

REPORT

# Plant species richness and community productivity: why the mechanism that promotes coexistence matters

Nicolas Mouquet,<sup>1,\*</sup> Joslin L. Moore<sup>2,†</sup> and Michel Loreau<sup>1</sup>  
<sup>1</sup>Laboratoire d'Ecologie, UMR 7625, École Normale Supérieure, 46 rue d'Ulm, F-75230 Paris Cedex 05, France. E-mail: mouquet@bio.fsu.edu

<sup>2</sup>NERC Center for Population Biology Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY, U.K.

\*Present address: Department of Biological Science and School of Computational Science & Information Technology, Florida State University, Tallahassee, FL 32306–1100, U.S.A. Office Location: CSIT, Oirac Library 4th floor.

†Present address: Conservation Biology, Department of Zoology, University of Cambridge, 15 Downing Street, Cambridge, CB2 3EJ, U.K.

## Abstract

This paper stresses that the mechanism of coexistence is the key to understanding the relationship between species richness and community productivity. Using model plant communities, we explored two general kinds of mechanisms based on resource heterogeneity and recruitment limitation, with and without any trade-off between reproductive and competitive abilities. We generated different levels of species richness by changing model parameters, in particular the number of species in the regional pool, the degree of recruitment limitation, and the level of heterogeneity. Different diversity–productivity patterns are obtained with different coexistence mechanisms, indicating there is no reason to expect any general relationship between species richness and productivity. We discuss these results in the context of the within-site and across-site aspects of the relationship between species richness and productivity. Furthermore, we extend these results to hypothesize the relationship between species richness and productivity for other coexistence mechanisms not explicitly considered here.

## Keywords

Biodiversity, coexistence mechanism, competition-colonization trade-off, model, plant community, productivity, recruitment limitation, resource heterogeneity, regional species pool, species richness.

Ecology Letters (2002) 5: 56–65

## INTRODUCTION

The relationship between species richness and aggregate community properties such as productivity has become a central issue of community and ecosystem ecology (see Tilman 1999, Waide *et al.* 1999 and Loreau 2000 for reviews). It is a unifying fundamental question that requires merging concepts from ecosystem and community ecology. In itself, merging these two different fields of ecology is a challenge for modern ecology. Moreover, the current loss of species diversity stresses the need for understanding of the relationship between species diversity and community properties. An important question has been whether a species-rich community is more productive than is a species-poor community. Some recent experimental studies in which species richness was manipulated have demonstrated a positive relationship between species richness and productivity (Tilman *et al.* 1996; Hector *et al.* 1999),

although the interpretations of these results have been debated (Aarssen 1997; Grime 1997; Huston 1997; Loreau 1998a; Wardle 1999; but see Loreau & Hector 2001).

Here, we develop an important distinction, related to the 'kind of diversity' that is maintained in a community. We know from the theory of community ecology that species richness within a community can be determined by a number of different mechanisms (see Tilman & Pacala 1993 and Chesson 2000 for reviews). By extension, the identity of coexisting species and the characteristics of species assemblages will depend strongly on which mechanism is acting to promote coexistence. Some authors have predicted a positive relationship between productivity and species richness (Tilman *et al.* 1997; Loreau 1998b) but their models were based on niche complementarity. However, if we consider that coexistence may be based on different mechanisms, this result may no longer be valid. For example, Loreau (1998b) has shown that when species are 'redund-

ant', productivity is not correlated with species richness. Moreover, if regional processes such as immigration mediate coexistence, productivity can either remain constant or decrease as the number of locally coexisting species increases (Loreau & Mouquet 1999). The recent work by Cardinale *et al.* (2000) also concerned this limitation, showing that the cause of the diversity–productivity relationship changed with environmental context.

These contrasting examples emphasize the need for study of aggregate community properties in the light of the mechanisms that promote coexistence. Invasibility was discussed in this context in a previous paper, where it was shown that species richness is likely to be a poor predictor of invasion resistance (Moore *et al.* 2001). Community stability has also been analysed in such a context recently (Hughes & Roughgarden 2000; Lehman & Tilman 2000). Here, we present a theoretical model focusing on the relationship between species richness and community productivity in herbaceous plant communities at equilibrium. We focus exclusively on some spatial mechanisms promoting local coexistence at equilibrium: resource heterogeneity (MacArthur & Levins 1967) with and without recruitment limitation (Hastings 1980; Tilman 1994; Hurtt & Pacala 1995). Using these mechanisms we generate different levels of species richness and examine community productivity. We focus only on these mechanisms because they can be easily derived from the same general model, and, as we will show, they provide sufficiently contrasting results to illustrate our point. We speculate in the discussion as to how other mechanisms may affect the relationship between species richness and productivity.

## MODELS AND METHODS

We present a model of a community in which each species has a competitive advantage or disadvantage depending on environmental conditions or life-history strategy. We consider a very general model of recruitment limitation in heterogeneous habitats (RLHH) derived from the models developed by Chesson (1985), Pacala & Tilman (1994) and Hurtt & Pacala (1995). We then derive a more specific model similar to the classical competition–colonization trade-off model developed by Hastings (1980) and Tilman (1994).

