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# Species richness peaks for intermediate levels of biomass in a fractal succession with quasi-neutral interactions

**David Mouillot and Nicolas Mouquet**

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The mechanisms that promote species richness, including net community interactions, are considered central to the investigation of the consequences of biodiversity loss for ecosystem functioning. Recently, some empirical studies at large spatiotemporal scales suggest that increasing species richness within natural communities results in a finer division of biomass among species rather than an increase in total biomass. In parallel, the most common pattern observed in nature is the peaked relationship between diversity and productivity estimated as total biomass. Thus, the aim of our study is to provide model predictions for the diversity–biomass relationship with various levels of net species interactions within communities: negative, neutral, quasi-neutral and positive. Using a scaling relationship between the number of species and total community biomass, we propose a new self-similar process of biomass partitioning during a community assembly process. At each step of the succession, K more species appear that are A times less abundant on average giving $K = A^d$; the parameter d being a fractal dimension related to the nature of interactions among coexisting species. Our results, compared to those from meta-analyses about empirical diversity–productivity relationships, illustrate that quasi-neutral interactions among coexisting species lead to the most commonly observed pattern: an 'envelope' where diversity peaks at intermediate values of total biomass, i.e. that the area below the hump-backed line (considered as the upper boundary) is filled with data points.

*David Mouillot (mouillot@univ-montp2.fr), UMR CNRS-UMII 5119 Ecosystèmes Lagunaires, Univ. Montpellier II CC 093, FR-34095 Montpellier Cedex 5, France. – N. Mouquet, UMR 5554, ISEM, Univ. Montpellier II CC 065, FR-34095 Montpellier Cedex 5, France.*

In a natural world increasingly transformed by human activities, ecologists are faced with the challenge of understanding the processes behind species coexistence, as well as the relationship between species richness and ecosystem processes (Loreau et al. 2001). Preserving biodiversity is assumed to maximize the probability of a viable response of communities to global change by increasing the variability of potential alternative ecological organizations to disturbances and changing environmental conditions (Peterson et al. 1998).

An increasing number of studies have highlighted the role of species interactions in shaping the relationship between species coexistence (richness) and functioning in ecological communities (Cardinale et al. 2002, Mouquet et al. 2002). Local coexistence between competing species can be explained by two opposing views of ecological communities: the niche-assembly and the neutral-assembly perspectives. In the former, community assembly rules are based on species ecological niches or functional roles (Weiher et al. 1998, Tokeshi 1999, Sugihara et al. 2003) whereas in the latter, communities are assemblages of species largely thrown together by chance and history (Caswell 1976, Hubbell 2001, Chave 2004). In this context, contrasted predictions can be

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done based on the nature of species interactions within the communities. (1) Positive interactions among species lead to a positive relationship between species richness and ecosystem functioning given complementarity and facilitation among coexisting species (Loreau and Hector 2001, Petchey 2003). Species-rich communities are more prone to be productive, stable and resistant to invasion by using a larger range of resources and by filling a higher amount of the whole niche space (Tilman et al. 1997, Naeem et al. 2000, Moore et al. 2001, Fargione et al. 2003). (2) Antagonistic interactions may weaken considerably the diversity–function relationship. For instance fungi secrete chemical substances which act to reduce competition from other microbes (Semighini et al. 2006). Increasing the diversity of fungi might thus lead to more chemical inhibition, in turn reducing ecosystem functioning, as for example litter decay efficiency (Hattenschwiler et al. 2005). (3) Neutral interactions (Hubbell 2001) imply functional redundancy between coexisting species, and would lead to the absence of relationship between species richness and ecosystem functioning. For instance, Wardle (2001) reported that there was no evidence for diversity effect on productivity in Mediterranean shrublands suggesting a neutral role of diversity on ecosystem functioning under certain circumstances (Jonsson et al. 2001, Orwin et al. 2006). Within the context of the diversity–function debate, positive interactions among species have been mainly reported while antagonistic and neutral interactions have been largely overlooked (but see Jonsson et al. 2001, Orwin et al. 2006).

