

Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model

Alexandra Goudard^{1,2,*} and Michel Loreau^{3,†}

1. Biogéochimie et Ecologie des Milieux Continentaux, Unité Mixte de Recherche 7618, Ecole Normale Supérieure, 46 rue d'Ulm, F-75230 Paris cedex 05, France;

2. Université Pierre et Marie Curie, 4 place Jussieu, 75252 Paris cedex 05, France;

3. Department of Biology, McGill University, 1205 avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada

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ABSTRACT: Research into the relationship between biodiversity and ecosystem functioning has mainly focused on the effects of species diversity on ecosystem properties in plant communities and, more recently, in food webs. Although there is growing recognition of the significance of nontrophic interactions in ecology, these interactions are still poorly studied theoretically, and their impact on biodiversity and ecosystem functioning is largely unknown. Existing models of mutualism usually consider only one type of species interaction and do not satisfy mass balance constraints. Here, we present a model of an interaction web that includes both trophic and nontrophic interactions and that respects the principle of mass conservation. Nontrophic interactions are represented in the form of interaction modifications. We use this model to study the relationship between biodiversity and ecosystem properties that emerges from the assembly of entire interaction webs. We show that ecosystem properties such as biomass and production depend not only on species diversity but also on species interactions, in particular on the connectance and magnitude of nontrophic interactions, and that the nature, prevalence, and strength of species interactions in turn depend on species diversity. Nontrophic interactions alter the shape of the relationship between biodiversity and biomass and can profoundly influence ecosystem processes.

Keywords: biodiversity, ecosystem functioning, nontrophic interactions, interaction modifications, mass balance, model.

* E-mail: alexandra.goudard@ac-paris.fr.

† Corresponding author; e-mail: michel.loreau@mcgill.ca.

The relationship between biodiversity and ecosystem functioning has emerged as a central issue in ecology in the last decade. Human activities contribute to species extinction, and biodiversity loss can cause loss of ecological services (Pimm et al. 1995; Vitousek et al. 1997; Sala et al. 2000; Loreau et al. 2001, 2002; Kinzig et al. 2002; Hooper et al. 2005). Therefore, a better understanding of the effects of biodiversity on ecosystem properties is critically needed.

The relationship between biodiversity and ecosystem processes has mostly been studied experimentally and theoretically in plant communities. Theoretical models usually predict that primary productivity increases with plant species richness but saturates at high diversity (Tilman et al. 1997; Loreau 1998, 2000). Controlled experiments conducted in different localities (Hector et al. 1999; Spehn et al. 2005) or over several years (Tilman et al. 2001) often exhibit the predicted pattern. The positive effects of species diversity on ecosystem functioning have been explained by two main mechanisms (Tilman 1999; Loreau and Hector 2001): a complementarity effect, which emerges from facilitation or niche differentiation, and a selection effect arising from the dominance of species with particular traits. These models, which focus on a single trophic level, are based on niche theory and plant competition for a limiting nutrient. Food web models with several trophic levels, however, predict that plant biomass does not always increase with plant diversity and that changes in diversity can lead to complex changes in ecosystem functioning (Thébaud and Loreau 2003; Ives et al. 2005). Recent experiments (Jonsson and Malmqvist 2000; Downing and Leibold 2002; Duffy 2002; Paine 2002; Duffy et al. 2003, 2005) have showed that trophic interactions can indeed profoundly affect the relationship between biodiversity and ecosystem functioning.

Thus, the relationship between biodiversity and biomass or productivity has been mostly studied in plant communities or in food webs. The only form of direct species interaction considered in these studies is the trophic in-

teraction (exploitation competition for a shared resource is an indirect effect of the consumer-resource trophic interaction). Some experiments, however, suggest that nontrophic interactions, such as facilitation, may play an important role in ecosystem functioning (Mulder et al. 2001; Cardinale et al. 2002; Rixen and Mulder 2005). For instance, Rixen and Mulder (2005) showed that water retention increases with species diversity through increasing facilitation and leads to increased productivity in arctic tundra moss communities. Experiments suggest that different kinds of species interactions do not act in isolation from each other in nature but co-occur within the same community (Callaway and Walker 1997). Evidence for the importance of indirect interactions is also accumulating. Habitat modification is one type of indirect interaction that has been studied experimentally (Bertness et al. 1999; Mulder et al. 2001; Cardinale et al. 2002; Rixen and Mulder 2005). For instance, Bertness et al. (1999) have shown that algal canopy reduces physical stress such as temperature or water evaporation and thus has positive effects on organism recruitment, growth, and survival in rocky intertidal communities, but habitat modification by algal canopy can also have negative effects by increasing consumer pressure.

Although there is growing recognition of the significance of nontrophic interactions in communities and ecosystems, these interactions are still poorly studied theoretically, and we still know little about general patterns and mechanisms. Therefore, an important current challenge is to understand how nontrophic interactions affect the relationship between biodiversity and ecosystem functioning. More generally, there is an urgent need to include nontrophic interactions in ecological theory (Borer et al. 2002; Bruno et al. 2003). There are some models of mutualism (Goh 1979; Heithaus et al. 1980; Addicott 1981; Ringel et al. 1996; Holland et al. 2002), but these models are specific, as they consider only one kind of species interactions. We lack general models of interaction webs that include all types of direct species interactions (interference competition, mutualism, exploitation, commensalism, amensalism) as well as their indirect effects. Simple models of mutualism based on Lotka-Volterra equations also have the unrealistic property of leading to explosive systems because they do not respect the physical principle of mass conservation (Ringel et al. 1996). Mass balance is crucial for understanding the functional processes of natural ecosystems. Thus, it is necessary to construct interaction web models that satisfy mass balance constraints. Arditi et al. (2005) recently made a first step in that direction by adding interaction modifications to a food web model; they showed an increasing proportion of super-efficient systems as the magnitude of interaction modifications was increased. Here, we expand this approach to

study the structural and functional properties of interaction webs and hence the relationships between biodiversity and ecosystem properties that emerge in complex ecosystems.

We need theories and models to provide generalizations on the role of nontrophic interactions in ecosystem functioning. It is therefore necessary to construct the most general possible model of an ecosystem—a model of an interaction web that includes both trophic and nontrophic interactions and that respects the principle of mass conservation. Here, we present a theoretical model that meets this need. Despite its generality, our model is too complex to be analytically tractable. Therefore, we study it using numerical simulations that mimic a community assembly process. This allows us to investigate the relationship between biodiversity and ecosystem functioning under more realistic constraints than would an analytical equilibrium study of special cases, in agreement with Loreau et al.'s (2001) recommendation to study the relationship between biodiversity and ecosystem functioning with a dynamic approach. Using this assembly model, we study the relationship between biodiversity and ecosystem properties, such as the biomass and productivity of the various trophic levels, in an interaction web in comparison with a food web. This comparison allows us to examine the effects of nontrophic interactions on the biodiversity-ecosystem functioning relationship. Thus, our interaction web model provides a useful basis for reaching greater generality regarding the impact of species diversity and species interactions on the functional properties of complex ecosystems.

Model and Methods

The Interaction Web Model

The model is an extension of a model developed by Thébault and Loreau (2003) for a nutrient-limited ecosystem with three trophic levels containing an arbitrary number of plants, herbivores, and carnivores. Plants take up a limiting nutrient in their rhizosphere, thus creating species-specific resource depletion zones and allowing plant coexistence under some conditions (Loreau 1996, 1998). These species-specific resource depletion zones may be viewed as physical soil volumes, but they may also be viewed in a more abstract way as different niche spaces available to different species.

Here, we add nontrophic interactions to this food web to construct an interaction web model that satisfies mass balance constraints. Nontrophic interactions are included in the form of interaction modifications: each species can modify the trophic interaction between any two species.

The model is described by the following dynamic equations and figure 1:

$$\begin{aligned}
 \frac{dC_i}{dt} &= \sum_{j=1}^S q_C a_{C,H_j} \mu_{C,H_j} H_j C_i - u_{C_i} C_i, \\
 \frac{dH_i}{dt} &= \sum_{j=1}^S q_H a_{H,P_j} \mu_{H,P_j} P_j H_i \\
 &\quad - \sum_{j=1}^S a_{C,H_j} \mu_{C,H_j} C_j H_i - u_{H_i} H_i, \\
 \frac{dP_i}{dt} &= a_{P,L_i} \mu_{P,L_i} L_i P_i \\
 &\quad - \sum_{j=1}^S a_{H,P_j} \mu_{H,P_j} H_j P_i - u_{P_i} P_i, \\
 \frac{dL_i}{dt} &= \gamma \left(R \frac{V_i}{V_R} - L_i \right) - a_{P,L_i} \mu_{P,L_i} P_i L_i, \\
 \frac{dR}{dt} &= I - \lambda_R R - \sum_{i=1}^S \gamma \left(R \frac{V_i}{V_R} - L_i \right) \\
 &\quad + \sum_{i=1}^S (1 - \lambda_{P_i}) u_{P_i} P_i + \sum_{i=1}^S (1 - \lambda_{H_i}) u_{H_i} H_i \\
 &\quad + \sum_{i=1}^S (1 - \lambda_{C_i}) u_{C_i} C_i \\
 &\quad + \sum_{i=1}^S \sum_{j=1}^S (1 - q_C) a_{C,H_j} \mu_{C,H_j} H_j C_i \\
 &\quad + \sum_{i=1}^S \sum_{j=1}^S (1 - q_H) a_{H,P_j} \mu_{H,P_j} P_j H_i, \tag{1}
 \end{aligned}$$

where

$$\mu_{xy} = \sum_{e_z=1}^n m_{xyz} \log(1 + X_z) = \prod_{z=1}^n (1 + X_z)^{m_{xyz}}. \tag{2}$$

Here, S is the number of species per trophic level, $n = 3S$ is the total number of species, and P_i , H_i , and C_i are the nutrient stocks of plant, herbivore, and carnivore species i , respectively.