### Presentation of the models

#### *Recruitment limitation in a heterogeneous habitat (RLHH)*

We consider the habitat as partitioned into sites that cannot be used by more than one individual at a time. We assume that sites show different combinations of environmental variables and that each species is best adapted to one of these combinations. Consider  $N_{\text{reg}}$  species (that constitute the regional pool) in competition for a number of free sites

$V$  from a total number of sites  $Q$ . We use a fixed number of sites to allow for the possibility of rare-species extinction through demographic stochasticity. The model is not spatially explicit. The environment encountered at a site  $k$  is represented by a value  $H_k$  chosen randomly between 0 and 1 from a beta distribution. The beta distribution allows us to vary the degree of environmental variability from homogeneous to very heterogeneous (Fig. 1a). We use  $1/\beta$  (see Fig. 1a) as a measure of heterogeneity. The different  $H_k$  values are not correlated, and they do not change with time. By heterogeneous environment, we mean an environment constituted by cells that differ in their conditions. To a certain extent, increasing heterogeneity is equivalent to increasing the number of different niches available.

Let  $X_i$  be the number of sites occupied by species  $i$  at time  $t$ . We model  $\Delta X_i$  as the change in  $X_i$  between  $t$  and  $t + 1$ . Sites are vacated when adult plants die, with probability  $m$ , which is density independent and the same for all species. For each species,  $G_{ik}$  is the probability that a propagule of species  $i$  successfully establishes itself at an unoccupied site  $k$ . Our model is very similar to spatial lottery models (Chesson & Warner 1981) in the sense that plants compete for a vacant site through recruitment. The probability of recruitment  $G_{ik}$  is the product of two independent probabilities that indicate species  $i$ 's ability to reach a site,  $S_i$ , and its probability of being the best competitor for the conditions encountered at site  $k$ ,  $C_{ik}$ . The general model reads:

$$\Delta X_i = \left( \frac{\sum_k G_{ik}}{Q} \right) \left( \sum_i^N mX_i + (Q - \sum_i^N X_i) \right) - mX_i \quad (1)$$

where

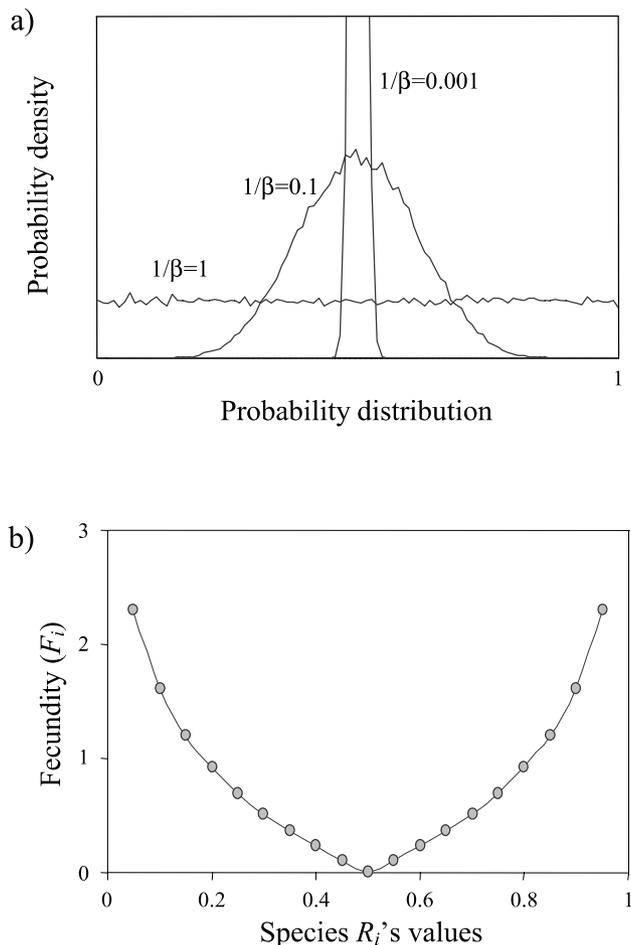
$$G_{ik} = S_i \times C_{ik} \quad (2)$$

The probability that a species reaches a site,  $S_i$  obeys a Poisson distribution the mean of which is a function of the species' fecundity,  $F_i$ , and of its relative abundance in the previous time step:

$$S_i = 1 - \exp\left(-F_i \frac{X_i}{Q}\right) \quad (3)$$

For simplicity we consider the fecundity of all species,  $F_i$  to be equal to mean fecundity,  $F_m$ , which can vary between 0 and infinity.

Each species  $i$  is defined by the value  $R_i$  which is randomly chosen from a uniform distribution between 0 and 1. For a species  $i$ , the probability of being the best competitor for the conditions encountered at site  $k$ ,  $C_{ik}$ , is determined from the difference between  $R_i$  and  $H_k$ , i.e.



**Figure 1** (a) Three probability distributions generated with the beta function defined by  $(p(x : \alpha, \beta) = x^{\alpha-1}(1-x)^{\beta-1} / \int_0^1 x^{\alpha-1}(1-x)^{\beta-1} dx)$ . Each distribution has the same mean (0.5) and is symmetrical. In our model, we set  $\alpha = \beta$  and consider  $\beta$  in the interval  $[1, +\infty[$ . As  $\beta$  increases, the variance converges to 0. We use  $1/\beta$  as a measure of environmental heterogeneity and illustrate the beta distribution for three different values of  $1/\beta$ . This measure will be equal to 1 when the habitat is completely heterogeneous and tend to zero as the habitat becomes more homogeneous. (b) Illustration of the trade-off curve between competitive ability and fecundity defined by equation 4 ( $F_{mn} = 1$ ).

species  $i$  is competitively dominant at a site  $k$  if its  $R_i$  value is closest to the  $H_k$  value of the site.

