Diversity–Stability Relationships in Community Ecology: Re-Examination of the Portfolio Effect

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Diversity–Stability Relationships in Community Ecology: Re-Examination of the Portfolio Effect

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In plant communities, the portfolio effect, also called "statistical averaging effect", expresses the fact that stability in aggregate community properties such as biomass productivity generally rises with species diversity, simply because of the statistical averaging of the fluctuations in species' properties. This paper essentially upgrades the previous formulations of the portfolio effect, first developed by Doak and collaborators and then by Tilman. It uses a theoretical approach based on simple statistical relationships and some simplifying assumptions proposed by these authors. The new formulation presented extends and improves the previous relationships in the sense that it takes into account simultaneously a varying scaling power of the variance, the interaction effect between species, the heterogeneity in species productivity and interspecies correlated responses to the environment. It appears that the simple statistical averaging, as inferred from this formulation, does not necessarily lead to a positive correlation between species diversity and community stability. © 2002 Elsevier Science (USA)

Key Words: biodiversity; stability; intraspecific and interspecific variability; statistical averaging; species interaction; covariance effect.

1. INTRODUCTION

The relationship between biological diversity and community stability has been the subject of many studies during the last decades, both experimental and theoretical (e.g., Clay and Allard, 1969; Marshall and Brown, 1973; McNaughton, 1977). In a recent historic perspective of the diversity–stability debate McCann (2000) enhances four main facts. (i) Up to the 1970s most ecologists believed that more diverse communities increased ecosystem stability (Odum, 1953; Elton, 1958). (ii) These early intuitive ideas were challenged by May (1973) who showed, using statistical analysis based upon random processes, that diversity tends to destabilize community dynamics. (iii) Later, Yodzis (1981) contra-

dicted this result by showing that models constructed on biologically plausible interactions strengths tended to prove that stability and diversity were positively correlated. The same conclusion is reached when environmental feedback, specifically between the biota and their climate, is included in the model (Harding, 1999). (iv) Recent investigations on the subject follow two distinct lines: one, statistical, searching for general diversity–stability relationships (Haydon, 1994; Tilman, 1996; Yachi and Loreau, 1999), and a second one, more mechanistic, seeking relationships between food-web structure and stability (Naeem and Li, 1997; Loreau and Behera, 1999; Kassen *et al.*, 2000). In a recent study based on the utilization of three markedly different models of multi-species competition, Lehman and Tilman (2000) showed for instance that diversity increases temporal stability at the community level, but decreases stability at the population level. Looking for a new reconciling perspective, Loreau *et al.* (2001) also

outlined the importance of considering the ecological levels of organization in analyzing stability–diversity relationships. Investigating the statistical line of research, Doak *et al.* (1998) put forward the interesting fact that simple statistical averaging might explain stability–diversity correlations independent of any ecological mechanism due to species interactions. Using basic relationships on stochastic processes, they essentially showed that stability always rises with species diversity because of the statistical averaging of the fluctuations in species' abundances: it is the portfolio effect.

As pointed out by Tilman *et al.* (1998), Doak *et al.*'s theory relies on the assumption that the coefficients of variation for all species are identical. This assumption implies that the variance σ^2 in the abundance of each species increases as the square of its mean abundance μ ($\sigma^2 = c\mu^z$ with $z = 2$). Tilman (1999) reformulated the approach pioneered by Doak *et al.* (1998) by using a non-prescribed value of the scaling power z of the variance. He introduced also a possible "yielding effect", which expresses the fact that total community biomass may change as diversity changes, due to positive or negative interactions between species (mutualism, facilitation, competition or allelopathy). His reformulation shows that stability can rise or fall with the number of species, depending on the value of the scaling power z. For instance, when $z < 1$, stability decreases with diversity in the absence of overyielding, a result not expected from Doak *et al.*'s formulation. However, this reformulation takes into account neither the fact that species abundances can be unequal, nor the fact that correlated responses of species to environmental variations can exist, as Doak *et al.*'s analysis does.

The purpose of this study is to address the discrepancy between the two models by showing that their formulations are not irreconcilable and can be combined into a more general formula. It extends the work of Doak *et al.* (1998) by considering the more general case where the scaling power z can take any positive value and where the interaction effect (equivalent to Tilman's overyielding) is explicitly accounted for. It also extends Tilman's (1999) work by taking into account simultaneously the interspecific heterogeneity in average abundance and the possible correlated responses of the species within the community. A general formula that synthesizes and extends the previous approaches on the subject is proposed and discussed. Also are explored the consequences of this new formulation on the relationships between community stability and species diversity.