While these studies focused on the relationship between the conditions that maintains species richness and ecosystem functioning, others have focused on the general patterns of species diversity and ecosystem properties (Waide et al. 1999, Mittelbach et al. 2001). For instance, Enquist et al. (2002) introduced a new perspective on the processes that regulate species coexistence and diversity across years and broad geographical gradients. Using a worldwide database including different sites, they found a regular taxonomic partitioning of total biomass in species assemblages, suggesting that increasing species richness within natural communities results in a finer division of biomass between taxa, rather than a total biomass increase. The power function found by Enquist et al. (2002) suggests that scaling processes may shape the distribution of biomass among species. This general pattern at large spatial and temporal scale needs now to be re-interpreted in the context of species interactions within communities. Regular taxonomic partitioning of total biomass gives support to the absence of relationship between species richness and ecosystem functioning due to functional redundancy, or neutrality, between coexisting species (Enquist et al. 2002). This interpretation does not contradict recent experimental studies that have found positive relationship between community biomass and species richness (Hector et al. 1999) because these experiments were considering local scales (within sites sensu Lawton et al. 1998) while the results of Enquist et al. (2002) concern large scales (between sites), but this example highlights the need for a common framework.

In our article we propose to link the mechanistic approaches based on species interaction coefficients and the large scale patterns observed by Enquist et al. (2002). To this aim, we compare diversity–biomass relationships obtained by sampling communities of different stages of a succession at the scale of a landscape but with knowing the mechanisms underlying succession dynamics. Classical succession theory was originally developed for terrestrial plant communities and has been used to predict how an assemblage will change over time (Whittaker 1967, Odum 1969, Horn 1974, Walker and Chapin 1987). We developed a fractal model of succession to predict the diversity–biomass relationship under various levels of net species interactions within communities (from negative to neutral and to positive interactions). By varying the fractal exponent (linked to the nature of average interactions between species), we simulated various levels of net species interactions within communities (from negative to neutral and to positive interactions) and found various patterns of biomass–diversity relationship empirically observed at a macroecological scale: positive, negative, and peaked. We discuss our results in the context of the debate opposing the classical view of community ecology to the approach proposed by the neutral theory (Hubbell 2001).

## Biomass partitioning among successional species

The main driver of succession is the impact that established species have upon their own environments (Pickett et al. 1987). In this context, each establishment of a new species during the succession depends on the previous realization of particular conditions. Thus, the relationship between the number of species and the partitioning of total biomass during the course of a succession can be described as a fractal process where species diversity is a fractal property of biomass (Frontier 1994, Mouillot et al. 2000). More conceptually, a tree can summarize the succession in which, at each step, K more branches (species) are present of length divided by a factor A (biomass partitioning); this tree being fractal (Frontier 1994) (Fig. 1). The branches at any step can be species surviving from the previous step of the succession. However, the original environment may have been optimal for the first species, but the newly altered environment is often optimal for some other species of plant or animal, so new species will be able to enter and some species present in previous steps are

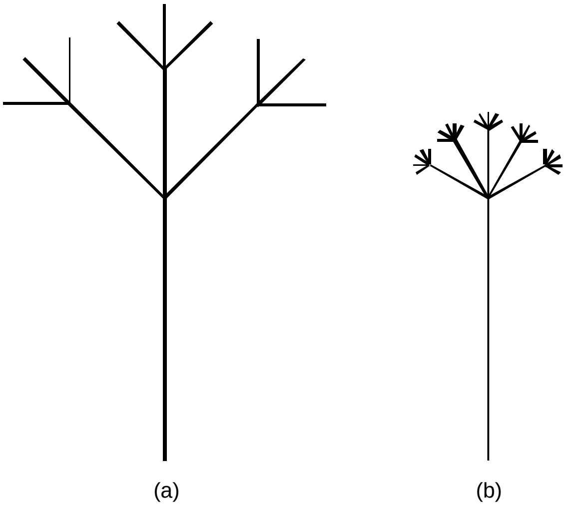

Fig. 1. Fractal trees with two sets of parameters ($K = 3$, $k = 2$ for (a); $K = 5$, $k = 4$ for (b)). At each of the three steps of the fractal process, K more branches (species) are present of length divided by a factor A (biomass partitioning).