We assume the stoichiometric composition of each species to be constant; hence, its nutrient stock is proportional to its biomass. Parameter a_{xy} is a per capita potential consumption rate, that is, the intensity of the trophic interaction between predator species x and prey species y in the absence of interaction modification ($a_{xy} \geq 0$). Parameter a_{P,L_i} is the nutrient uptake rate of plant species i . Each herbivore or carnivore species x may be more or less spe-

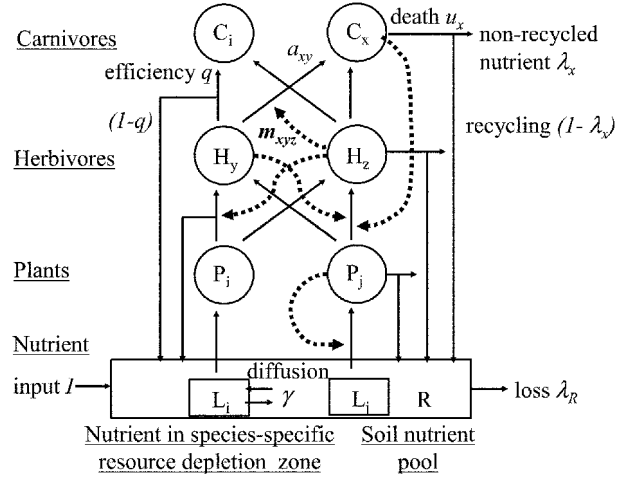


Figure 1: Interaction web model. Solid arrows represent nutrient flows. For clarity of the figure, flows of nonassimilated nutrient returned to the soil nutrient pool during consumption by carnivores and herbivores are represented only on the left trophic chain, and flows of nutrient either recycled or lost from the ecosystem following death are represented only on the right trophic chain. Dotted lines represent interaction modifications. Only five examples of interaction modifications are represented here for the sake of clarity. For instance, herbivore species H_z modifies the trophic interaction between herbivore species H_y and carnivore species C_x , with a magnitude of interaction modification of m_{xyz} . The modification of the nutrient flow between plant species P_j and its species-specific resource depletion zone L_j corresponds to intraspecific competition or facilitation.

cialist (if one of its potential consumption rates a_{xy} is much higher than the others) or generalist (if all its potential consumption rates a_{xy} are of similar magnitude), with a preference for certain prey species. The constants q_H and q_C are the conversion efficiencies of herbivores and carnivores, respectively (see app. A in the online edition of the *American Naturalist* for parameter values).

Nontrophic interactions are introduced into the model by adding nontrophic modifications of trophic interactions: each species z is allowed to modify the trophic interaction between species x and y with an effect that depends on both its biomass X_z and a magnitude of interaction modification of m_{xyz} (fig. 1). Parameter μ_{xy} is the nontrophic coefficient: it is the total nontrophic effect of all species of the community on the trophic interaction between species x and y . Thus, species x consumes species y with a realized consumption rate $a_{xy} \mu_{xy}$. The function that describes nontrophic effects (eq. [2]) was chosen such that it satisfies several conditions. First, it is a strictly increasing function of both the magnitude of interaction modification m_{xyz} and biomass X_z . Second, if either $m_{xyz} = 0$ or $X_z = 0$, then $(1 + X_z)^{m_{xyz}} = 1$, and species z does not affect the trophic interaction between species

x and y . Thus, in the absence of interaction modifications, $\mu_{xy} = 1$, and the realized consumption rate $a_{xy}\mu_{xy}$ is equal to its potential value a_{xy} . Third, the function for nontrophic effects is strictly positive, so that the sign of the realized consumption rate $a_{xy}\mu_{xy}$ does not change. The magnitude of interaction modification m_{xyz} can be positive or negative without changing the sign of $a_{xy}\mu_{xy}$. Whatever the nontrophic effects of other species, the nutrient flow between species x and y is never reversed. Fourth, while the magnitude of interaction modification m_{xyz} comes as the exponent of a power function to keep the function positive, we chose a linear dependence on biomass X_z : preliminary results showed that a power dependence on biomass is strongly destabilizing. A positive m_{xyz} leads to multiplication of the potential consumption rate a_{xy} by a factor $(1 + X_z)^{|m_{xyz}|}$, whereas a negative m_{xyz} leads to division of a_{xy} by this factor.

In the presence of interaction modifications, each species can affect any other species x by modifying one or several trophic interactions that involve species x and hence increasing or decreasing the population growth rate dX_x/dt of species x . In the absence of interaction modifications, the only direct species interaction is predation, and our model web reduces to a food web. When interaction modifications are added, each species can have a positive (facilitation), negative (inhibition), or null effect on the population growth rate of any other species, and thus all types of species interactions are possible (competition, mutualism, exploitation, commensalism, amensalism), including intraspecific (negative or positive) effects ($m_{xxx} \neq 0$ for species x). Our model web is then a full interaction web that includes both trophic and nontrophic interactions.

Our interaction web model respects the principle of mass conservation: a nontrophic interaction, such as mutualism or competition, does not affect the total quantity of matter in the ecosystem as a whole. Interaction modifications change the material flow between a resource and a consumer by multiplying it by some factor, but there is mass conservation overall.

The model also includes nutrient cycling. The constant μ_x is the loss or death rate of species x , and λ_x is the nonrecycled (lost) proportion of nutrient coming from species x . The variable R is the nutrient mass in the soil nutrient pool with volume V_R ; L_i is the nutrient mass in the set of species-specific resource depletion zones, with total volume V_p , of plants from species i . Nutrient is transported between species-specific resource depletion zones and the soil nutrient pool at a diffusion rate γ per unit time. In our simulations, γ was quite high ($\gamma = 10$) to allow rapid soil homogenization and strong indirect plant competition for the limiting nutrient. Parameter I is the

nutrient input in the soil nutrient pool per unit time, and λ_R is the rate of nutrient loss from the soil nutrient pool.

Community Assembly

We constrained our interaction web model as little as possible in order to explore its general properties. Accordingly, we randomly assigned the various biological parameters (potential consumption rates, intensities of interaction modifications, death rates, nonrecycled proportions of nutrient) to a regional pool of species from a uniform distribution within appropriate intervals and let the local ecosystem assemble spontaneously. The establishment of a species depends on both its intrinsic traits (parameter values) and its interactions with the other species already present in the ecosystem.

The model was simulated numerically using C++ programming, and numerical integration of the dynamic equations was performed with a Runge-Kutta method of order 4 and a time step of 0.01 during 1,000 iterations, that is, 100,000 time steps (100,000 numerical integrations). The local ecosystem results from an assembly process that involves species' successive introductions and eliminations. Species were introduced with a biomass equal to 0.01 that was subtracted from the soil nutrient pool, and they were considered extinct if their biomass was smaller than 0.005, in which case this biomass was returned to the soil nutrient pool. Species were picked at random from a regional species pool with species richness $n = 3S$ (S species at each trophic level) and introduced regularly to the community. Each successive introduction occurred after a constant period irrespective of whether a new equilibrium was reached (thus, if the introduction period was 100 time steps, there were 1,000 introduction events during a simulation).

Local species richness is the total number of species in the locally assembled ecosystem (to be distinguished from regional species richness). The total volume of the soil was kept constant irrespective of local species richness: $V_{\text{soil}} = V_R + \sum_{i=1}^S V_p$, where $V_i = 0$ if species i was not present in the community. Thus, when a plant species became extinct, the volume of its species-specific resource depletion zones was set to 0 and added to the volume of the soil nutrient pool. When a plant species was introduced, the volume of its species-specific resource depletion zones was created and subtracted from the volume of the soil nutrient pool. This volume allocation rule respects the conservation of total soil volume while at the same time allowing different plant species to occupy complementary resource depletion zones in the soil. Complementarity between plant species has both theoretical and empirical justifications (Loreau 1998; Loreau and Hector 2001). To be consistent, however, this allocation rule requires that the

total soil volume be greater than the sum of the volumes of the depletion zones of all possible plant species, which was the case in our simulations (app. A). Mass conservation was also satisfied upon extinction of a plant species by adding the nutrient stocks in its residual biomass and in its resource depletion zone to the soil nutrient pool and, conversely, upon introduction of a plant species by subtracting these nutrient stocks from the soil nutrient pool (app. B in the online edition of the *American Naturalist*).