2. THEORY

2.1. Basic Community Relationships

We consider a community of plants (cultivated or natural) with N species and different replicates of this community. These replicates can be either spatially or temporally distributed, but we refer specifically to stability as temporal constancy (see Grimm and Wissel (1997) for other definitions of stability). The total number of plants in a replicate is $n = k_1 + \cdots + k_N$ where k_i is the number of plants belonging to species i. Variable p_i characterizes a trait such as biomass production per plant, i.e., the biomass produced by one plant of a given species in a given environment corresponding to a given replicate (it would be equivalent to consider any other measurable plant function). This implies that the total biomass production of a given species in a given replicate is $m_i = k_i p_i$ and the total production of the entire community ($m_{c,N}$) is the sum of the m_i. As k_i and p_i are assumed to be independent variables, the mean values of m_i and $m_{c,N}$ (calculated over all replicates) can be written as

$$\mu_i = \overline{k_i p_i} = \overline{k_i}\,\overline{p_i}, \qquad \mu_{c,N} = \sum_{i=1}^{N} \overline{k_i}\,\overline{p_i}. \qquad (1)$$

Additionally, following the idea of Tilman (1999) concerning the impact of diversity on community productivity, we will assume that the mean value of biomass production per plant for a given species is parameterized according to the relationship

$$\overline{p_i} = b_i/N^y, \qquad (2)$$

where b_i characterizes the mean plant productivity for a given species grown in pure population and N^y takes into account the species interaction effect with y the interaction coefficient. If $y < 0$, biomass production per plant of a given species increases with diversity (positive interaction). If $y > 0$, it is the contrary: biomass production decreases with diversity (negative interaction). If $y = 0$, the effect is null and the mean value of biomass production per plant is simply equal to b_i. We do not use the same terminology as Tilman because his definition of the overyielding effect differs from the classic one, which commonly refers to a particular monoculture (generally the most productive one) and not to the total community (Trenbath and Harper, 1973; Austin, 1982). It seems preferable to call the effect described here "species interaction effect", a more neutral term than "overyielding". We have to note also that the effect of species interaction represented by

Eq. (2) is modeled slightly differently from the one called overyielding by Tilman (1999, Eq. (5)). Our coefficient y is related to Tilman's coefficient x by $y = x - 1$. The reason of this difference is that Tilman applies the interaction effect (N^x in his formulation) to the mean production of the species (represented here by μ_i) and not to the mean production per plant (b_i), as we do in Eq. (2).

The variance in total community biomass is the sum of all terms in the full $N \times N$ covariance matrix. Introducing the correlation coefficients $r_{i,j}$ for all pairs of species in the community and putting $\sigma_i^2 = \text{Var}(m_i)$, the total variance can be written as

$$\sigma_{c,N}^2 = \sum_{i=1}^{N} \sigma_i^2 + 2 \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} r_{i,j} \sqrt{\sigma_i^2 \sigma_j^2}. \qquad (3)$$

Following Tilman (1999), temporal stability (S) is defined as the ratio of mean biomass to its standard deviation (i.e., the inverse of the coefficient of variation). This implies that the stability of a community containing N species is $S_{c,N} = \mu_{c,N}/\sigma_{c,N}$, and for a single-species community, stability is written as $S_{c,1} = \mu_{c,1}/\sigma_{c,1}$. In this study, the ratio of $S_{c,N}$ to $S_{c,1}$ used by Tilman (1999) will be termed "community relative stability", $\text{RS}_{c,N} = S_{c,N}/S_{c,1}$. In a similar way, stability of an individual species living in a community of N species (i.e., population stability) is defined as its mean abundance divided by the standard deviation in its abundance (Tilman, 1999): $S_{i,N} = \mu_i/\sigma_i$. The ratio of the stability of a single species in the community ($S_{i,N}$) to that of this single species living by itself ($S_{i,1}$) will be termed "population relative stability": $\text{RS}_{i,N} = S_{i,N}/S_{i,1}$. Let us note that $S_{i,1} = S_{c,1}$.

To go further with the mathematical development, an important assumption is made concerning the averaging effect on the variance (Doak et al., 1998; Schläpfer and Schmid, 1999). It consists in admitting that the variance σ_i^2 in the biomass of species i scales with its mean biomass μ_i as a power function

$$\sigma_i^2 = \lambda \mu_i^z, \quad z > 0, \quad \lambda > 0, \qquad (4)$$

where λ and z are constants for a given community and characterize the intraspecific variability in biomass production over time. For a given value of z the temporal variance σ_i^2 increases with the mean μ_i. This type of scaling relationship has been thoroughly examined in population dynamics by Anderson et al. (1982), Murdoch and Stewart-Oaten (1989) and also reviewed by Tilman et al. (1998) and Tilman (1999). It seems that for most species in natural communities the scaling power z of the variance lies between 1 and 2.