likely to disappear in a species replacement process largely documented for successions (Horn 1974). In our paper we consider only cases where $K > 1$ which implies that more species are expected to be present at each new step of the succession, both new ones as well as ones surviving from previous steps. This "constraint" seems rather realistic in the sense that there are usually larger numbers of late successional species than there are early successional species (Whittaker 1967). This may lead to a self-similar process generating a potentially infinite tree, each branch being a miniature model of the whole tree (Frontier 1994, Mouillot et al. 2000, Fig. 1). Based on theses simple considerations, we developed a conceptual model in order to investigate the co-evolutionary relationship between species richness and total biomass in a community assembly process where interactive species partition resources.

In mathematical terms, during each step of the process of ecological succession, K more species are present which are A times less abundant on average giving $K = A^d$ (with d the fractal dimension and K and A multiplicative factors). For instance, let's apply a fractal succession with $K = 2$ and $A = 2$ ($d = 1$) to a community of 10 species sharing a total biomass of 100 units (10 units by species on average). At the next step this community will contain 20 species (times more) with a mean abundance of 5 units by species (two times less) and the same total biomass of 100 units. The fractal dimension d is interpreted as a simple measure of the average interactions within a community during a succession, i.e. d is related to the global nature of interactions among coexisting species (not to the global strength of these interactions). We define interactions on the basis of the effects of species interactions on community properties. Four cases can be considered:

1) If $d = 1$ (neutrality): the number of species increases at the same rate as the average biomass per species decreases. Thus, the community partitions the same biomass regardless of the number of species (sensu Enquist et al. 2002). Species are equivalent or functionally redundant and thus competition is perfectly symmetric (Wardle et al. 1997, Loreau 2004). This corresponds to the neutral view of community ecology (Caswell 1976, Hubbell 2001).
2) If $d > 1$ (positive interactions): the number of species increases at a higher rate than the biomass per species decreases. New species added to the community during the succession are able to utilize new resources or to help previous installed species to utilize more resources. This corresponds to niche complementarity (Tilman et al. 1997, Loreau 1998) or facilitation (including mutualism) (Cardinale et al. 2002).
3) If $d < 1$ (negative interactions): the number of species increases at a slower rate than the biomass per species decreases which means that as the number of species increases the total biomass decreases. In other words, new species added during the succession decrease the ability of the community to utilise resources. This corresponds to asymmetric competition (Levine and Rees 2002, Rajaniemi 2003), antagonistic relationship between species (Finke and Denno 2002, Lombardero et al. 2003) or inhibition (Connell and Slatyer 1977, Hattenschwiler et al. 2005). Contrary to asymmetric competition, antagonism and inhibition have been poorly considered in the debate on the relationship between species richness and ecosystem functioning.
4) We will also consider quasi-neutral cases with d values close to 1. These communities build with quasi-neutral interactions among species can be defined as communities where species are quasi-redundant in the way that niche complementarity, facilitation or antagonistic relationships are not strong enough to enhance either a consistent positive or a negative trend in the species richness along a biomass gradient. This concept was already suggested by Zobel (2001) in a different context to describe small-scale richness formation where interspecific competition is not a significant factor to be considered in explaining plant species co-existence.

## The fractal model

Given that $B_0$ is the total biomass, in our model at the initial stage with only one species and that K more species are present ($K > 1$) in the next stage that are on average A times less abundant, the biomass $B_t$ can be expressed as:

$$B_1 = K\frac{B_0}{A}$$

$$B_2 = K\frac{B_1}{A} = K^2\frac{B_0}{A^2}$$

$$\ldots$$

$$B_t = K^t\frac{B_0}{A^t} \tag{1}$$

With $A = K^{\frac{1}{d}}$ and $S_t = K^t$ we have:

$$B_t = B_0(S_t)^{\left(\frac{d-1}{d}\right)} \tag{2}$$

with $S_t$ the number of species at the time step t. The total biomass at the step t depends thus on the fractal parameter d that determines the biomass partitioning between species. The biomass ratio between two time steps can be expressed as:

$$\Delta_B = \frac{B_{t+1}}{B_t} = K^{\left(\frac{d-1}{d}\right)} \tag{3}$$

It is independent of the time step t considered, and depends only on the number of new species added at each step of the succession and on the fractal parameter d. As mentioned earlier, if $d = 1$ (neutral interaction among species) $\Delta_B = 1$, if $d > 1$ (positive interaction among species) $\Delta_B > 1$ and if $d < 1$ (negative interaction among species) $\Delta_B < 1$. Since the number of species is continuously increasing during the succession ($K > 1$), simple predictions of the relationship between the number of species and the total biomass are obtained: positive relationship if $d > 1$, negative if $d < 1$ and no relationship if $d = 1$ (Fig. 2).

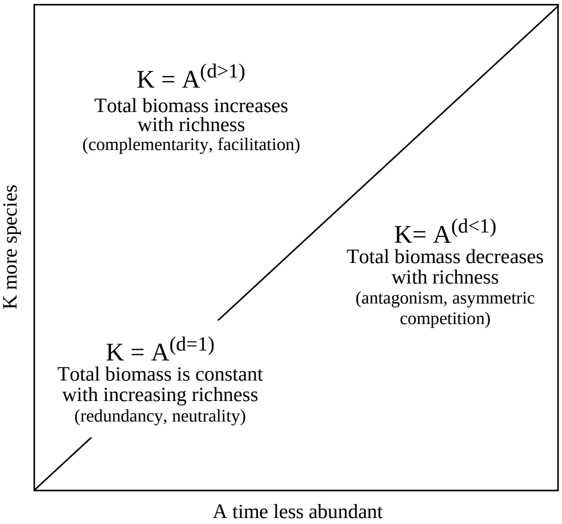

Fig. 2. Expected relationships between species richness and total community biomass for different values of K and A. During the succession, at each step, K more species appear that are on average A times less abundant: $K = A^d$ with d a fractal exponent related to the nature of interactions between species during the succession build up.

In its simplest form, this model is deterministic and predicts a perfectly regular succession of species through time. However, stochastic processes are also likely in species assemblage (Hubbell 2001, Tilman 2004) and, as a consequence, the rate of species richness increase (K) is more likely to be a number with a fraction than a whole number. In this case, the fractal succession of species can no longer be represented by a simple fractal tree but by a statistically self-similar probability branching diagram (Mandelbrot 1977, 1982), with the relationship between the total biomass and the number of species during a succession becoming a Bayesian stochastic process. For example, if one species is present at the beginning of the succession and $K = 1.2$, so that more species appear at each step that are $A = 2$ times less abundant, there are two possibilities: either two new or only one new species will appear, in each case with biomass lowered by a factor of two. A probability can be attributed to each of these two possibilities: $p = K - \text{int}(K) = 0.2$ the probability of having two new species and $p = \text{int}(K) + 1 - K = 0.8$ of having only one new species ('int' is the integer part, i.e. rounding down). During the second step of the succession, 1, 2 or 4 new species can appear, each two times less abundant on average than in the first step, a probability being associated to each event (Fig. 3). More generally, when the initial biomass $B_0$ is partitioned among $S_0$ species, the total biomass of the $S_1$ species at the first succession step ($B_1$) can be expressed as:

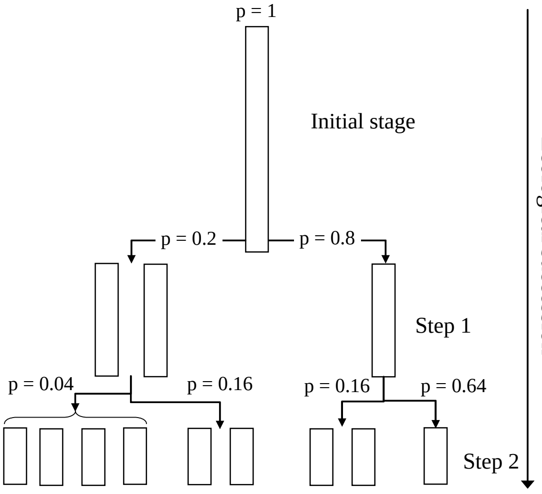

Fig. 3. Two steps of a Bayesian stochastic process during a fractal ecological succession where 1.2 new species appear 2 times less abundant; each rectangle is a species with a length proportional to its abundance. Different probabilities are associated to each branch.