#### Competition-colonization trade-off (CC)

We assume a trade-off between competitive ability (allocation to biomass) and fecundity (allocation to reproduction). We consider the habitat homogeneous so that the environment is characterized by a unique value ( $1/\beta \rightarrow 0$ ,  $H_k = 0.5, \forall k$ ). Seedlings of inferior competitors can establish themselves only at sites where propagules of better competitors are absent. In contrast with previous models

(Hastings 1980; Tilman 1994), ours considers only competition for vacant sites; i.e. adults cannot be excluded by seedlings of other species. The trade-off is given by

$$F_i = F_{mn} [\ln(0.5) - \ln(0.5 - |0.5 - R_i|)] \quad (4)$$

We present the trade-off curve in Fig. 1(b). The most competitive species is the one whose  $R_i$  value is closest to 0.5, at which value fecundity is zero.

Let the species be ranked from 1 to  $N$  with species 1 being the best competitor. The probability that species  $i$  is the best competitor for the conditions encountered at site  $k$  is equal to the probability that a better competitor will not reach the site:

$$C_{ik} = \exp\left(-\sum_{j=1}^{i-1} F_j \frac{X_j}{Q}\right) \quad (5)$$

#### Simulations

We used simulations to study the properties of the different models. The habitat consisted of 4900 sites. Each site  $k$  was characterized by a value  $H_k$  between 0 and 1 chosen randomly from the beta distribution. We determined the regional pool of species by choosing the  $R_i$  values randomly between 0 and 1 from a uniform distribution. At the beginning of each simulation, we distributed seeds of all species equally over the habitat so that two-thirds of sites were initially occupied. We chose to assemble the community simultaneously rather than sequentially because there is no clear evidence, to our knowledge, that either of these processes is dominant in natural communities. Moreover, simultaneous assemblages drastically reduce the time to equilibrium.

Each time step consisted of three different events: (1) the total seed rain for each species was calculated as the product of its fecundity and the number of individuals present; (2) for each adult, mortality occurred with probability  $m$  ( $m = 0.4$  for all species and models in the simulations presented here); and (3) we simulated recruitment. For the RLHH model, we calculated the probability that each species reached a site,  $S_k$ , during the seed-rain event (equation 3). Competition for the site then occurred such that the species with the highest competitive ability for the conditions encountered at that site won. If no individuals reached a site, it remained empty. For the CC model, for each site, a random number between 0 and 1 was drawn from a uniform distribution and compared to the  $C_{ik}$  given by equation 5 to determine whether the best competitor reached the site. If it did, it won the site. If not, another random number was drawn to determine whether the second-best competitor reached the site. This process was continued until the site was occupied or no species had successfully reached the site.

One simulation set compared the community properties of assemblages generated by use of each of the different

coexistence mechanisms with a given regional pool of species and a particular habitat. For each coexistence mechanism, community properties were measured after 500 time steps, which proved to be a sufficient time to reach a stable equilibrium in our simulations. Each simulation set was repeated 30 times with a new species pool and a new habitat, so that results could be presented with means and standard deviations. In all our simulations, the default values for  $F_{mn}$  and  $N_{reg}$  were fixed at 5 and 20, respectively.

### Community measures

At the end of each set of simulations, we measured species richness as the number of species still present in the community. For each site we assumed that each species' productivity was inversely proportional to the match between species and site values. As a species' competitive ability for the conditions present at a site increased, so did its productivity. Total productivity was then a function of both species abundances and species' competitive abilities and was calculated as:

$$\Phi = \sum_i^N \sum_k^Q 1 - (2 \times |H_k - R_i|) \quad (6)$$

This equation assumes that the maximal productivity at a site is 1 when the match between species and site values is maximal ( $H_k = R_i$ ). Clearly, this measure of productivity is indirect and requires the assumption that competitive ability is equivalent to efficiency of resource utilization, but it is consistent with the measure used by Tilman *et al.* (1997), who assumed that each species' productivity was linked to its competitive ability for a limiting nutrient,  $R^*$ .

## RESULTS

We generated different levels of species richness for each model by changing parameter values. In particular, we varied the number of species in the regional pool,  $N_{reg}$ , the mean fecundity,  $F_{mn}$  and the level of heterogeneity,  $1/\beta$ . Varying the mean fecundity and the level of habitat heterogeneity is equivalent to varying the environmental conditions through variation in the species characteristics incorporated into the model. We first present results on how species richness and productivity are affected by changes in the parameters. We then compare the results of the different models in a search for an overall relationship between species richness and community productivity.