Community and Ecosystem Properties

We examined the relationship between the structure and functioning of interaction webs and the impact of nontrophic interactions by analyzing the effects of regional species richness, nontrophic connectance, and maximal nontrophic magnitude (independent parameters of the regional species pool) on various properties of the local ecosystems, that is, local species richness, species richness at each trophic level, proportions of the various types of species effects and species interactions, interaction web connectance, total biomass (total biomass of all species in the local ecosystem), biomass of each trophic level, and production of each trophic level. When we varied regional species richness, we kept equal numbers of species (S) at all trophic levels in the regional species pool.

Food web connectance of the regional species pool was defined as the number of realized trophic interactions divided by the number of possible trophic interactions and was kept constant in all simulations. Its value was close to 1 because consumers were assumed to be more or less generalist, with potential consumption rates randomly drawn from a uniform distribution between 0 and 0.01 (and hence with a very small probability of being exactly 0). Note that our definition differs from the conventional definition of food web connectance because feeding links within trophic levels and between plants and carnivores were not allowed in our model.

Interaction modifications were assigned in two steps: (1) there was a certain probability that $m_{xyz} \neq 0$; (2) if $m_{xyz} \neq 0$, the magnitude of the interaction modification was chosen in a uniform distribution. We call the probability that $m_{xyz} \neq 0$ the nontrophic connectance of the regional species pool, which is the probability that a species modifies the trophic interaction between any two species:

$$\text{nontrophic connectance} = \frac{\text{number of realized interaction modifications}}{\text{number of possible interaction modifications}} \quad (3)$$

The number of possible interaction modifications in the

regional species pool is equal to the number of species multiplied by the number of possible trophic interactions between species at adjacent trophic levels in the pool, that is, $3S(S^2 + S^2 + S)$.

We also varied the range of values of the magnitude of interaction modification. Parameter m_{xyz} was randomly taken between a maximum value called “maximal nontrophic magnitude” and a symmetrical minimum equal to minus the maximal nontrophic magnitude. The maximal nontrophic magnitude was then allowed to take on different values. Thus, we explored the impacts of nontrophic interactions by manipulating both the nontrophic connectance and the maximal nontrophic magnitude of the regional species pool.

We analyzed the community and ecosystem properties in the local ecosystems that resulted from the assembly process. We measured the proportions of species effects (facilitation, inhibition, or no effect) and species interactions (mutualism, competition, exploitation, commensalism, amensalism, or neutral interaction) based on the sign of the net species effects. The net species effect E_{ig} (including trophic and nontrophic effects) of species g on species i was measured by the partial derivative of the growth rate dX_i/dt of species i with respect to the biomass X_g of species g :

$$E_{ig} = \frac{\partial(dX_i/dt)}{\partial X_g} \quad (4)$$

If $E_{ig} > 0$, the effect of species g on species i is a facilitation. If $E_{ig} < 0$, it is an inhibition. If $E_{ig} > 0$ and $E_{gi} > 0$, the interaction between species i and g is a mutualism. If $E_{ig} < 0$ and $E_{gi} < 0$, species i and g are in competition. If $E_{ig} > 0$ and $E_{gi} < 0$, the species interaction is an exploitation (including nontrophic forms of exploitation). If $E_{ig} = 0$ and $E_{gi} > 0$, it is a commensalism. If $E_{ig} = 0$ and $E_{gi} < 0$, it is an amensalism. Density-mediated indirect interactions (Abrams 1995), such as exploitative nutrient competition, do not enter into the calculation of E_{ig} . The species interactions thus defined are phenomenological net interactions, just as they are defined traditionally in ecology. A phenomenological rather than a mechanistic definition was necessary to account for the wide variety of trophic and nontrophic effects in a simple unified framework. This allowed us to investigate the effects of regional species richness, nontrophic connectance, and maximal nontrophic magnitude on the prevalence and strength of species effects and species interactions.

Interaction web connectance of the local community was measured by the proportion of nonneutral species interactions among all possible species interactions, that is, by the proportion of species interactions in which at

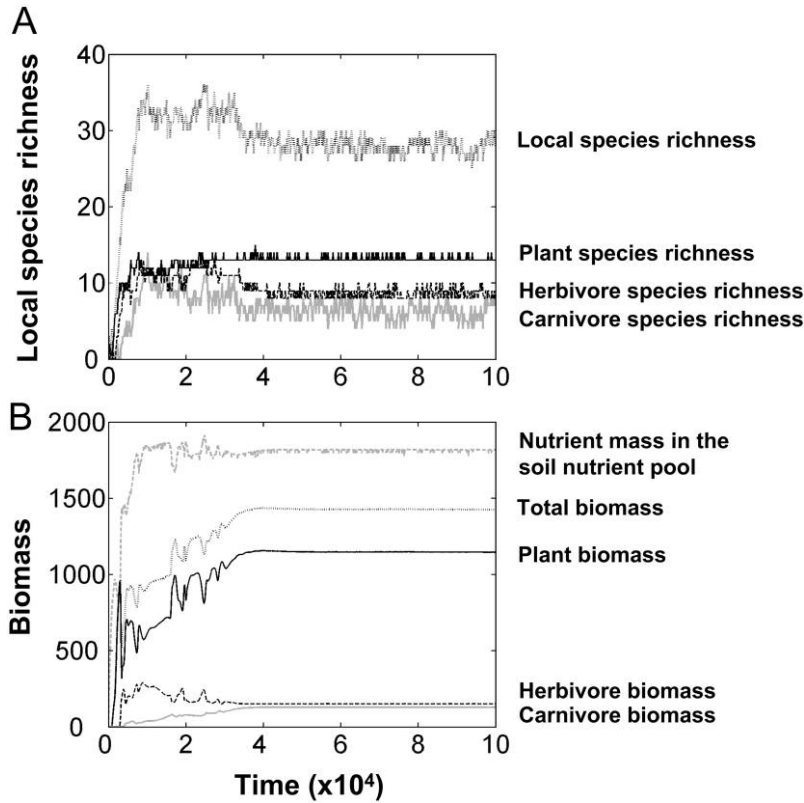


Figure 2: Temporal changes in local species richness (A) and biomass (B) during the ecosystem assembly process. Biomass and local species richness are shown for the community as a whole (black dotted lines), all plants (black solid lines), all herbivores (black dashed lines), and all carnivores (gray solid lines). The gray dashed line represents the nutrient mass in the soil nutrient pool. Regional species richness = 45, nontrophic connectance = 0.2, maximal nontrophic magnitude = 0.2.

least one of the two net species effects (E_{ig} or E_{gi}) is non-zero:

$$\begin{aligned} \text{interaction web connectance} &= \\ \frac{\text{number of nonneutral species interactions}}{\text{local species richness (local species richness - 1)/2}} \\ &= 1 - \text{proportion of neutral species interactions.} \end{aligned} \tag{5}$$

We call “mean value of facilitation” the mean value of all positive net species effects, and we call “mean value of inhibition” the mean value of all negative net species effects.

We calculated the proportions, mean values, and standard deviations of species effects and the proportions of species interactions both in the community as a whole and within each trophic level. We then considered only interspecific species effects and interactions without taking into account the effect of a species on itself (E_{ii}).

The production of each trophic level was measured by its nutrient inflow (nutrient mass per unit time):

$$\begin{aligned} \text{carnivore production} &= \sum_{i=1}^S \sum_{j=1}^S q_{C_i H_j} \mu_{C_i H_j} H_j C_i, \\ \text{herbivore production} &= \sum_{i=1}^S \sum_{j=1}^S q_{H_i P_j} \mu_{H_i P_j} P_j H_i, \tag{6} \\ \text{primary production} &= \sum_{i=1}^S a_{P_i L_i} \mu_{P_i L_i} L_i P_i. \end{aligned}$$

We measured all these community and ecosystem properties during the course of community assembly. After a transition phase, however, the ecosystem systematically reached a quasi-stationary regime (fig. 2), that is, a phase where aggregated variables such as local species richness and biomass showed small variations around a constant temporal mean value. Therefore, we compared the community and ecosystem properties in the quasi-stationary regime by calculating the temporal mean during the last

10% of the simulation iterations. For each value of regional species richness, nontrophic connectance, or maximal nontrophic magnitude, we performed eight simulations with different random compositions of the regional species pool, as is often done in experiments (Hooper and Vitousek 1997; Hector et al. 1999; Knops et al. 1999; Tilman et al. 2001), and we calculated the mean and standard deviation of the measured properties for these eight replicates. We present below figures for a relatively high regional species richness (45 species, i.e., 15 species per trophic level), but the results are qualitatively similar whatever the number of species. In the figures below that describe the effects of regional species richness, both nontrophic connectance and maximal nontrophic magnitude were set to 0.2.