$$B_1 = \frac{B_0}{A} \times \text{int}(K) \times P(S_1 = S_0 \times \text{int}(K)) + \frac{B_0}{A} \times (\text{int}(K)+1) \times P(S_1 = S_0 \times (\text{int}(K)+1)) \quad (4)$$

with,

$$P(S_1 = S_0 \times \text{int}(K)) = K - \text{int}(K)$$
$$P(S_1 = S_0 \times (\text{int}(K)+1)) = \text{int}(K) + 1 - K$$

The ratio of the total community biomass between two steps of the succession, with K more species A less abundant at each step is given by:

$$\Delta_B = \frac{B_{t+1}}{B_t} = \frac{\text{int}(K) \times P(S_{t+1} = S_t \times \text{int}(K)) + (\text{int}(K)+1) \times P(S_{t+1} = S_t \times (\text{int}(K)+1))}{A} \quad (5)$$

with,

$$P(S_{t+1} = S_t \times \text{int}(K)) = K - \text{int}(K)$$
$$P(S_{t+1} = S_t \times (\text{int}(K)+1)) = \text{int}(K) + 1 - K$$

The last equation (5) determines a Bayesian stochastic process that determines biomass partitioning among the coexisting species through a fractal succession.

Our model includes migration or speciation events adding new species to the community but also includes extinction in the sense that it does not suppose that the species present during one step of a succession will also be present during the next step. For simplicity, our model does not consider any disturbances that are commonly considered in ecological successions (Connell and Slatyer 1977, Turner et al. 1998). In our model, species accumulation does not asymptote because we consider an infinite regional pool of species. We will consider these limitations in the discussion. Our model was developed to provide biomass and richness distributions along a large scale succession gradient corresponding to a limited number of stages (non-equilibrium). The samples used to construct the richness–biomass relationship must be understood as being either spatially or temporally separated.

## Simulations and results

Using this Bayesian fractal process we simulated the dynamics of species richness and total community biomass during a succession. We fixed $K = 2.3$ and varied A to obtain five different scenarios:

Positive interaction ($A = 1.81 \rightarrow d = 1.4$),
Quasi-neutral positive interaction ($A = 2.13 \rightarrow d = 1.1$),
Redundancy ($A = 2.3 \rightarrow d = 1$),
Quasi-neutral negative interaction ($A = 2.5 \rightarrow d = 0.9$) or
Negative interaction ($A = 4 \rightarrow d = 0.6$).

We iterated the succession for 10 steps and repeated this process for 100 replicates. Ten steps are long enough to observe various diversity–biomass patterns according to the parameters and short enough to avoid unrealistic patterns obtained when too many species accumulate (since there are no disturbance or limited regional pool). Each succession started with 1 species and a total biomass of 100. For each scenario, the 100 simulated replicates obtained were represented on a total biomass vs species richness plot (Fig. 4).

Depending of the nature of the interaction (d), we obtained various diversity/total-biomass relationships (Fig. 4) corresponding to the various relations observed in the field (Waide et al. 1999, Mittelbach et al. 2001). With positive interaction among species (Fig. 4a), there was a positive relationship between species richness and total biomass because at each step of the succession, there is 2.3 more species that are two times less abundant (total biomass increases with the number of species). When there was negative interaction (Fig. 4b), we found a negative relationship (hyperbolic shape) between species richness and total biomass. In this case, at each time step of the succession there were 2.3 more species that were 4 times less abundant, thus whatever the realized increase of species richness was in the stochastic process (either 2 or 3) the total biomass always decreased with the number of species.