2.2. Extension of Previous Expressions for Community and Population Stability

General expressions for $\text{RS}_{c,N}$ and $\text{RS}_{i,N}$ can be derived from the basic relationships given above. This derivation is detailed in Appendix 2. However, to go further in the examination of the general equations obtained, it is necessary to specify how the number of plants (k_i) and their productivity (b_i) vary according to the species and what the correlation coefficients ($r_{i,j}$) between species are. In the following section, we will use assumptions that simplify the mathematical formulation while retaining a certain generality. Three major assumptions, made by Doak et al. (1998), are successively used. (i) Each species in the community has the same number of individuals, which means that all k_i are equal to n/N. (ii) The correlation coefficients for all pairs of species in a community are identical and equal to r ($-1 < r < +1$). (iii) Mean plant productivity b_i varies with species following an exponential decline with rank. As the same correlations exist between all species, there is a mathematical constraint in how negative a correlation can be for a given number of species. In fact, r cannot take all the possible values between -1 and $+1$ (see below, Fig. 5 and comments). By taking into account the first two assumptions, Eqs. (2.4) and (2.5) of Appendix 2 simplify into

$$\text{RS}_{c,N} = \frac{b_1^{(z/2-1)} N^{(y+1)(z/2-1)} \sum_{i=1}^{N} b_i}{[\sum_{i=1}^{N} b_i^z + 2r \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} b_i^{z/2} b_j^{z/2}]^{1/2}}, \qquad (5)$$

$$\text{RS}_{i,N} = N^{(y+1)(z/2-1)}. \qquad (6)$$

Population relative stability is independent of species biomass productivity (b_i) and depends only on scaling coefficients z and y. By putting $x = y + 1$, Eq. (6) transforms into the equation given by Tilman (1999, Eq. (7)).

To account for a variation in mean plant productivity, all species are ranked from 1 to N, with 1 indicating the most productive species and N the least productive. Following the idea of Doak et al. (1998), an exponential decline in mean productivity with rank i is assumed

$$b_i = b_1 \exp[-a(i-1)/(N-1)] \qquad (7)$$

with i comprised between 1 and N. Parameter a is an extinction coefficient that indicates how different mean productivities are between species grown in pure population. It is expressed as $a = \ln(b_1/b_N)$ with $a > 0$, b_1 being the highest value of b_i and b_N the lowest. The greater a, the greater the difference between the highest

and the lowest productivity. a cannot be too great, however, because it is defined on a logarithmic scale: when $b_1 = 2b_N$, $a = 0.69$ and when $b_1 = 5b_N$, $a = 1.6$. It is also worthwhile stressing that Eq. (7) is different from the one originally used by Doak *et al.* (1998, p. 266) in the sense that $N - 1$ appears in the denominator of the exponential. The original formula makes that a formally depends on $N - 1$ ($a = [\ln(b_1/b_N)]/(N - 1)$), which is not recommendable. Taking into account Eq. (7), and after some manipulations specified in Appendix 3, community relative stability defined by Eq. (5) can be rewritten in a more concise form as

$$\text{RS}_{c,N} = \frac{\left[\frac{(1-e^{-aN/(N-1)})(1-e^{-az/2(N-1)})}{(1-e^{-a/(N-1)})(1-e^{-azN/2(N-1)})^{1/2}}\right] N^{(y+1)(z/2-1)}}{\left[\frac{1-e^{-az(N+1)/2(N-1)}+(2r-1)e^{-az/2(N-1)}(1-e^{-az/2})}{1+e^{-az/2(N-1)}}\right]^{1/2}}. \quad (8)$$

Equation (8) gives the relative community stability with respect to a single-species community containing the highest ranking species (with productivity b_1), namely the species with the highest productivity. The most productive species is also the most stable when $z < 2$ (since $\sigma_i/\mu_i = \lambda^{1/2}\mu_i^{z/2-1}$ according to the scaling relationship of the variance). This criterion appears to be more appropriate to evaluate the performance of a multi-specific community than the average value of all the single-species communities (Vandermeer and Schultz, 1990; Garnier *et al.*, 1997), but this point is discussed more thoroughly below.

