decreases with the level, either because  $n^{(l)}/N_c$  decreases with  $l$ , Eq. (7), or because the minimal width of the productivity distribution,  $\Delta_l$ , grows with  $l$ , Eq. (8). Thus, our model food webs present a maximum in the distribution of the biodiversity per level in a broad region of parameter space (Lässig et al., 2001). This result is consistent with studies of real food webs, where the maximum of biodiversity is attained at the second or third trophic level (Cohen et al., 1990).

Eventually, biodiversity is limited by either of the two mechanisms to just one species. This defines the maximum food web length in our model.

The qualitative description outlined above is supported by numerical computations of the full effective model, and by simulations of the species assembly model.

Summarizing, in the framework of this model the biodiversity profile is shaped by two very simple processes: horizontal (within level) competition, limiting

the maximum biodiversity at each trophic level, and vertical (across level) hardening of competition, either due to the propagation of fluctuations (the growth of  $\Delta_l$  with the level), or energy dissipation (the decrease of  $n_l$  with the level).

### 6. Propagation of perturbations along a food chain

Here, we justify the assumption that the minimal width of the distribution of rescaled growth rates increases for higher levels along a food web:  $\Delta_l \propto \exp(l/l_0)$ . This assumption was used in the previous section to yield a limitation on biodiversity at high levels, and ultimately to constrain the maximal length of food webs.

For simplicity, we consider a food chain with just one species per level. In this way, we do not have to consider the number of species at each level as an additional unknown parameter coupled to  $\Delta_l$  through Eq. (5). We start from the system of equations that determine the fixed point of a food chain with linear prey-dependent functional responses,

$$\eta\gamma_l n_{l-1} - \alpha_l - n_l - \gamma_{l+1} n_{l+1} = 0. \tag{11}$$

As usual, the level specific densities  $n_l$  and the parameters  $\gamma_l$  (coefficients of the functional response) and  $\alpha_l$  (death rate) have been rescaled so that the coefficient of the self-damping term equals one.

The equations can be solved iteratively starting from the lowest level in the form

$$n_l = p_l - \frac{\gamma_{l+1} n_{l+1}}{B_l}, \tag{12}$$

where the rescaled growth rates  $p_l$  and the rescaled self-damping terms  $B_l$  are recursively given by

$$p_l = \frac{p_{l-1} - \alpha_l / (\eta\gamma_l)}{\gamma_l / B_{l-1} + 1 / (\eta\gamma_l)}, \tag{13}$$

$$B_l = 1 + \frac{\eta\gamma_l^2}{B_{l-1}}. \tag{14}$$

We now consider a perturbation that changes the (fictitious) growth rate at level zero by a relative amount  $\Delta_0 = (p'_0 - p_0)/p_0$ . This perturbation propagates along the food chain, leading to relative changes in the growth rates equal to

$$\Delta_l = \frac{\Delta_{l-1}}{1 - \alpha_l / (\eta\gamma_l p_{l-1})} > \Delta_{l-1}. \tag{15}$$

This is larger than  $\Delta_{l-1}$  because all the factors in the denominator are strictly positive and, moreover,  $\eta$  is smaller than one. Since  $p_l$  decreases at higher levels, the factor  $1/(1 - \alpha_l / (\eta\gamma_l p_{l-1}))$  also increases with the level, so that  $\Delta_l$  increases even faster than exponentially with  $l$ . This rapid amplification of perturbations along the food chain justifies our expectation that the

distribution of rescaled growth rates becomes broader with the level.

### 7. Discussion

In this paper, we have generalized to transient ecological communities far from fixed points the coexistence conditions derived in the companion paper for systems at the fixed point. Also in the general case, species with rescaled growth rates much lower than average will disappear very rapidly and will not be observed.

For systems maintained out of equilibrium through immigration, the relevant time-scale is given by the inverse of the immigration rate. A non-zero ratio between the immigration rate and typical growth rates of the population dynamics,  $1/\langle p \rangle T_{mig}$ , makes it easier to fulfill the coexistence condition. This analytical result leads to the prediction that the biodiversity in the stationary state of the species assembly model increases with the immigration rate, as observed in the simulations.

Coupling the coexistence condition with the unavoidable fluctuations in productivity values (due to environmental noise with time-scale much smaller than that of population dynamics), we predicted in our previous paper that competition and fluctuations limit the maximum biodiversity that can be hosted in a trophic level. This result complements, but does not contradict the prediction that environmental fluctuations with a time-scale comparable to that of population dynamics enhance species coexistence (Chesson, 2003a,b). It would be desirable to develop a more general theory of the interaction between environmental fluctuations and population dynamics from which the two results can be derived.

The coexistence condition also depends on the typical competition overlap between species at the same trophic level. We have defined the competition overlap to be proportional to the predation overlap  $q_{ij}$ , defined through Eq. (2). The distribution of the overlap is a useful property for characterizing the structure of ecological networks. Our modified model of species assembly through immigration and speciation yields overlap distributions in good agreement with those obtained from three well-studied natural food webs: the Ythan estuary, the Little Rock lake, and the Silwood Park system.

These steps allowed us to define an effective model for the variation of biodiversity across the levels of a hierarchical food web. In our model, two main processes control biodiversity: competition, on the horizontal within-level direction; and modulation of competition, on the vertical across-level direction.

In the framework of the effective model, this last process controls the decay of the number of species across higher levels, and therefore the length of food webs, an issue that received a considerable attention in ecological literature (see for instance Post, 2002 for a recent review). Accommodating more competing species becomes harder at higher levels, because of two complementary mechanisms: the dissipation of metabolic energy across the food web, which make energetic constraints more difficult to fulfill, and the propagation of environmental perturbations across the food web, which makes it more difficult to finely tune ecological parameters in order to accommodate new species.

The first mechanism is reminiscent of the so-called productivity hypothesis for the length of food webs, which goes back almost 80 years (Elton, 1927). However, weak or no correlation was found between food chain length and primary productivity in field studies (Briand and Cohen, 1987; Post et al., 2000). These and other results suggest that resources limit the length of food chains below some threshold level, above which other factors come into play (Post, 2002).

The other mechanism proposed here, relating food chain length to the amplification of environmental perturbations across the chain, is a novel variant of the stability hypothesis that states that environmental disturbance limits the length of food webs (Menge and Sutherland, 1987). This hypothesis was originally grounded on the observation that the dynamical stability of model ecosystems decreases as chain length increases (Pimm and Lawton, 1977). However, the generality of this model result was questioned later (Sternler et al., 1997). The mechanism proposed here constitutes a new theoretical justification for the disturbance hypothesis, which is supported by some empirical evidence, but only indirectly (Post, 2002).

In addition, simulations of the species assembly model provide a third mechanism that may limit the length of food webs. In the simulations, longer food webs can be generated by increasing the immigration rate, which makes the coexistence condition more permissive and increases the overall biodiversity, therefore allowing more opportunities for dynamically generating longer networks. A positive relation between colonization and food chain length was also suggested in another model of species assembly (Holt, 1996). Assuming a relation between the size of the ecosystem and the immigration rate, the effect of the immigration rate may explain the observed positive correlation between food chain length and ecosystem size (Post, 2000), to date the strongest empirical determinant of food chain length found in field studies.

This work can be extended in several directions. The most important, in our opinion, would be to build a mechanistic model in which environmental fluctuations are explicitly modeled, instead of including them in an

effective way as we have done here. This might permit a more quantitative comparison between model results, parameters, relevant mechanisms, and variables operating in natural ecosystems.

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