When species were redundant (neutral interactions) there was a peaked envelope (sensu Schmid 2002) relationship between richness and total biomass in the community (Fig. 4c). We define this peaked envelope as the biomass–richness space which contains all the points and which peaks for intermediate biomass values. The species richness was increasing at each step of the succession but the total biomass was alternatively increasing or decreasing due to the stochastic nature of the succession process: there was a probability of 0.7 that 2 new species appeared 2.3 times less abundant leading to a decreasing total biomass in the community and a probability of 0.3 that 3 new species appeared 2.3 times less abundant leading to an increasing total biomass. There was a higher probability that interspecific interactions are negative (0.7) than positive (0.3) but, on average, over several steps of succession, the probability to increase total community biomass with species richness equals to zero which is in accordance with the neutral case. When 2 new species appear 2.3 times less abundant, we obtained a total biomass divided by 1.15 (2.3/2) with a probability of 0.7. Conversely, when 3 new species appear 2.3 times less abundant we obtained a

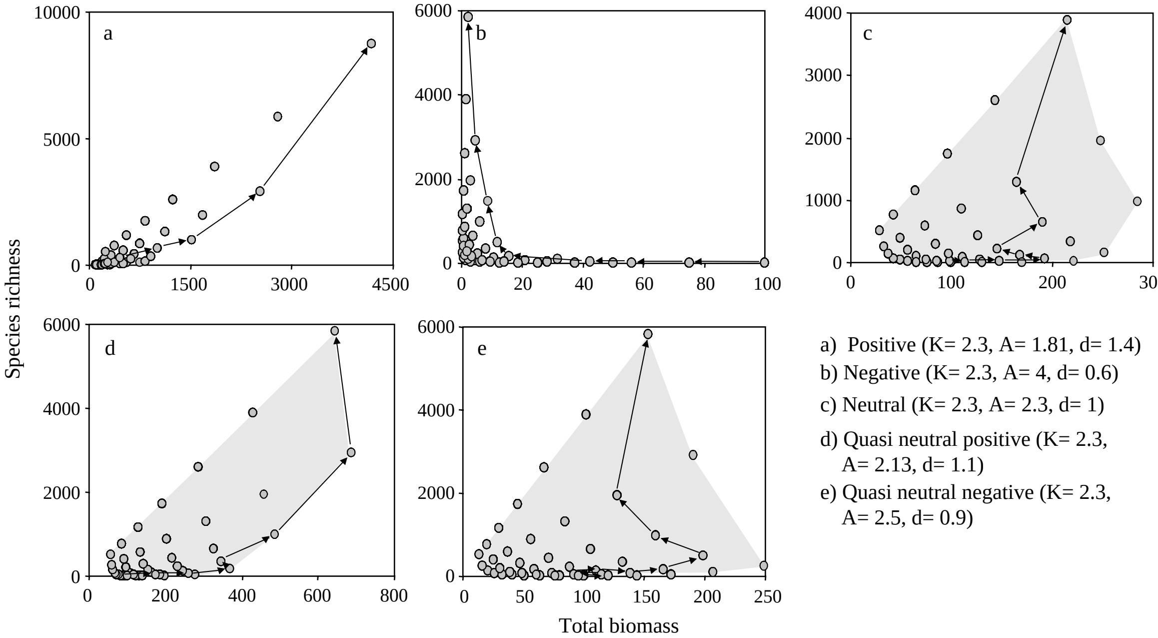

Fig. 4. Species richness–total biomass relationships for various fractal ecological successions. Each point represents the species richness and the total biomass of the community under assemblage process. We ran the succession for 10 steps and repeated this process for 100 replicates. Each succession started with 1 species and a total biomass of 100. The parameters were K more species (2.3) A times less abundant (1.81 for (a): positive interaction, 0.6 for (b): negative interaction among species, 2.3 for (c): neutral interaction, 2.13 for (d): quasi neutral positive interaction and 2.5 for (e): quasi neutral negative interaction). To illustrate the relationship between species richness and total biomass during community assembly, we drew one succession pathway directly on each figure.

total biomass divided by 0.77 (2.3/3) with a probability of 0.3. Overall the total biomass along the richness gradient is divided by $1.15 \times 0.7 + 0.77 \times 0.3 = 1$.