Eq. (8) represents an extension of the formulations previously proposed by Doak *et al.* (1998) and Tilman (1999) for community relative stability. This new equation is more general than the equation proposed by Doak *et al.* (1998, Eq. (6)) in the sense that it is valid for any value z of the scaling power of the variance and not only for the particular value $z = 2$. It is also more general than the equation proposed by Tilman (1999, Eq. (6)) in the sense that it includes the effects due to different species productivities ($a \neq 0$) and to correlated responses to the environment ($r \neq 0$). In Appendix 4, we show how Eq. (8) can be downgraded to the simplified formulae given by Doak *et al.* (1998) and Tilman (1999). On the other hand, the formula giving population stability (Eq. (6)) is exactly the same as the one derived by Tilman (1999, Eq. (7)) and will not be re-examined here, since it has already been discussed by this author. For $z > 2$ population stability increases when diversity increases, whereas for $z < 2$ population stability decreases as diversity increases. In the following section we will only examine numerical results inferred from the equation giving community relative stability (Eq. (8)).

3. RESULTS AND DISCUSSION

3.1. Metric for the Diversity–Stability Relationships

Some authors think it sounder to calculate the relative community stability with respect to the mean ranking species (with productivity b_m) than with the highest ranking species as represented by Eq. (8) (Naeem *et al.*, 1996; Hector *et al.*, 1999). In that case, taking into account Eq. (3.2) of Appendix 3 leads to

$$b_m = \frac{1}{N}\sum_{i=1}^{N} b_i = \frac{b_1}{N}\frac{1-e^{-aN/(N-1)}}{1-e^{-a/(N-1)}} \quad (9)$$

and the community relative stability is calculated as

$$\text{RS}'_{c,N} = \beta\text{RS}_{c,N}, \qquad \beta = \left[\frac{1}{N}\frac{1-e^{-aN/(N-1)}}{1-e^{-a/(N-1)}}\right]^{(z/2-1)}. \quad (10)$$

The difference between $\text{RS}_{c,N}$ (relative stability with respect to the most productive species) and $\text{RS}'_{c,N}$ (relative stability with respect to a species having the mean productivity of the community) is essentially encapsulated in the β coefficient. Figure 1 shows the variation of β as a function of N for different values of z and a given value of a. For $z < 2$, β is greater than 1 and tends to increase the community relative stability when passing from RS to RS'. According to most empirical observations and theoretical developments z lies between 1 and 2 (Anderson *et al.*, 1982; Murdoch and Stewart-Oaten, 1989). Consequently, this result illustrates how the stability of multi-species communities generally outweighs that of monocultures when the
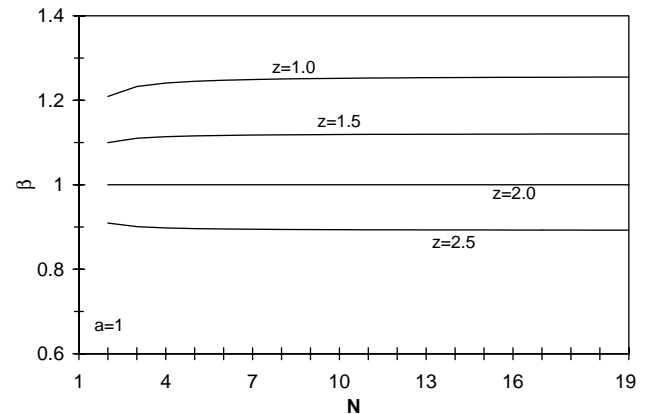

FIG. 1. Variation of the coefficient β relating $\text{RS}_{c,N}$ (community relative stability with respect to the most productive species) to $\text{RS}'_{c,N}$ (community relative stability with respect to the species having a mean productivity) (Eq. (10)).

comparison is based on the mean of all possible monocultures rather than on the most productive or most stable one (Garnier *et al.*, 1997). Conversely, for $z > 2$, β is lower than 1 and consequently decreases the community relative stability. For $z = 2$, $RS_{c,N} = RS'_{c,N}$. Whatever the value of z, the effect of β also appears nearly independent of the number of species N and changing the value of a does not alter the general behavior. One can note that these results are in agreement with the fact stressed above, namely, when $z < 2$ the most productive species is also the most stable. It should be noted also that, when $z > 2$, i.e., when intraspecific variability is high, the result is opposite, which is logical since in that case the most productive species becomes the least stable one. The β coefficient making no decisive impact on the variation of relative stability with N, the influence of the four parameters (z, y, a, r) involved in the general formulation will be documented using only Eq. (8) as a basis. The differences with the previous results obtained by Doak and Tilman will be duly emphasized.