### Variation of the size of the species regional pool

For the RLHH model, because the degree of heterogeneity was maximal, coexistence was always possible. The number

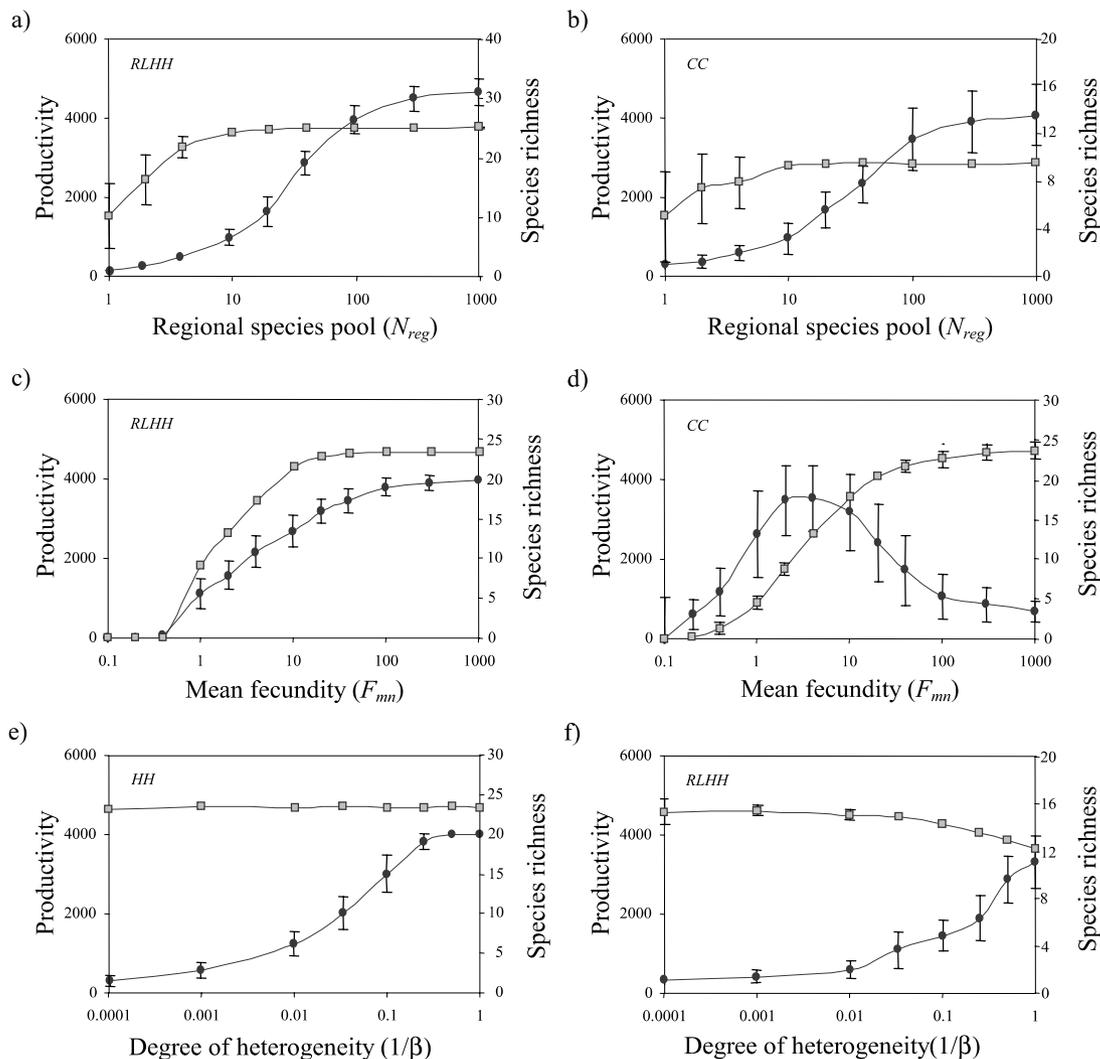
of species coexisting at equilibrium increased with  $N_{reg}$  and reached a plateau due to recruitment limitation (Fig. 2a). As the number of coexisting species increased, each species occupied a smaller proportion of space, so the probability of that its seeds would occupy a site decreased (equation 3), and species richness rapidly became limited. Productivity increased with  $N_{reg}$  (Fig. 2a) because, as the number of species in the regional pool increased, the distribution of  $R_i$ 's in the species pool could better approximate the distribution of  $H_k$ 's, so the match between species' competitive parameters ( $R_i$ ) and the environments ( $H_k$ ) tended to be maximized. This is a kind of sampling effect (Aarssen 1997; Huston 1997; Tilman *et al.* 1997), a signature of which is the high standard deviation of productivity for low values of  $N_{reg}$  (Fig. 2a).

For the CC model, when the regional pool increased, the number of coexisting species increased and reached a plateau (Fig. 2b). As demonstrated by Kinzig *et al.* (1999), the trade-off between fecundity and competitive ability means that the potential for coexistence increases with the competitive ability of the most competitive species. In our simulations, the probability of drawing a very competitive species increased with the size of the regional pool of species,  $N_{reg}$ . Species richness reached a plateau because both the number of sites and maximum fecundity were finite (Goldwasser *et al.* 1994). Productivity increased with  $N_{reg}$  and reached a plateau (Fig. 2b). First, because of a kind of sampling effect, productivity cannot be maximal when the regional pool is too small. Second, one would expect productivity to decrease when  $N_{reg}$  increases because the best competitor (which has a very low fecundity) occupies fewer sites, but this effect is counterbalanced by the increase in abundance of less competitive species. Thus, when the regional pool is so large that the sampling effect disappears, productivity stays constant.