Results

Local species richness and species richness at each trophic level in the quasi-stationary regime increased with regional species richness in both food webs and interaction webs (fig. 3A, 3B). Therefore, the results obtained as functions of regional species richness or local species richness were very similar.

Impact of Nontrophic Interactions and Species Richness on the Prevalence and Strength of Species Interactions

Diversity of Species Interactions in Interaction Webs. Nontrophic connectance has an important effect not only on ecosystem properties but also on the nature of species interactions. When nontrophic connectance increased, the proportion of 0 species effects decreased, while the pro-

portions of facilitation and inhibition increased up to a plateau (fig. 4A). In a food web, the only direct species interaction is exploitation between trophic levels (fig. 4B, when nontrophic connectance = 0, and fig. 4F). In an interaction web, the proportion of neutral interactions decreased to 0 as nontrophic connectance increased, and hence interaction web connectance increased to 100%. The proportions of commensalism and amensalism first increased and then decreased to 0 as nontrophic connectance increased, while the proportions of mutualism, competition, and exploitation increased as nontrophic connectance increased (fig. 4B). Thus, interaction modifications created nontrophic interactions between species (such as mutualism or competition).

Impact of Interaction Modifications on the Prevalence and Strength of Species Effects. As either nontrophic connectance (fig. 4A) or maximal nontrophic magnitude (fig. 4E) increased, the mean value of facilitation increased and the mean value of inhibition decreased; that is, the mean absolute values of species effects increased, and the standard deviation of species effects also increased. As maximal nontrophic magnitude increased, the proportion of 0 species effects first fluctuated and eventually increased (fig. 4E). Thus, both nontrophic connectance and maximal nontrophic magnitude had an impact on the prevalence, strength, and variability of species effects.

The increase in the mean value of species effects with nontrophic connectance is a consequence of the assumption that nontrophic effects act multiplicatively on consumption rates. Since the magnitude of interaction modification m_{xyz} is randomly taken from a uniform distribution, it has the same probability of being positive or

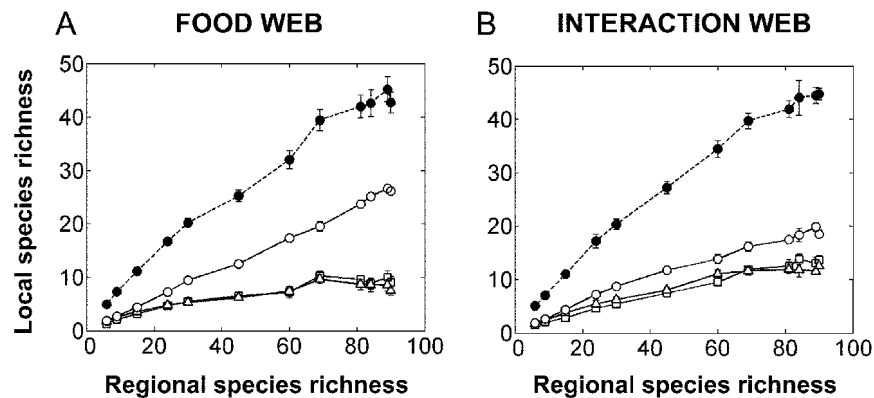


Figure 3: Local species richness in the quasi-stationary regime as a function of regional species richness in food webs (A; nontrophic connectance = 0, maximal nontrophic magnitude = 0) and in interaction webs (B; nontrophic connectance = 0.2, maximal nontrophic magnitude = 0.2). We present the mean and standard deviation for local species richness (filled circles), plant species richness (unfilled circles), herbivore species richness (triangles), and carnivore species richness (squares).

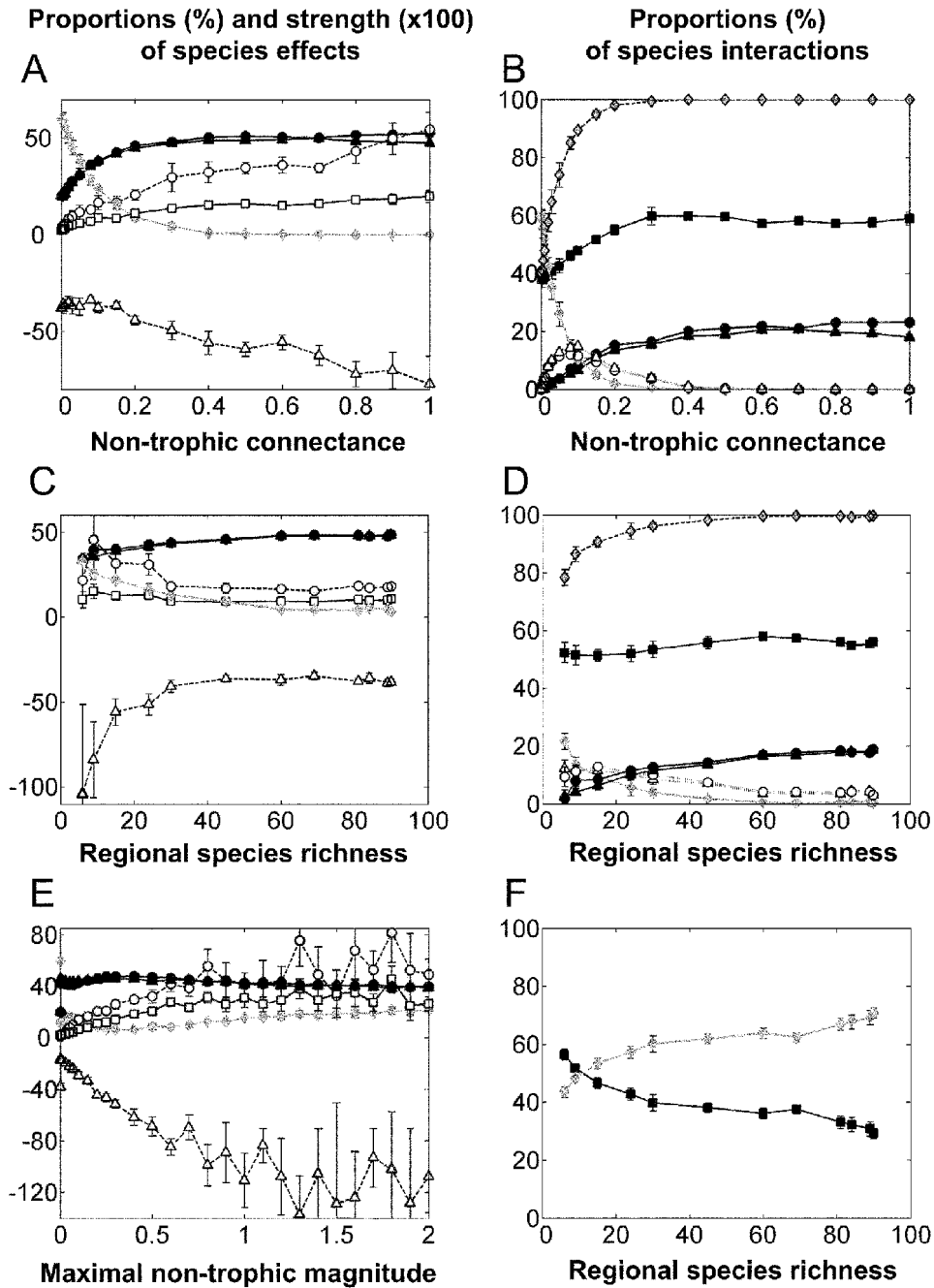


Figure 4: Proportions and strength of species effects (A, C, E) and proportions of species interactions (B, D, F) in the community as a whole in the quasi-stationary regime as functions of nontrophic connectance (A, B; regional species richness = 45, maximal nontrophic magnitude = 0.2) and regional species richness in interaction webs (C, D; nontrophic connectance = 0.2, maximal nontrophic magnitude = 0.2). E shows the proportions and strength of species effects as functions of maximal nontrophic magnitude (regional species richness = 45, nontrophic connectance = 0.2). F shows the proportions of species interactions as functions of regional species richness in food webs (nontrophic connectance = 0, maximal nontrophic magnitude = 0). A, C, and E show the mean and standard deviation for the proportions of neutral effects (gray diamonds, gray lines, $\times 100$), facilitation (filled circles, $\times 100$) and inhibition (filled triangles, $\times 100$), the mean and standard deviation for the mean value of facilitation (unfilled circles, $\times 100$), the mean value of inhibition (unfilled triangles, $\times 100$), and the standard deviation of species effects (unfilled squares, $\times 10$). B, D, and F show the mean and standard deviation for the proportions of mutualism (filled circles, $\times 100$), competition (filled triangles, $\times 100$), exploitation (filled squares, $\times 100$), commensalism (unfilled circles, $\times 100$), amensalism (unfilled triangles, $\times 100$), and neutral interactions (gray diamonds, gray lines, $\times 100$). Dashed lines (gray-filled outlined diamonds, $\times 100$) represent interaction web connectance.

negative; thus, the potential consumption rate that it modifies has the same probability of being multiplied by a factor or divided by the same factor (eq. [2]). On the other hand, the net species effect E_{ig} of a species g on another species i is proportional to the magnitude of the realized consumption rates, $a_{ij}\mu_{ij}$, that are affected by species g . The difference between the multiplicative effect of interaction modifications on the magnitude of realized consumption rates and the additive effect of realized consumption rates on the net species effect E_{ig} explains why, on average, nontrophic interactions tend to increase net species effects. On average, 50% of the μ_{xy} will be in the range 0–1 and 50% will be in the range 1– ∞ . Therefore, with increasing nontrophic connectance, the arithmetic mean of the realized consumption rates $a_{xy}\mu_{xy}$ will increasingly exceed a_{xy} , leading to an increasing average strength of both inhibition and facilitation.