3.2. Effect of Variation in Mean Plant Productivity

For the particular case where $z = 1$ (with $y = a = r = 0$), Tilman finds that community relative stability $RS_{c,N}$ is equal to unity whatever species diversity N. However, as shown in Fig. 2, when productivity differs between species ($a \neq 0$) $RS_{c,N}$ becomes lower than unity, while remaining approximately constant and hence nearly independent of diversity. The greater the dispersion coefficient a, the lower the community relative stability $RS_{c,N}$. Consequently, when species biomass follows any random distribution for which variance increases linearly with mean biomass ($z = 1$), community stability decreases with the heterogeneity in species productivity (a) and species diversity (N) makes a very low impact on stability. It is also worthwhile noting that for $z = 2$ (the particular case examined by Doak *et al.* (1998)), the power of N in Eqs. (8) and (6) is equal to zero, whatever the value of the interaction coefficient (y). This implies that species interaction has no impact on community stability and, as already stressed by Tilman (1999), diversity has no impact on population stability.

The effect of the interspecific heterogeneity in biomass productivity with respect to the previous analysis made by Tilman (1999, Fig. 1) is outlined in Fig. 3. It shows how the variation of relative stability as a function of N and for different values of z is displaced by the introduction of a strong heterogeneity in productivity. It is important to stress that for $z > 1$, a strong heterogeneity can inverse the relationship between relative stability and diversity with respect to the trend given by Tilman (1999, Fig. 1). Moreover, when interspecific heterogeneity is high, the trend can change with N, as exemplified for the case $z = 1.2$ with $a = 3$ (Fig. 3). Parameter a gives an index of interspecific functional diversity based on the ranking of the individual species productivities in monoculture. This simple ranking often allows one to predict dominance in multi-specific communities (Keddy, 1990). The effects of both species dominance and functional diversity on community stability (Sankaran and McNaughton, 1999; Wardle *et al.*, 2000) received less attention than those on community productivity which are widely debated (e.g.,
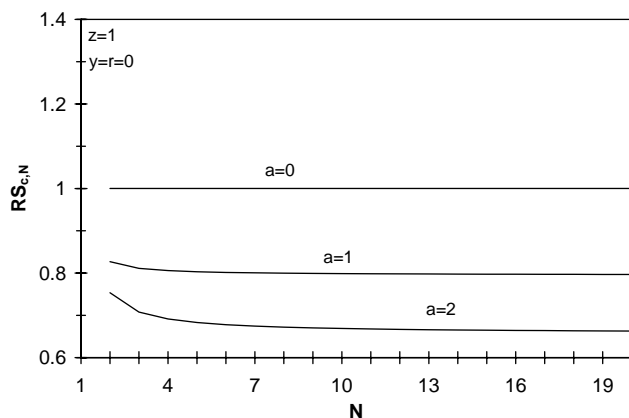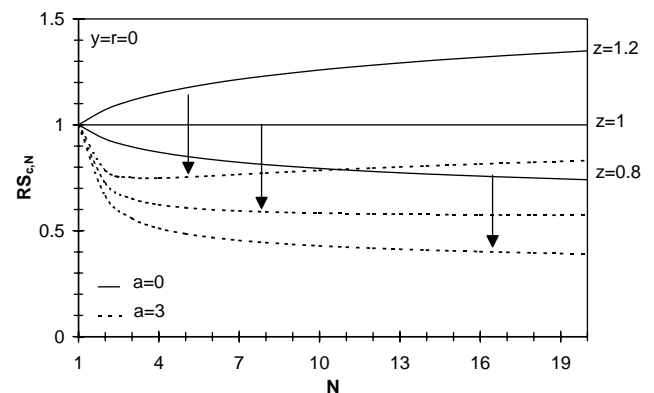

FIG. 2. Effect of varying productivity ($a \neq 0$) on the relationship between community relative stability and species diversity for a scaling power $z = 1$.

FIG. 3. Effect of a strong heterogeneity among species ($a = 3$) on the relationship between community relative stability and species diversity for different values of z (0.8, 1.0, 1.2).

Aarssen, 1997; Grime, 1997; Wilsey and Potvin, 2000). There is still a controversy over the interpretation of results of several experiments where primary production exhibits a positive relationship with plant species and functional-group diversity, in contradiction with patterns often observed in nature (Loreau *et al.*, 2001). Our theoretical examination, however, suggests that their global effect, as indexed by *a*, systematically offsets the portfolio effect. This seems a paradoxical result when considering other theoretical studies which hold dominance and functional diversity as determinant for the insurance effect (Yachi and Loreau, 1999; Loreau, 2000). This apparent contradiction stems from our hypothesis of an equal density of the species in the community, which precludes any selection effect in favor of the most productive species (Loreau, 2000, pers. comm.).