We found roughly the same results with quasi-neutral interactions, be they positive (Fig. 4d) or negative (Fig. 4e). Note that the three peaked relationships (Fig. 4c–e) are asymmetric because the probability of obtaining 2 species was higher than the probability of obtaining 3 species (0.7 vs 0.3). A symmetric peaked relationship would have been obtained with $K = 2.5$ because at each step of the succession the probability of having 2 more or 3 more species would be the same (0.5).

## Discussion

We have shown that a simple fractal model of ecological succession, based on the nature of the mean interaction among species during the course of a succession, can predict the different relationships found in the field between species richness and total community biomass by comparing sites at different stages of a succession or as in between sites comparative studies (Lawton et al. 1998, Loreau et al. 2001, Schmid 2002). The stochastic version of our model confirms these results and highlights that the relationship between species richness and total biomass was less predictable for quasi-neutral interactions, but that they converge to the results found for neutral interactions: an envelope where diversity peaks at intermediate values of total biomass, i.e. that the area below the hump-backed line (considered as the upper boundary) is filled with data points (sensu Schmid 2002). The "envelope" relationship, obtained for neutral interactions among species, simply results from a random increase and decrease of the total biomass during the different steps which produces an intermediate richness peak for intermediate biomass (Fig. 4c). This result was less trivial for quasi-neutral interactions in communities because on average species interactions are either positive or negative and may lead to monotonic increase or decrease of species richness along biomass gradient but not to a peaked relationship (Fig. 4d, 4e).

Positive interaction between species ($d > 1$) can result from two main processes, either complementarity (Loreau and Hector 2001, Petchey 2003) or facilitation (Cardinale et al. 2002). Complementarity among species is classically invoked to explain a positive relationship between diversity and total biomass or productivity: when species niches are complementary, more the niche space is filled and hence the community biomass or productivity is higher (Tilman 1999, Loreau and Hector 2001, Petchey 2003). Facilitation between interacting species is also supposed to promote higher total biomass or productivity during a succession (Cardinale et al. 2002). For example, shrubs may buffer harsh abiotic conditions and facilitate tree recruitment (Bertness and Callaway 1994, Raffaele and Veblen 1998). Moreover, facilitation and complementarity can occur simultaneously, for example in coastal dune shrubs, where non-nitrogen fixing shrubs facilitates establishment of a nitrogen-fixing species enabling increasing richness and total biomass simultaneously (Rudgers and Maron 2003).

Negative interactions ($d < 1$) have curiously been much less considered in the debate on the relationship between species richness and total biomass than positive interactions. They can arise from many ecological situations, e.g. indirectly by habitat modification (Crooks 2002) or directly by intra-guild predation (Finke and Denno 2002) or antagonistic effects (Semighini et al. 2006). For example, the exotic goldfish *Carassius auratus* is considered as an "ecosystem engineer invader" of ponds and lakes (Richardson et al. 1995). This species destroys the habitat of the existing species and induces high levels of turbidity by its foraging activity, reducing the foraging success of other competitors. Within the context of ecological succession, inhibition mechanisms are often invoked to explain why established species prevent or slow new species invasion and reduce both diversity and total biomass. This kind of inhibition generally occurs more strongly between species of the same functional guild (Fargione et al. 2003) and may weaken biodiversity–ecosystem relationship (Hattenschwiler et al. 2005).