This property might be viewed as a limitation of the mathematical formulation of our model, which involves both multiplicative and additive effects while there is no distribution of numbers in which both their product and their sum are equal to 1. But it might be realistic, because biological rates do have a lower bound of 0 and no upper bound, so that nontrophic interactions may be expected to have the effects predicted by our model. Ultimately, this issue will have to be resolved using empirical data on nontrophic effects in natural ecosystems, but these data are currently sorely lacking.

The Interaction Web Connectance Increases with Species Richness. As regional species richness (and hence also local species richness) increased, the proportion of 0 species effects decreased, while the proportions of facilitation and inhibition increased (fig. 4C). Accordingly, the proportion of neutral species interactions decreased to very low values (fig. 4D), whereas the proportions of commensalism and amensalism first increased and then decreased, the proportions of mutualism and competition increased, and the proportion of exploitation was unchanged. Thus, interaction web connectance increased with species richness to nearly 100%: the more numerous species are, the more they interact with other species.

In food webs, the proportion of neutral species interactions increased with regional species richness (fig. 4F) whereas the proportion of exploitation decreased. Thus, the increase in interaction web connectance with species richness in interaction webs (fig. 4D) is due to the presence of nontrophic links between species.

The increase in interaction web connectance with species richness is a general property of interaction webs that can be explained intuitively as follows: as regional species richness increases, the number of trophic links of a given species increases (as long as consumers are not strict spe-

cialists), which increases the probability for this species to have at least one trophic link modified by any other species in the web. The fact that interaction web connectance tends to 100%, however, is due to the assumption that consumers are generalists in our model. Other food web configurations may lead to smaller upper limits.

The Strength of Species Effects Decreases with Species Richness. As regional species richness increased (fig. 4C), the mean value of facilitation decreased and the mean value of inhibition increased; that is, the mean absolute values of species effects decreased. Thus, species effects tended to be denser, that is, proportionally more numerous, and weaker as regional species richness increased in interaction webs (fig. 4C). Weak average interaction strength probably buffers the destabilizing effects of interaction web connectance and species richness. Note that average interaction strength also decreased with regional species richness in food webs (the mean absolute value of inhibition decreased; results not shown).

Species Effects and Species Interactions within the Various Trophic Levels. Patterns within the various trophic levels were very similar to those reported in figure 4 for the community as a whole. The only difference concerned the prevalence of facilitation and inhibition, and hence of interspecific competition and cooperation, among plants as nontrophic connectance increased (fig. C1 in the online edition of the *American Naturalist*). In plants, the proportion of inhibition increased more rapidly than that of facilitation, whereas in the community as a whole (fig. 4A) or in other trophic levels (results not shown), the proportions of inhibition and facilitation varied in the same way. In the same manner, the proportion of interspecific competition increased more rapidly than that of mutualism in plants, whereas these proportions varied in the same way in other trophic levels or in the whole community (fig. 4B).

Impacts of Nontrophic Interactions on Biodiversity and Ecosystem Properties

Nontrophic Interactions and Ecosystem Properties. Nontrophic connectance and maximal nontrophic magnitude had an important effect on ecosystem properties. Local species richness decreased as either nontrophic connectance (fig. 5A) or maximal nontrophic magnitude (fig. 5B) increased, except at a low level of nontrophic parameters. Plant species richness decreased as either nontrophic connectance (fig. 5A) or maximal nontrophic magnitude (fig. 5B) increased. In contrast, consumer species richness was less affected by variations in nontrophic connectance; it

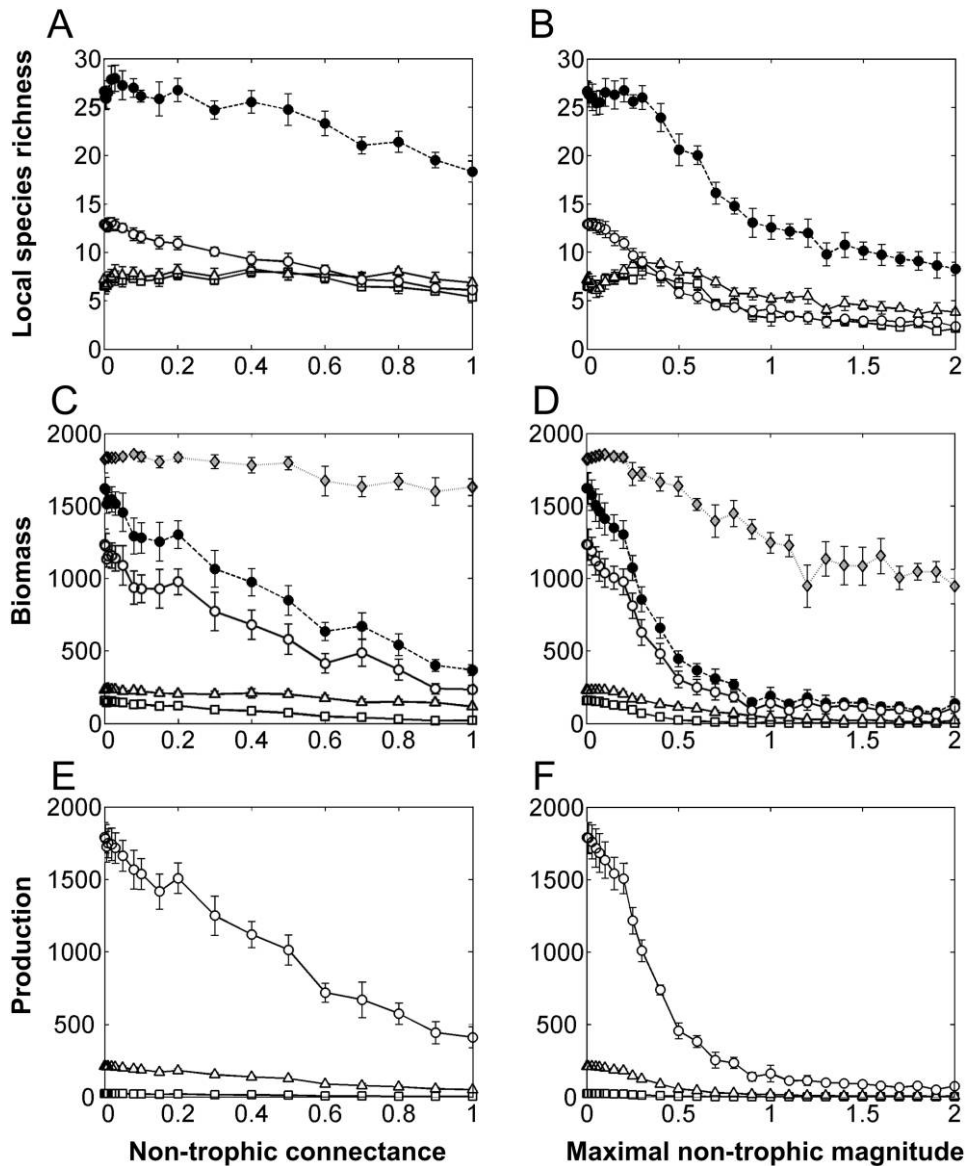


Figure 5: Local species richness, biomass, and production in the quasi-stationary regime as functions of nontrophic connectance (A, C, E; regional species richness = 45, maximal nontrophic magnitude = 0.2) and maximal nontrophic magnitude (B, D, F; regional species richness = 45, nontrophic connectance = 0.2). We present the mean and standard deviation for total (filled circles) local species richness and biomass and plant (unfilled circles), herbivore (triangles), and carnivore (squares) local species richness, biomass, and production (per unit time). Dotted lines represent the nutrient mass in the soil (diamonds).

decreased as maximal nontrophic magnitude increased, except at a low level of maximal nontrophic magnitude.