### Variation in mean fecundity

In the RLHH model, the number of coexisting species increased with mean fecundity (Fig. 2c). As  $F_{mn}$  increased, the degree of recruitment limitation decreased, and coexistence was easier; maximal species richness was determined by the size of the regional pool ( $N_{reg} = 20$ ). Productivity was low at low values of fecundity because species were not able to colonize all sites, but it rapidly became maximal as fecundity increased (Fig. 2c).

For the CC model, increasing mean fecundity had two effects on species richness (Fig. 2d). The number of coexisting species first increased because all species were better able to persist at a given mortality, but as  $F_{mn}$  increased, very competitive species could persist, whereas they could not at low values of  $F_{mn}$  (their realized fecundity, given in equation 4, was too low). Space was therefore



**Figure 2** Community properties for the RLHH (a, c, e and f) and the CC (b and d) models as a function of the size of the regional species pool  $N_{reg}$  (a and b), the mean fecundity  $F_{mn}$  (c and d), and the degree of heterogeneity  $1/\beta$  (e and f). We present means and standard deviations for species richness (●) and productivity (□).

rapidly saturated, and poor competitors were progressively excluded by the most competitive species. Species richness then declined. Productivity increased with increasing mean fecundity (Fig. 2d) because the best competitor occupied more sites and the match between species traits and habitat values improved.

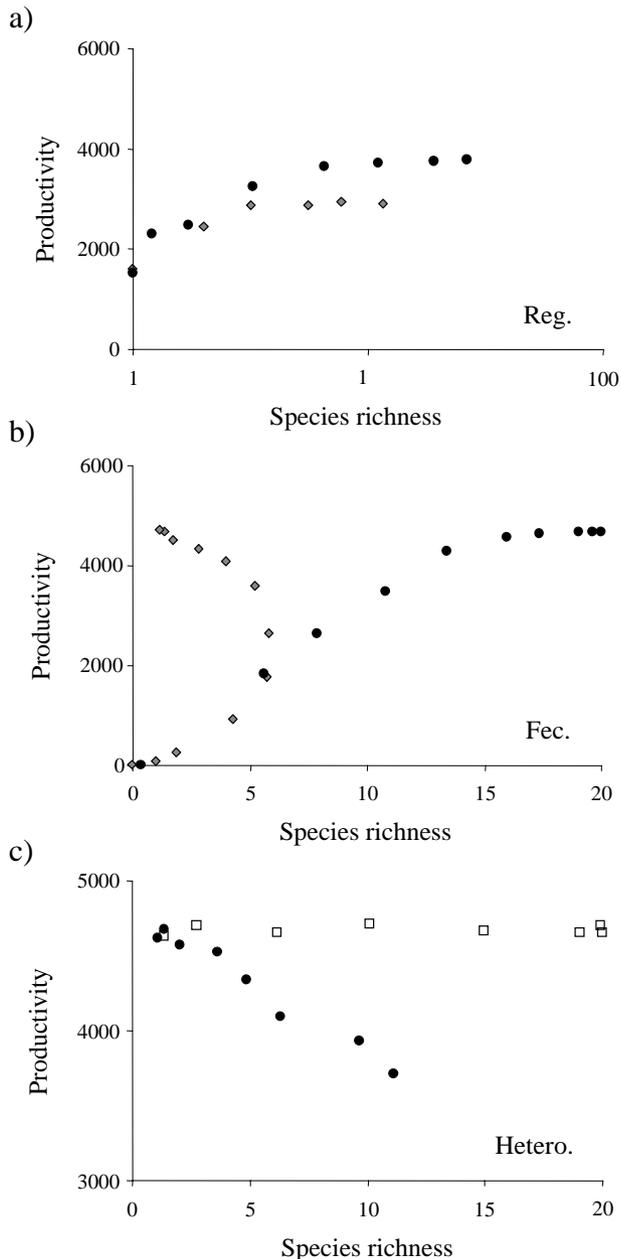
### Variation in heterogeneity

This section concerns only the RLHH model, but we consider also an extreme case in which there is no recruitment limitation (called HH), which helps to explain the results of the RLHH model.

For the HH case, as the environment became more heterogeneous, the number of coexisting species increased

(Fig. 2e). When the habitat was totally homogeneous ( $1/\beta \rightarrow 0$ ), coexistence was impossible because the species with the highest competitive ability had seeds at every site. When the habitat was totally heterogeneous ( $1/\beta \rightarrow 1$ ), coexistence was maximal and only limited by the size of the regional pool ( $N_{reg} = 20$ ). We found the same tendency for the RLHH general model (Fig. 2f), but fewer species coexisted because of the limited fecundity.

Productivity was maximal and constant for the HH case, whatever the degree of heterogeneity (Fig. 2e). Fecundity was not limiting, so there were seeds at every site. The match between species and environment was therefore purely a function of the number of species in the regional pool, which in this case was constant. In the RLHH general case, however, productivity decreased as the degree of hetero-



**Figure 3** Relationships between species richness and productivity for the different models studied in the present paper: RLHH (●), CC (◆), and HH (□). Variation in species richness was driven by variation of the size of the regional pool (a), mean fecundity (b), and the degree of heterogeneity (c).

genity increased (Fig. 2f). When the environment was homogeneous ( $1/\beta \rightarrow 0$ ), there was competitive exclusion by the species with the  $R_i$  closest to 0.5, and productivity was high. When heterogeneity was maximal ( $1/\beta \rightarrow 1$ ), all species coexisted, but because species fecundity and the regional pool were limited, the match between a species'

competitive ability and the environment of the site that it occupied was lower than when the environment was homogeneous, and productivity therefore declined.