3.3. Effect of Interaction and Correlation between Species

As already pointed out by Tilman (1999), positive interaction ($y < 0$) generally has a positive impact on the stability–diversity relationship (i.e., enhances relative stability), whereas negative interaction ($y > 0$) has a negative impact. This effect is illustrated in Fig. 4. Counteracting *a*, positive interaction ($y < 0$) might potentially reinforce the dependence of community stability on diversity. Nevertheless, its experimental demonstration remains questionable and fiercely debated (e.g., Huston *et al.*, 2000). Figure 5 shows the effect of the correlation coefficient between species (*r*). Negative covariance can be generated by interspecific competition whereas positive covariance generally represents a common response to environmental variations. As could be anticipated, a negative value of *r* tends to considerably enhance community relative stability, but at the same time it generates a mathematical limitation in the number of species simply because all the correlation coefficients are assumed to be identical. This limitation does not appear when different values of the coefficient of correlation between individual species are allowed (e.g., Yachi and Loreau, 1999). Interspecific heterogeneity ($a \neq 0$) slightly compensates for this limitation, allowing the community to maintain more species in competition while retaining sufficient overall stability. For instance, with the following combination of parameters ($z = 1.5$, $y = 0$, $r = -0.1$), the maximum number of species in competition can be $N = 10$ for $a = 0$, $N = 11$ for $a = 1$ and $N = 13$ for $a = 2$. Conversely, positive values of *r* lower the community relative stability, and this effect can be strong enough to reverse the expected direction of variation of stability with diversity. The slope of the curve can also shift from positive to negative as a function of the value of *N*, as exemplified for the case $r = 0.1$ (Fig. 5): relative stability begins to increase with *N* up to a value $N = 9$ and then decreases.

It is important to note at last that the correlation coefficient between species *r* can be made dependent on the number of species *N*, since the only requisite in deriving Eq. (8) is that all the correlation coefficients are equal. This can be useful since Lehman and Tilman (2000), using different models of multi-species competition, have shown that the summed covariances fall to a minimum and then rise again as *N* increases. However, making *r* a function of *N* would lead us beyond the scope of the present analysis.
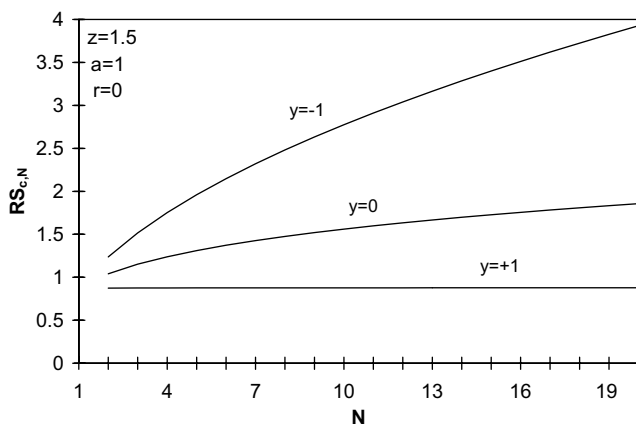

FIG. 4. Effect of the species interaction coefficient (*y*) on the relationship between community relative stability and species diversity ($z = 1.5$).
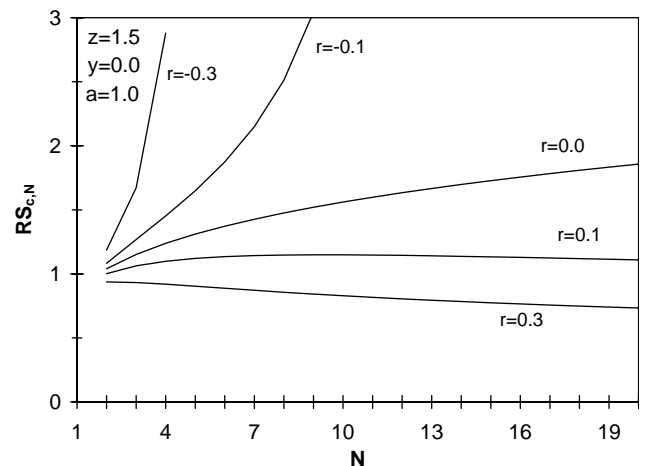

FIG. 5. Effect of the correlation coefficient between species (*r*) on the stability–diversity relationship for $z = 1.5$.