When species are redundant ($d = 1$), all the species are functionally and competitively equivalent so the community utilizes the same amount of resources whatever the number of species present. Neutrality among individuals and, thus, among species is a controversial issue at the moment (McGill 2003, Chave 2004, Poulin 2004), but it can be viewed as a clear-defined extreme case of species interaction: perfect symmetry or equivalence in competitive abilities. We show that stochasticity of community assembly during succession generates a peaked relationship between species richness and total community biomass: an envelope as defined by (Schmid 2002). Redundancy or neutrality sensu stricto among species is certainly impossible (Loreau 2004), but we have found similar results for quasi-neutral interactions allowing for generalization. If, as some authors claim, interactions in ecological communities are quasi neutral or neutral (Caswell 1976, Hubbell 2001) we should expect an absence of clear relationship between species richness and total biomass during the course of a succession. This result must be interpreted in the context of the actual debate that opposes the classical view of ecological communities, provided by the niche theory and the vision proposed by the neutral theory (reviewed by Chave 2004). Despite the criticisms against the neutral theory for failure in main assumptions (Poulin 2004) and lack of power to explain observed patterns (McGill 2003), considering species as quasi neutral (as we have done with interaction near the neutral case $d = 1$) can lead to predictions of observed patterns. This does not rule out other hypothesis that have been proposed to explain the nature of the relationship between species richness and ecosystem functioning (Loreau et al. 2001) but it will enable ecologists to consider neutral or quasi-neutral perspectives when they study this relationship.

However some caution is needed when comparing our results to the neutral community drift model. Firstly, our fractal model does not stipulate a strict neutral relationship among species and individuals along the whole succession process; $d = 1$ can be obtained by a combination of net negative and positive interactions among species while d would be consistently equal to 1 without any variation in a pure neutral model. Secondly, we simulate a process of species accumulation while neutral models consider species richness at equilibrium (Hubbell 2001). Our model was rather developed to provide richness–biomass patterns predicted along a succession gradient with a limited number of stages where interactions are not forced to be equivalent between each pair of species (as in a pure neutral model) but where these interactions are quantified on average at the level of the whole community over all succession steps (a variability of d is allowed). Despite these differences, we would expect the same relationship to emerge from a truly neutral community drift model. In a pure neutral model with species having different biomass but equal interaction coefficients we would expect more variability in biomass composition in low diversity communities than in high diversity communities generating the same envelop as found in Fig. 4c. Low diversity communities would be composed of only high, low or mixture of species biomass generating the whole spectrum of total community biomass (bottom of the envelope) while high diversity communities will only have a mixture of species biomass thus generating intermediate community biomass (the peak of envelope).

Like all modeling approaches with few parameters and simple assumptions (McGill and Collins 2003), our model is not supposed to mimic perfectly the reality and its extreme complexity but rather to provide simple predictions at the marcoecological scale. Patterns of species richness and biomass partitioning during a community assembly are certainly ruled by more complex mechanisms. For example, the parameter d, that summaries average interaction between species, is likely to vary during the assembly process (Sans et al. 2002, Jackson 2003). For instance, Mullineaux et al. (2003) reported that species colonization patterns during succession on cubic basalt blocks revealed both positive (facilitation) and negative (antagonistic) biological interactions. The history of species interactions can thus hardly be encapsulated within a single constant parameter. This simplification is partly overcome by the stochastic character of our model where d may vary from one step to another but not in the same range as what we can expect in real ecological successions. We can predict what would happen with varying d during succession. If, for instance, there are two phases during succession, the first with strong positive interactions and the second with strong negative ones, one would expect to find a unimodal relationship with maximal species richness at intermediate biomass values. This may happen during the colonization of a vacant space because more positive interactions might occur in the first stages in order to buffer harsh abiotic conditions and facilitate recruitment (Bertness and Callaway 1994, Raffaele and Veblen 1998) while some more negative interactions may occur lately in the succession when interspecific competition limits community growth (Ramseier and Weiner 2006). If, however, we consider d as a random number centered on one, then one would expect to find either an absence of relationship or a peaked relationship (envelope) as the one found for the neutral case (Fig. 4c). More generally, the nature of species interactions is obviously not the only factor that explains the shape of the diversity-productivity relationship (Mouquet et al. 2002). Many other factors can play an important role such as disturbances (Venterink et al. 2001, Allcock and Hik 2003), history of community assembly (Fukami and Morin 2003), regional processes (Mouquet and Loreau 2003), as well as the spatial scale examined (Mittelbach et al. 2001, Chase and Leibold 2002).

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