### Relationship between species richness and productivity

We did not find any general relationship between species richness and productivity. When variation in species richness was driven by increases in the number of species in the regional pool (Fig. 3a), we found a positive relationship in all cases. However, when variation in species richness was driven by increasing mean fecundity (Fig. 3b), the relationship was positive for the RLHH model but either positive or negative for the CC model. Finally, when variation in species richness was driven by increasing degree of heterogeneity (Fig. 3c), the relationship was negative or zero, depending on the degree of recruitment limitation.

## DISCUSSION

### Generation of species-richness gradients

We generated the different mechanisms by changing assumptions about how species interact and coexist in a community, and we obtained the species-richness gradient by changing parameters within a given model.

Changing the size of the regional pool has two major effects on species composition. It makes species richness increase and it makes species composition at equilibrium more closely match local environmental conditions. Our models show that, in such context, it is realistic to expect an overall positive relationship between species richness and community properties such as productivity. This result can be interpreted as a sampling effect (Aarssen 1997; Huston 1997; Tilman *et al.* 1997) or as a positive selection effect (Loreau 2000). For the RLHH model, however, one can also interpret this pattern as the result of a complementarity effect between coexisting species (Tilman *et al.* 1997; Loreau 1998b), because each species is a good competitor in a different habitat. Therefore, when the degree of habitat heterogeneity is high, a combination of different species will use the habitat more efficiently than will a single species. This result illustrates the difficulty of clearly differentiating between complementarity and sampling effects: when the environment is homogeneous, the increase in productivity stems from a pure sampling effect, and as it becomes more heterogeneous it arises from both sampling and complementarity effects.

When variation in species richness is generated by changes in fecundity, recruitment limitation in a heterogeneous habitat (RLHH) lowers the match between a species' competitive ability and the local environment in which it is found. When heterogeneity is maximal, both species richness and productivity decrease with decreasing  $F_{min}$ ;

these are then positively correlated. The results obtained for the CC model can be interpreted in the context of succession theory. In this model, species richness is maximal at intermediate levels of  $F_{ms}$ , when, because of the trade-off, less-competitive species are abundant and competitive species are rare. However, productivity is low because the community contains many poor competitors that use the habitat inefficiently. Such communities are characteristic of early stages of a succession, which have a high species richness but a low efficiency of resource use and thus a low productivity (Odum 1969). It is interesting to note that in the CC model the relationship between species richness and productivity can be either positive or negative depending only on the degree of recruitment limitation in the community.

Finally, when we generate a species-richness gradient by altering the degree of habitat heterogeneity, the number of species increases with increasing heterogeneity, but productivity stays constant or declines. This result differs from intuitive expectation based on other theoretical studies that have examined the effects of niche differentiation on productivity by means of the complementarity effect (Tilman *et al.* 1997; Loreau 1998b). Tilman *et al.* (1997) and Loreau (1998b) have considered that niche differentiation allows different species to occupy the same site. In their studies, as the number of available niches (the degree of heterogeneity, in our model) increased, both species richness and productivity increased. In contrast, we did not permit different species to occupy the same site. Under these conditions, when heterogeneity increased, species richness increased because of niche differentiation; but space was limited, and all species occupied relatively fewer sites: adding new species to the community produced no strong additional effect on productivity. For this kind of complementarity, we propose the term 'weak complementarity' because total resource use, usually regarded as a component of complementarity (and the basis for measures such as overyielding, Loreau 1998a), does not increase.

Like any model, ours involves a number of simplifying assumptions. In particular, we assumed that species competitive ability and productivity are correlated, that communities reach a steady state, and that mortality is constant. We used an indirect measure of productivity, assuming that competitive ability is equivalent to efficiency of resource utilization. Although the relationship between productivity and competitive ability is still controversial (Grime 2001), this hypothesis has been used by other authors (Tilman 1994; Cardinale *et al.* 2000). Moreover, changing this assumption would not drastically change our results because neither the complementarity nor the selection effect depends on a particular competition mechanism. Nonequilibrium situations are observed in many natural systems, such as grasslands maintained by

management or in a successional transition. Because our results focus on their long-term equilibrium behaviour, there is a potential mismatch in time scale between theory and potential experimental tests. It would be interesting as a future direction to investigate how the results obtained from theoretical models that explore the relationship between species richness and productivity may change when transient dynamics is considered. We have also assumed the mortality rate to be constant and equal among species. In our model, mortality determines the rate at which sites become vacant, so in most cases (except in the trade-off model) varying a common mortality rate would only change the speed at which the equilibrium is reached and the number of species that coexist at equilibrium, without affecting any of the general tendencies that we found. In contrast, varying mortality between species would generate new scenarios of coexistence, but it would result in a new level of complexity without providing fundamentally new insights into the question we investigate here.