The biomass and production of each trophic level decreased sharply as either nontrophic connectance (fig. 5C, 5E) or maximal nontrophic magnitude (fig. 5D, 5F) increased. Interaction webs with high levels of either nontrophic connectance or maximal nontrophic magnitude were systems in which the biological processes of pro-

duction and recycling were very low and inorganic flows prevailed. Such high levels of nontrophic connectance and magnitude are presumably absent in natural ecosystems.

The Impacts of Nontrophic Interactions on Ecosystem Processes Are Mediated by Changes in Realized Consumption Rates and Species Interactions. The decrease in biomass and production at all trophic levels as nontrophic con-

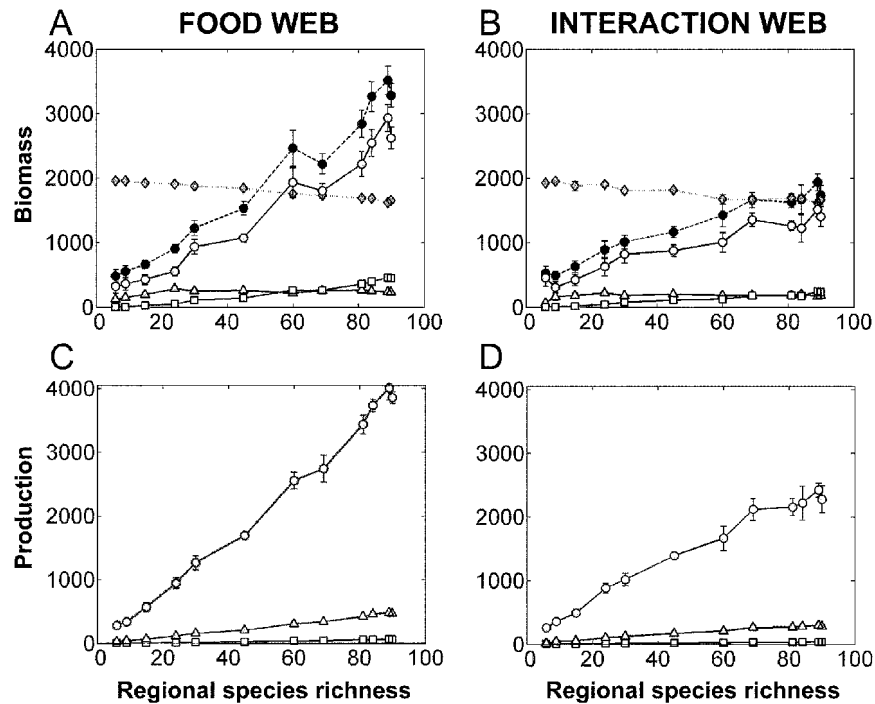


Figure 6: Biomass and production in the quasi-stationary regime as functions of regional species richness in food webs (A, C; nontrophic connectance = 0, maximal nontrophic magnitude = 0) and in interaction webs (B, D; nontrophic connectance = 0.2, maximal nontrophic magnitude = 0.2). We present the mean and standard deviation for total biomass (filled circles), total plant (unfilled circles), total herbivore (triangles), and total carnivore (squares) biomass and production (per unit time). Dotted lines represent the nutrient mass in the soil (diamonds).

nectance or maximal nontrophic magnitude increases can be explained by the impacts of nontrophic interactions on realized consumption rates and species interactions (fig. 4). First, mean realized consumption rates increase with nontrophic connectance, as mentioned above, which contributes to a decrease in the biomass and production at the next lower trophic level. These declines in the biomass and production of lower trophic levels cascade up the food web and lead indirectly to decreased carnivore biomass and production. Increasing nontrophic connectance also leads to more intense competition between consumers for their resource and a smaller resource-use complementarity, which contributes to a decrease in herbivore and carnivore biomass and production.

Second, the proportions of inhibition and competition increase more than those of facilitation and mutualism in plants when nontrophic connectance increases. Thus, nontrophic interactions tend to make competition between plant species stronger, which may also partly explain the decrease in primary production and plant biomass and hence indirectly in consumer production and biomass.

The Biodiversity–Ecosystem Functioning Relationships in Food Webs and Interaction Webs

Effects of Species Richness on Ecosystem Processes in Food Webs and Interaction Webs. In both food webs and interaction webs, total biomass increased with regional species richness and hence with local species richness (fig. 6A, 6B). Plant and carnivore biomasses increased in parallel, which suggests a bottom-up control of plants on carnivores. In contrast, herbivore biomass was less affected by species richness, which suggests a top-down control of carnivores on herbivores. The soil nutrient concentration decreased as species richness increased, which shows a better exploitation of the limiting nutrient by plants.

Production at all trophic levels increased with regional species richness (fig. 6C, 6D). Primary production increased with species richness because of the better exploitation of the limiting nutrient by plants; as a result, the increase in plant biomass was much higher than the decrease in the soil nutrient stock, and primary production increased (eq. [6]; fig. 6A, 6B). Herbivore production depends on plant biomass and herbivore biomass (eq. [6]),

and herbivore biomass was top-down controlled; therefore, herbivore production showed the same pattern as plant biomass (cf. fig. 6A, 6C and 6B, 6D). In the same manner, carnivore production depends on herbivore and carnivore biomasses (eq. [6]), but herbivore biomass was top-down controlled; therefore, carnivore production followed carnivore biomass. Production (especially in plants and herbivores) was generally high compared with the inorganic nutrient input, I . This results from the high recycling efficiency of ecosystems in the quasi-stationary regime, after a long assembly process. This high recycling efficiency also explains why the amount of nutrient in the soil often remained relatively high.

Differences between food webs and interaction webs highlight the role of nontrophic interactions in ecosystems. The increase in biomass and production with regional (fig. 6) and local (fig. 7) species richness was less rapid in interaction webs than in food webs. Differences between food webs and interaction webs were greater at higher levels of regional species richness (fig. 6A, 6B). The positive effect of nontrophic interactions on the average realized consumption rate as species richness increases explains why nontrophic effects are more important in species-rich ecosystems than in species-poor ecosystems in our model. Higher realized consumption rates make species more efficient but also more competitive.

Biodiversity–Ecosystem Functioning Relationships. We studied the relationship between total biomass and local species richness at the quasi-stationary regime that emerged from variations in one of the parameters of the regional species pool, that is, regional species richness, nontrophic connectance, or maximal nontrophic magnitude (fig. 7). Whatever the parameter driving variations in local species richness, there was a positive relationship between total biomass and local species richness. However, the shape of this relationship differed. The relationship was roughly linear in both food webs and interaction webs when regional species richness varied, but it was nonlinear and concave-up when nontrophic connectance or maximal nontrophic magnitude varied in interaction webs. This concave-up relationship between local species richness and total biomass is explained by the greater effect of nontrophic interactions on biomass than on species richness (fig. 5). Thus, our model predicts a positive relationship between species richness and biomass in naturally assembled ecosystems, but with a strong impact of nontrophic interactions on the shape of the diversity-biomass relationship. Specifically, nontrophic interactions are expected to decrease the magnitude of biomass and production, but changes in their frequency or strength are expected to increase the dependency of biomass and production on local species richness.

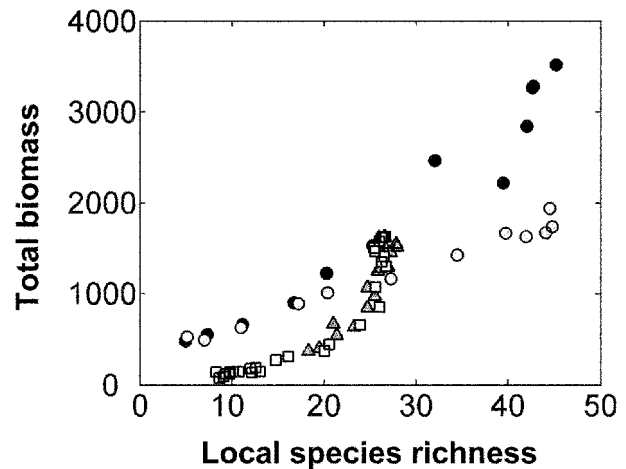


Figure 7: Relationships between local species richness and total biomass driven by variations of different properties of the regional species pool: regional species richness in food webs (*filled circles*; nontrophic connectance = 0, maximal nontrophic magnitude = 0), regional species richness in interaction webs (*unfilled circles*; nontrophic connectance = 0.2, maximal nontrophic magnitude = 0.2), nontrophic connectance in interaction webs (*triangles*; regional species richness = 45, maximal nontrophic magnitude = 0.2), and maximal nontrophic magnitude in interaction webs (*squares*; regional species richness = 45, nontrophic connectance = 0.2).

Discussion

Our theoretical model shows that species diversity and nontrophic interactions affect strongly and nonintuitively the community and ecosystem properties in communities that have assembled through repeated colonization events. Our main results can be summarized as follows.