4. CONCLUSION

The main point of this study has been to upgrade previous formulae concerning the relationship between community stability and species diversity. The new equation proposed (Eq. (8)) extends Doak *et al.*'s equation (1998, Eq. (6)) by including (through the parameter *z*) a varying scaling power of the variance. It also extends Tilman's equation (1999, Eq. (6)) by including (through *a*) a varying mean productivity and (through *r*) a varying common correlation coefficient for all pairs of species. This extended equation partially contradicts the results previously obtained by Doak *et al.* and Tilman. For the former authors, stability necessarily increases with diversity, whatever the values of the coefficients involved. For Tilman, the stabilizing effect of diversity only occurs when the scaling power of the variance (*z*) is greater than a given function of the interaction coefficient (*x*) (Tilman, 1999, Fig. 1C). Contrary to these previous results, the new formulation shows that, even for a scaling power *z* greater than this function, interspecific heterogeneity in mean productivity or positive correlation between species can invert the effect of diversity on stability. Furthermore, for a given set of parameters, the effect of diversity on stability can change with the increasing number of species (*N*). Consequently, it is clear now that the simple statistical averaging (or portfolio effect) does not necessarily lead to a positive correlation between species diversity and community stability: the "statistical inevitability" is avoidable in certain circumstances. Unfortunately, the equation linking community stability with species diversity (Eq. (8)) involves too many parameters to provide a clear mapping of combinations of parameter values yielding positive or negative relationships, as Tilman (1999, Fig. 1C) did for an equation with only two parameters.

To conclude and at the risk of denigrating the validity of the present theory, it seems worthwhile stressing that the formulations developed here, as those they stem from, rely on a basic scaling relationship represented by Eq. (4). This equation relating the mean and its variance through a scaling factor *z* represents indeed the corner stone of the present theory. Although this scaling relationship has been extensively discussed and seems verified in studies on population dynamics (Anderson *et al.*, 1982; Murdoch and Stewart-Oaten, 1989), its validity for functional processes like fluxes of energy or matter in plant communities is still unknown and requires more experimental and theoretical evidences.

APPENDIX 1. LIST OF MAIN SYMBOLS

a	coefficient defined by Eq. (7) indicating the variation of productivity among species
b_i	mean biomass productivity of one plant in a given species (with $y = 0$)
k_i	number of plants in the community belonging to species i
p_i	biomass production of species i per plant
n	number of plants in the community
N	number of species in the community
r	correlation coefficient between species
$RS_{c,N}$	community relative stability
$RS_{i,N}$	relative stability of species i (population relative stability)
$S_{c,N}$	stability of a community of N species
$S_{i,N}$	stability of species i within a community of N species (population stability)
$m_{c,N}$	biomass production of the whole community
m_i	biomass production of species i
x	interaction coefficient in Tilman's formulation
y	interaction coefficient in our formulation
z	variance scaling coefficient
β	coefficient relating $RS'_{c,N}$ to $RS_{c,N}$ (Eq. (10))
λ	constant parameter
μ_i	mean biomass production of species i
$\mu_{c,N}$	mean biomass production of the entire community
σ_i	standard deviation in biomass production of species i
$\sigma_{c,N}$	standard deviation in biomass production of the entire community

APPENDIX 2. EXPRESSIONS FOR COMMUNITY AND POPULATION STABILITY

Taking into account Eqs. (1)–(4) leads to the following expression for community stability:

$$S_{c,N} = \mu_{c,N}/\sigma_{c,N}$$

$$= \left[\lambda^{-1/2} N^{y(z/2-1)} \sum_{i=1}^{N} \overline{k_i} b_i\right] \Bigg/ \left[\sum_{i=1}^{N} \overline{k_i}^z b_i^z + CE\right]^{1/2}, \tag{2.1}$$

where parameter CE, which represents the global correlation effect, is defined by

$$CE = 2 \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} r_{i,j} \overline{k_i}^{z/2} \overline{k_j}^{z/2} b_i^{z/2} b_j^{z/2}. \tag{2.2}$$

For a single-species community we have: $N = 1$, $k_i = n$, $b_i = b_1$. In this case community stability is written as

$$S_{c,1} = \mu_{c,1}/\sigma_{c,1} = \lambda^{-1/2}(nb_1)^{(1-z/2)} = \lambda^{-1/2}M_1^{(1-z/2)}, \quad (2.3)$$

where $M_1 = nb_1$ represents the mean value of the total biomass produced by a single-species community. The community relative stability is expressed as

$$\mathrm{RS}_{c,N} = S_{c,N}/S_{c,1} = \frac{M_1^{(z/2-1)}N^{y(z/2-1)}\sum_{i=1}^{N}\overline{k}_i b_i}{[\sum_{i=1}^{N}\overline{k}_i^z b_i^z + \mathrm{CE}]^{1/2}}. \quad (2.4)$$