### The relationship between species richness and productivity

Our results show that the nature of the relationship between species richness and productivity depends on both the mechanism of coexistence and the cause of the species-richness gradient. In summary, our different models suggest that a positive relationship between species richness and productivity is likely to occur under several conditions, which can act alone or in combination. (1) For all models, a positive relationship is expected if the size of the regional species pool increases so that a positive selection or complementarity effect can act. (2) As shown by the RLHH model, the habitat must be sufficiently heterogeneous that niche differentiation between species can be expressed and that coexisting species are complementary. Moreover, this differentiation must be such that species can occupy overlapping physical sites; otherwise complementarity is weak, and no relationship between species richness and productivity is expected. (3) Finally, as shown by recruitment-limited models, species must have access to all sites so that the match between species traits and habitat values is good. Conversely, if the process that increases species richness results in the creation of free or badly exploited sites (recruitment limitation), the relationship between species richness and productivity will probably be negative.

The relationship between species richness and productivity has traditionally been studied in two ways. First, ecologists have asked whether a productive environment supports a higher number of species than an unproductive environment. 'Productive environment' is there defined as a combination of environmental variables (rainfall, nutrient supply, etc.) allow-

ing a high net primary productivity. This question has been addressed by field studies that have compared established plant communities with different productivities. It is likely that different mechanisms and different environmental conditions were acting to maintain species richness, and under those conditions, as shown in our results, all kinds of relationships are possible. This is indeed what has been found, with almost every new study producing a new relationship (see Waide *et al.* 1999 for review). Second, ecologists have investigated whether, in a particular environment, a species-rich community has a higher productivity than a species-poor community. Recent theoretical and experimental work has shown that in this context the relationship between species richness and productivity can be positive because of either a complementarity effect or a sampling effect (see Tilman 1999 and Loreau 2000 for reviews). Because environmental variables are more likely to vary among sites than within sites, the former approach can be viewed as considering across-site relationships and the latter within-site relationships (Lawton *et al.* 1998; Loreau 1998b, 2000).

Our work is at the interface between these two approaches because we consider environmental conditions (the habitat) to determine in part the characteristics of the species pool, and these in turn determine community productivity. Productivity is thus responding to both environmental conditions and species richness. Environmental constraints set the range of variation of potential productivity, and local coexistence mechanisms determine realized productivity within this range. In our model, varying different parameters allows us to simulate the two traditional approaches mentioned above. Variation of the regional species pool generates, at least in part, a variation of species richness that is independent of within-site environmental conditions, whereas variation of other parameters such as fecundity and heterogeneity mimics the effects of variation in environmental conditions across sites. It is interesting to note that we found positive relationships between productivity and species richness when we obtained the gradient of species richness by varying the size of the regional pool, just as in local experimental studies in which environmental conditions were homogeneous (Naeem *et al.* 1996; Tilman *et al.* 1996; Hooper & Vitousek 1997; Naeem & Li 1997; Hector *et al.* 1999). In contrast, when we obtained the gradient of species richness by varying parameters representing the effects of environmental conditions, we found either positive, null, or negative relationships, just as in across-site comparative studies (see Waide *et al.* 1999 for a review). Although the small numbers of scenarios studied here does not allow further generalization, our results illustrate the complexity of the relationship between productivity and species richness, which differs among scales because of the different causal relationships between variables at different scales.

### Implications for some other models of species coexistence

In the present paper, we have focused on two main models of species coexistence driven by habitat heterogeneity and recruitment limitation, but other mechanisms might permit coexistence between species. We now briefly discuss how these other mechanisms may affect the relationship between species richness and productivity. We consider temporal fluctuations, intermediate disturbance, local similarity and regional influence. Clearly, this section is speculative but we hope it will provide stimulus for future studies.

Temporal fluctuations have been suggested as a possible explanation for permanent species coexistence. Coexistence has been demonstrated to be possible when rates of species recruitment fluctuate (Chesson & Warner 1981) or species respond nonlinearly to resource fluctuations (Levins 1979). Because growth rates must be nonlinear (so that periods of strong recruitment can more than compensate for periods of poor recruitment) and productivity should be broadly correlated with growth rate, one would expect a positive relationship between productivity and species richness when this type of mechanism is acting.

The intermediate-disturbance hypothesis (Grime 1973; see also Huston 1994 for a review) has been invoked by many authors to explain the maintenance of high species richness in plant communities (but see Wootton 1998). At intermediate disturbance intensities, the time to reach equilibrium is extremely long, so competitive exclusion does not occur within finite time periods. According to those authors, trophic diversity is expected to be maximal at intermediate disturbance frequencies or intensities, and thus ecosystem processes could then be maximized, generating a unimodal relationship between species richness and ecosystem processes.

Local similarity has also been invoked to explain coexistence between competitive species. Quasi-similar species can coexist because the time to competitive exclusion is extremely long (Hubbell 1979, 2001; Hubbell & Foster 1986). This pattern is reinforced by small stochastic events that may hide competitive differences (Ågren & Fagerström 1984). Because species are similar in their competitive ability and their pattern of resource utilization, additional species should have no effect on ecosystem functioning. Species are then functionally redundant (Walker 1992; Loreau 1998b).

Local coexistence can also be maintained by continuous immigration from an external source (MacArthur & Wilson 1967; Shmida & Ellner 1984; Loreau & Mouquet 1999; Hubbell 2001). Primary productivity is then expected either to decrease or to stay constant with increasing species richness, depending on the relationship between immigration and local reproduction (Loreau & Mouquet 1999).