First, increasing regional species richness leads to increased species richness, biomass, production, and interaction web connectance but decreased average interaction strength in local communities. Thus, species-rich interaction webs are expected to be more productive and more connected but to have weaker species interactions on average. Their lower interaction strength is probably what allows them to maintain a high diversity and connectance, in agreement with previous theory (May 1973; Kokkoris et al. 1999, 2002). Their high diversity in turn allows them to use the limiting nutrient more efficiently and hence have a higher production and biomass, as predicted by existing theory (Tilman et al. 1997; Loreau 1998, 2000; Tilman 1999).

Second, increasing the frequency and magnitude of nontrophic interactions in the regional species pool leads to decreased local species richness, biomass, and production. These counterintuitive effects result from the fact that nontrophic connectance and maximal nontrophic magnitude contribute to an increase in the magnitude of trophic con-

sumption fluxes, and hence the strength of species interactions, on average. Increased average interaction strength allows fewer species to coexist and imposes a higher mortality on lower trophic levels, which eventually deteriorates the functioning of the whole ecosystem.

Third, as a consequence, interaction webs that include trophic and nontrophic interactions are expected to have a lower local richness, biomass, and production than food webs that include only trophic interactions, all else (in particular, regional species richness) being equal. A positive diversity-biomass relationship emerges from the assembly of both food webs and interactions webs, but nontrophic interactions are expected to affect the shape of this relationship.

Thus, our results emphasize the need to take into account nontrophic interactions in theoretical ecology. Our simple, general model allows all types of species interactions to be incorporated by adding interaction modifications to a food web. This mass-balance constrained model of an interaction web provides a useful tool for studying the impact of diversity on the functional properties of complex ecosystems with more realism.

The Biodiversity-Ecosystem Functioning Relationship in Interaction Webs

Total biomass increases with regional species richness, and hence also with local species richness, in both food webs and interaction webs. In both types of web, carnivore biomass is bottom-up controlled by plants, herbivore biomass is top-down controlled by carnivores, and total biomass depends mostly on plant biomass. These control mechanisms are the same as in classical food webs, and our results concerning food webs are in qualitative agreement with previous theoretical studies (Thébault and Loreau 2003; Ives et al. 2005). Thébault and Loreau (2003), however, showed that in a two-level food web with generalist herbivores, plant biomass and herbivore biomass increase nonlinearly with regional species richness and can even decrease at a high level of species richness, whereas in our food web model, biomass does not decrease at a high level of species richness. This difference is probably explained by the presence of a third trophic level in our work and by the fact that, contrary to recent theoretical (Thébault and Loreau 2003; Ives et al. 2005) and experimental (Downing and Leibold 2002; Duffy et al. 2003) studies in which species richness is controlled, our work provides a dynamic approach to biodiversity and ecosystem functioning in which both factors result from an assembly process. Our model predicts that biomass and production are generally lower in interaction webs than in food webs. Nontrophic interactions are likely to generate strong constraints on species coexistence. The species present in the

community have higher realized consumption rates on average, which makes them more efficient but also more competitive. Therefore, the probability of observing extreme resource exploitation and negative effects on ecosystem properties is higher.

Species Diversity, Species Interactions, and Ecosystem Processes

Our work shows that species interactions depend on species richness: both the strength and the prevalence of these interactions are diversity dependent. In particular, the mean absolute values of interspecific facilitation and inhibition effects are expected to decrease with increasing species richness. These results agree with existing theory (Kokkoris et al. 1999, 2002). The analysis of natural food webs (Neutel et al. 2002) suggests that natural ecosystems are characterized by a majority of weak interactions and a minority of strong interactions.

Our model also predicts that interaction web connectance increases with species richness and that the proportions of the various types of species effects and species interactions depend on species richness. A higher species diversity increases the probability for each species to interact with any other species. Although the relationship between trophic connectance and species richness has been well studied in food webs (Martinez 1992; Montoya and Solé 2003), we lack knowledge concerning nontrophic connectance and interaction web connectance in ecosystems.

Species diversity is known to affect ecosystem functioning through functional complementarity between species that use different resources (Tilman et al. 1997; Loreau 1998; Loreau and Hector 2001). Our model further suggests that it can affect ecosystem functioning in more subtle ways by changing the nature, prevalence, and strength of species interactions. For instance, it can enhance ecosystem processes by increasing the probability of facilitation (Cardinale et al. 2002). Recent experiments have shown that a form of facilitation, whereby a species enhances the access of other species to resources through biophysical modifications, affects the productivity and the diversity-productivity relationship in bryophyte communities (Mulder et al. 2001; Rixen and Mulder 2005). Thus, species interactions, in particular nontrophic interactions, should be given more attention in studying the relationship between biodiversity and ecosystem properties.

Incorporating Nontrophic Interactions into Theoretical Ecology

Our work provides a consistent ecosystem model that incorporates nontrophic interactions in the form of inter-

action modifications. Although interaction modifications were regarded by Wootton (1994) as a class of indirect effects, they may be viewed as either direct or indirect trait-mediated interactions (Abrams 1995), depending on the context. The interaction may be direct if, for instance, the interaction modifier directly affects the behavior of the two species whose trophic interaction is affected. But it may also be indirect if, for instance, the interaction modification occurs through habitat modification, which in turn affects the ability of the predator to detect or catch its prey. Also, the direct or indirect nature of trait-mediated interactions is not necessarily reflected in a model's structure (Abrams 1995). Therefore, our measure of the net species effect, E_{ig} , of species g on species i includes both trophic and nontrophic direct effects as well as, potentially, trait-mediated indirect effects. The ambiguity of current terminology suggests that a reexamination of the concepts, definitions, and measures of direct and indirect effects might be useful.

Ecosystem engineers (Jones et al. 1994) are strong drivers of interaction modifications: by modifying their physical environment, they create many nontrophic species interactions. Autogenic or allogenic engineers can modulate resource flows or abiotic parameters that influences resource flows. Therefore, our modeling framework could be applied to the study of ecosystem engineers through specific nontrophic modifications of trophic interactions or through modifications of abiotic parameters such as those that govern the input, recycling, and loss of nutrients. Experimental studies show that ecosystem engineering can induce changes in community structural properties, such as species richness (Zhu et al. 2006), species composition (Badano et al. 2006), and species interactions (Collen and Gibson 2001), and ecosystem functional processes such as primary production (Zhu et al. 2006). Our model shows that interaction modifications of all kinds can profoundly affect ecosystem properties such as biomass and production at all trophic levels.

We view our interaction web model as a promising tool for merging the community and ecosystem perspectives in theoretical ecology. By incorporating nontrophic interactions in the form of modifications of trophic interactions, our model describes material flows in a consistent way and hence allows analysis of ecosystem properties. At the same time, it is a flexible and dynamic model that allows all kinds of species interactions to occur, and hence, it allows analysis of community properties such as species diversity and the connectance, prevalence, and strength of species interactions.

Model Limitations

Despite its strengths and generality, our model also has limitations. We represented nontrophic interactions in the

form of modifications of trophic interactions, but it would also be possible to introduce them in the form of modifications of nontrophic parameters such as intrinsic death rates and recycling rates. We assumed that nontrophic effects act multiplicatively on potential consumption rates because this led to the simplest functional form for interaction modifications that respects the direction of consumption fluxes between trophic levels. This assumption makes sense mathematically because biological rates have a lower bound of 0 and no upper bound; nontrophic modifications of these rates may have asymmetric effects, depending on whether they are positive or negative. But this assumption indirectly drives many of the observed effects of nontrophic interactions in our model, and empirical data to assess its validity are unfortunately sorely lacking. We also assumed that the various modifications of a given trophic interaction by different species are additive, but interaction modifications might interfere with each other and generate nonadditive effects. For instance, there could be a hierarchy of effects (one effect dominates over the others) or a synergy of effects (the effect of one species can only be expressed in, or is modified by, the presence of another species). Our linear approximation, however, is in line with the simplicity required for a general ecosystem model.

We assumed that there is a single limiting nutrient and that the stoichiometric composition of each species is constant, although the stoichiometric composition of plants is known to depend on factors such as environmental conditions and the presence of consumers. This simplification was made to avoid unnecessary complications in a model designed to explore the role of nontrophic interactions. In our model, the soil is compartmentalized, each plant taking up nutrient in its species-specific resource depletion zone. This assumption was meant to favor plant species resource-use complementarity and coexistence to some extent, although strong nontrophic interactions led to species-poor communities despite this assumption. We expect our results to be qualitatively robust to relaxation of this assumption, as suggested by preliminary simulation results. A decomposer compartment could be added, but it is unlikely to change the results because we have already included nutrient cycling in our model without detailing its mechanisms. Lastly, our current model considers an interaction web with three trophic levels. It would definitely be interesting to model an interaction web with a more realistic and flexible trophic structure by allowing consumers to feed on several trophic levels and blurring the separation between distinct trophic levels.