The relative stability of an individual species living in a community of N species (i.e., population relative stability) is expressed as

$$\mathrm{RS}_{i,N} = S_{i,N}/S_{i,1} = N^{y(z/2-1)}(\overline{k}_i/n)^{(1-z/2)}. \quad (2.5)$$

APPENDIX 3. DERIVATION OF Eq. (8)

Taking into account Eq. (7) and the following general property of geometric series:

$$\sum_{i=0}^{n} q^i = (1 - q^{n+1})/(1 - q), \quad q \neq 1, \quad (3.1)$$

where n is integer, the summations appearing in Eq. (5) transform into

$$\sum_{i=1}^{N} b_i = b_1 \sum_{i=1}^{N} (e^{-a/(N-1)})^{i-1} = b_1 \frac{1 - e^{-aN/(N-1)}}{1 - e^{-a/(N-1)}}, \quad (3.2)$$

$$\sum_{i=1}^{N} b_i^z = b_1^z \sum_{i=1}^{N} (e^{-az/(N-1)})^{i-1} = b_1^z \frac{1 - e^{-azN/(N-1)}}{1 - e^{-az/(N-1)}}, \quad (3.3)$$

$$\sum_{i=1}^{N-1} \sum_{j=i+1}^{N} b_i^{z/2} b_j^{z/2}$$
$$= b_1^z \sum_{i=1}^{N-1} (e^{-az/2(N-1)})^{i-1} \sum_{j=i+1}^{N} (e^{-az/2(N-1)})^{j-1}$$
$$= b_1^z e^{-az/2(N-1)} \frac{(1 - e^{-az/2})(1 - e^{-azN/2(N-1)})}{(1 + e^{-az/2(N-1)})(1 - e^{-az/2(N-1)})^2}, \quad (3.4)$$

which leads to Eq. (8).

APPENDIX 4. CORRESPONDENCE WITH DOAK'S AND TILMAN'S FORMULATIONS

When all the values of b_i are equal to a constant b (i.e., the mean value of biomass production is the same

for all species), $a = 0$ in Eqs. (7) and (8). However, Eq. (8) is not defined for $a = 0$. Consequently, we have to return to Eq. (5) to examine this particular case. Taking into account that the summation of the n first integers is $n(n + 1)/2$, we have

$$\sum_{i=1}^{N-1} \sum_{j=i+1}^{N} b_i^{z/2} b_j^{z/2} = b^z \sum_{i=1}^{N-1} \sum_{j=i+1}^{N} 1 = b^z N(N-1)/2 \quad (4.1)$$

and Eq. (5) transforms into

$$\mathrm{RS}_{c,N} = N^{y(z/2-1)+(z-1)/2}[1 + (N-1)r]^{-1/2} \quad (4.2)$$

with $r > -1/(N-1)$. Equation (4.2) is equivalent to Eq. (6) of Tilman (1999) by putting $y = x - 1$ and $r = 0$. We can also verify that Eq. (8) is mathematically equivalent to Eq. (4.2) when a tends to 0 (this can be easily demonstrated by noting that $\exp(\varepsilon)$ tends to $1 + \varepsilon$ when ε tends to 0). When $z = 2$ and $y = 0$, which is the case examined by Doak *et al.* (1998), Eq. (8) simplifies to

$$\mathrm{RS}_{c,N}$$
$$= \left[\frac{(1 - e^{-aN/(N-1)})(1 + e^{-a/(N-1)})}{1 - e^{-a(N+1)/(N-1)} + (2r-1)(1 - e^{-a})e^{-a/(N-1)}} \right]^{1/2}. \quad (4.3)$$

Equation (4.3) is equivalent to the formula given by Doak *et al.* (1998, Eq. (6)), which expresses the coefficient of variation for community biomass CV_{cb} when the coefficients of variation for all species are identical and equal to CV_s. However, a in our equation should be replaced by $a'(N-1)$ to account for the different writing by these authors of the exponential decline in mean productivity. Using the notations of Doak *et al.* (1998), their coefficient of variation is linked to our relative stability by $\mathrm{CV}_{cb} = \mathrm{CV}_s/\mathrm{RS}_{c,N}$ with $\mathrm{CV}_s = \lambda^{1/2}$.

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