## ACKNOWLEDGEMENTS

We thank S. Barot, A. Gonzalez, J. H. Lawton and G. Kokkoris for comments on the manuscript. A. Thistle kindly edited the manuscript. This collaboration was funded by the CNRS-PICS ('Dynamics of biodiversity: from species interaction to ecosystem functioning') and NERC. NM was supported by a grant from the French Ministry of Research, and JLM by a George Murray Scholarship from the University of Adelaide, South Australia.

## REFERENCES

- Aarssen, L.W. (1997). High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos*, 80, 183–184.
- Ågren, G.I. & Fagerström, T. (1984). Limiting dissimilarity in plants: randomness prevents exclusion of species with similar competitive abilities. *Oikos*, 43, 369–375.
- Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91, 175–183.
- Chesson, P.L. (1985). Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoret. Popul. Biol.*, 28, 263–287.
- Chesson, P.L. (2000). Mechanism of maintenance of species diversity. *Annu. Rev. Ecol. Systematics*, 31, 343–346.
- Chesson, P.L. & Warner, R.W. (1981). Environmental variability promotes coexistence in lottery competitive systems. *Am. Naturalist*, 117, 923–943.
- Goldwasser, L., Cook, J. & Silverman, E.D. (1994). The effect of variability on metapopulation dynamics and rates of invasion. *Ecology*, 75, 40–47.
- Grime, J.P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Grime, J.P. (1997). Biodiversity and ecosystem function: the debate deepens. *Science*, 277, 1260–1261.
- Grime, J.P. (2001). *Plant Strategies: Vegetation Processes and Ecosystem Properties*. Wiley, Chichester, England.
- Hastings, A. (1980). Disturbance, coexistence, history and the competition for space. *Theoret. Popul. Biol.*, 18, 363–373.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Höglberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Sherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troubis, A.Y., Woodward, F.I., Yachi, S. & Lawton, J.H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1126.
- Hooper, D.U. & Vitousek, P.M. (1997). The effect of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hubbell, S.P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203, 1299–1309.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Monographs in Population Biology 32. Princeton University Press, Princeton.
- Hubbell, S.P. & Foster, R.B. (1986). Biology, chance, and history and the structure of tropical rain forest tree communities. In: *Community Ecology*, eds Diamond, J. & Case, T.J. Harper & Row, New York, pp. 314–329.
- Hughes, J.B. & Roughgarden, J. (2000). Species diversity and biomass stability. *Am. Naturalist*, 155, 618–627.
- Hurttt, G.C. & Pacala, S.W. (1995). The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *J. Theoret. Biol.*, 176, 1–12.
- Huston, M.A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, New York.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–469.
- Kinzig, A.P., Levin, S.A., Dushoff, J. & Pacala, S. (1999). Limiting similarity, species packing, and system stability for hierarchical competition-colonization models. *Am. Naturalist*, 153, 371–383.
- Lawton, J.H., Naeem, S., Thompson, L.J., Hector, A. & Crawley, M.J. (1998). Biodiversity and ecosystem function: getting the Ecotone experiment in its correct context. *Funct. Ecol.*, 12, 848–852.
- Lehman, C.L. & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *Am. Naturalist*, 156, 534–552.
- Levins, R. (1979). Coexistence in a variable environment. *Am. Naturalist*, 114, 765–783.
- Loreau, M. (1998a). Separating sampling and other effects in biodiversity experiments. *Oikos*, 82, 600–602.
- Loreau, M. (1998b). Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl. Acad. Sci. USA*, 95, 5632–5636.
- Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3–17.
- Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M. & Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *Am. Naturalist*, 154, 427–440.
- MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Naturalist*, 101, 377–387.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Moore, J.L., Mouquet, N., Lawton, J.H. & Loreau, M. (2001). Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos*, 94, 303–314.
- Naeem, S., Hakansson, K., Lawton, J.H., Crawley, M.J. & Thompson, J. (1996). Biodiversity and plant productivity in a model assemblage of plant species. *Oikos*, 76, 259–264.
- Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507–509.
- Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262–270.
- Pacala, S.W. & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Naturalist*, 134, 222–257.
- Shmida, A. & Ellner, S. (1984). Coexistence of plant species with similar niches. *Vegetatio*, 58, 29–55.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.

- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *Proc. Natl. Acad. Sci. USA*, 94, 1857–1861.
- Tilman, D. & Pacala. (1993). The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds Ricklefs, R.E. & Schluter, D. University of Chicago press, Chicago, pp. 13–25.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999). The relationship between productivity and species richness. *Annu. Rev. Ecol. Systematics*, 30, 257–301.
- Walker, B.H. (1992). Biodiversity and ecological redundancy. *Conserv. Biol.*, 6, 18–23.
- Wardle, D.A. (1999). Is sampling effect a problem for experiments investigating biodiversity-ecosystem function relationships? *Oikos*, 87, 403–407.
- Wootton, J.T. (1998). Effects of disturbance on species diversity: a multitrophic perspective. *Am. Naturalist*, 152, 803–825.

Editor, P. Marquet

Received 18 June 2001

First decision made 30 July 2001

Second decision made 24 September 2001

Manuscript accepted 27 September 2001