Our theoretical study suggests several hypotheses that deserve to be tested experimentally. It would be useful to study the influence of species richness on species inter-

actions: does the strength of species effects (facilitation, inhibition) depend on species richness in experimental ecosystems? Does their connectance increase with species richness? It would also be useful to test the impacts of nontrophic interactions on ecosystem processes and their mechanisms: what is the influence of the connectance or magnitude of nontrophic interactions on biomass and production at various trophic levels? Do nontrophic interactions generally increase resource consumption, possibly leading to extreme resource exploitation?

Conclusion

We have developed a model of a full interaction web that includes both trophic and nontrophic species interactions and that respects the principle of mass conservation. This model shows the important role of species interactions, especially nontrophic interactions, in community and ecosystem properties and in the relationship between biodiversity and ecosystem functioning. The diversity-biomass patterns obtained with our interaction web model are not strikingly different from those shown in recent theoretical studies of food webs, but the mechanisms are far more complex. In particular, our model predicts that the nature, prevalence, and strength of species interactions change with regional and local species richness, which makes the mechanisms of the biodiversity–ecosystem functioning relationship more complex in an interaction web. Species interactions, and especially nontrophic interactions, should be given more attention to improve understanding and predictions of the ecological consequences of biodiversity loss.

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Appendix A from A. Goudard and M. Loreau, “Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model”

(Am. Nat., vol. 171, no. 1, p. 91)

Table A1
Parameter values

Parameter	Values
Numerical integration:	
Time step (Runge-Kutta of order 4)	.01
Simulation duration	1,000 iterations, i.e., 100,000 numerical integrations
Introduction period (p)	100 time steps
Introduction biomass	.01
Extinction biomass threshold	.005
Regional species pool (randomly taken from a uniform distribution):	
u_x (death rate)	$\forall x \in (1, \dots, n), .1 \leq u_x \leq .5$ per unit time
λ_x (nonrecycled proportion of dead organic matter)	$\forall x \in (1, \dots, n), .1 \leq \lambda_x \leq .3$
a_{xy}	Potential consumption rate of species y by species x per time and mass unit
Carnivore potential consumption rate	$\forall (x, y) \in (1, \dots, S)^2, 0 \leq a_{xy} \leq 0.01$ per time and mass unit
Herbivore potential consumption rate	$\forall (x, y) \in (1, \dots, S)^2, 0 \leq a_{xy} \leq 0.01$ per time and mass unit
Nutrient uptake rate by plants	$\forall i \in (1, \dots, S), 0 \leq a_{L,P_i} \leq 0.5$ per time and mass unit
q_C (carnivore conversion efficiency)	.15 (15%)
q_H (herbivore conversion efficiency)	.15 (15%)
m_{xyz} (magnitude of the nontrophic modification of the trophic interaction between species x and y , by species z)	$\forall (x, y, z) \in (1, \dots, S)^3, -\text{maximal nontrophic magnitude} \leq m_{xyz} \leq +\text{maximal nontrophic magnitude}$
μ_{xy}	Nontrophic coefficient of species y on species x
$a_{xy}\mu_{xy}$	Realized consumption rate of species y by species x per time and mass unit
Soil:	
V_{soil}	Total volume of soil: $V_{\text{soil}} = 100$
V_i (total volume of species-specific resource depletion zones of plant species i)	$V_i = 1$ if plant species i is present in the local ecosystem, else $V_i = 0$
V_R (volume of soil nutrient pool)	$V_{\text{soil}} - \sum_{i=1}^S V_i$
γ (diffusion rate)	10 per unit time
I (soil nutrient input)	100 per unit time
λ_R (soil nutrient loss rate)	.05 per time and soil nutrient mass unit
R_0 (initial nutrient mass in soil nutrient pool [randomly taken])	$1 \leq R_0 \leq 10$

Appendix B from A. Goudard and M. Loreau, “Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model”

(Am. Nat., vol. 171, no. 1, p. 91)

Program Algorithm

1. Choice of complexity parameters of the regional species pool: regional species richness, nontrophic connectance, and maximal nontrophic magnitude.
2. Creation of the regional species pool. The regional species pool consists of equal numbers of plant, herbivore, and carnivore species, without omnivory. The parameters of the pool species are randomly taken from a uniform distribution within appropriate intervals (app. A): death rate u_x , nonrecycled proportion λ_x of nutrient coming from species x , potential consumption rate a_{xy} , and magnitude of interaction modification m_{xyz} . The initial nutrient mass in the soil nutrient pool is also randomly taken from a uniform distribution.
At each introduction event (3–5):
 3. Community and ecosystem properties are calculated and recorded (proportions, strength and variability of species effects, proportions of species interactions, local species richness, species richness per trophic level, total biomass, biomass per trophic level, production at each trophic level, and mean consumption per species).
 4. A species is randomly taken from the pool of those that are not already present in the community. A species can thus be introduced, become extinct, and be reintroduced.
 5. The species is introduced into the community. The initial biomass of the introduced species is subtracted from the soil nutrient pool to respect the principle of mass conservation. When a plant species is introduced, the volume of its species-specific resource depletion zones is created, with a concentration equal to the soil nutrient pool concentration, and subtracted from the volume of the soil nutrient pool, and the nutrient mass of this species-specific resource depletion zone is subtracted from the soil nutrient pool.
- At each integration time step (6–7):
 6. Numerical integration of the dynamic equations (1) and (2) is performed with a Runge-Kutta method of order 4.
 7. Species whose biomass is smaller than the extinction biomass threshold are removed. Their biomass is added to the soil nutrient pool to respect the principle of mass conservation. When a plant species becomes extinct, the volume and the nutrient mass of its species-specific resource depletion zone are set to 0 and added to the volume of the soil nutrient pool.
8. Repeat steps 6–7 for 100 numerical integrations.
9. Repeat steps 3–8 for $100,000/100 = 1,000$ introduction events.
10. Repeat steps 2–9 for eight replicates.
11. Repeat steps 1–10 for each value of the studied parameter (regional species richness, nontrophic connectance, or maximal nontrophic magnitude).

Appendix C from A. Goudard and M. Loreau, “Nontrophic Interactions, Biodiversity, and Ecosystem Functioning: An Interaction Web Model”

(Am. Nat., vol. 171, no. 1, p. 91)

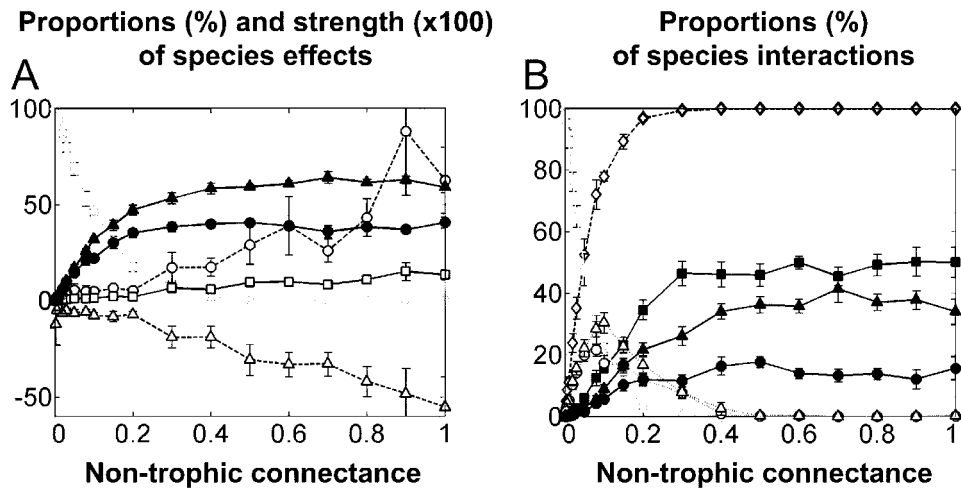


Figure C1: Frequency and strength of species effects (A) and species interactions (B) within the plant trophic level in the quasi-stationary regime as functions of nontrophic connectance (regional species richness = 45, maximal nontrophic magnitude = 0.2). A, Mean and standard deviation for the proportions of neutral effects (gray diamonds, gray lines, $\times 100$), facilitation (filled circles, $\times 100$) and inhibition (filled triangles, $\times 100$), the mean and standard deviation for the mean value of facilitation (unfilled circles, $\times 100$), the mean value of inhibition (unfilled triangles, $\times 100$), and the standard deviation of species effects (unfilled squares, $\times 10$). B, Mean and standard deviation for the proportions of mutualism (filled circles, $\times 100$), competition (filled triangles, $\times 100$), exploitation (filled squares, $\times 100$), commensalism (unfilled circles, $\times 100$), amensalism (unfilled triangles, $\times 100$), and neutral interactions (gray diamonds, gray lines, $\times 100$). Dashed line (gray-filled outlined diamonds, $\times 100$) represents interaction web connectance.