

LETTER

Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities

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Abstract

Recent experiments on grassland ecosystems have shown that biodiversity can enhance ecosystem processes such as plant biomass production. Functional complementarity is generally regarded as the main class of mechanisms generating these effects of biodiversity on ecosystem functioning. Although intuitively appealing and supported by some data, the complementarity hypothesis has been little explored theoretically using mechanistic approaches. Here, we present a simple dynamical model for a light-limited terrestrial ecosystem to assess the effects of species diversity on light competition and total biomass in plant communities. Our model shows that competitive relaxation (reduction in average light competition intensity) due to differences in foliar architecture among species enhances total plant biomass in mixtures, but that competitive imbalance (generated by the variance of the average light competition intensity experienced by different species) can either reinforce the effect of competitive relaxation or counteract it and contribute to reducing total plant biomass. Thus, complementary resource use is not enough to increase total plant biomass in species-rich communities; competitive balance among species also plays an important role. We propose an operational measure of light-use complementarity using empirical field data on light absorption to test the presence of complementarity in natural plant communities.

Keywords

Biodiversity, competitive imbalance, competitive relaxation, complementary resource use, ecosystem functioning, light competition model, light complementarity index, plant community.

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INTRODUCTION

Increasing human domination of natural ecosystems has raised great concern on the potential effects of biodiversity loss on ecosystem functioning during the last decade (syntheses in Kinzig *et al.* 2001; Loreau *et al.* 2001, 2002; Hooper *et al.* 2005). Experiments in grassland ecosystems have shown that biodiversity can enhance ecosystem processes, especially yearly biomass production, in a relatively short term (Naeem *et al.* 1994; Tilman *et al.* 1996, 1997a, 2001; Hector *et al.* 1999; Loreau & Hector 2001; van Ruijven & Berendse 2003; Hooper & Dukes 2004). The mechanisms that explain this enhancement of

ecosystem functioning, however, have been controversial. Several attempts to separate sampling or selection effects (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b; Loreau 2000) from other biodiversity effects such as resource-use complementarity (Naeem *et al.* 1994; Hooper 1998; Loreau 1998a, 2000) have been made, based on methods that compare species yields in monoculture and mixture (Trenbath 1974; Vandermeer 1988; Garnier *et al.* 1997; Jolliffe 1997; Hector 1998; Loreau 1998b; Loreau & Hector 2001). A number of studies have now established that selection effects are insufficient to explain observed experimental increases in plant biomass or yield with species diversity, and that some form of functional complementarity or

interspecific facilitation is involved in these ecosystem responses (Loreau & Hector 2001; Tilman *et al.* 2001; Hector *et al.* 2002; van Ruijven & Berendse 2003; Hooper & Duker 2004). Selection effects are often significant, but, counterintuitively, they are often negative, i.e. they often oppose the positive effect of functional complementarity on ecosystem processes.

The complementarity hypothesis (Naeem *et al.* 1994; Brisson & Reynolds 1997; Tilman *et al.* 1997b; Hooper 1998; Loreau 1998a, 2000, 2004) states that because of niche differences among species, individuals in a mixture on average experience less niche overlap as to resource use than in the corresponding monocultures. This reduced niche overlap leads to a more efficient utilization of resources (complementary resource use), which leads to an increase in the total biomass production of mixtures compared with monocultures. Although intuitively appealing, this hypothesis has been little explored theoretically using mechanistic approaches (Loreau 1998a), and still lacks robust theoretical foundations. In particular, complementarity in light exploitation was suggested as one possible mechanism yielding positive effects of plant species diversity on plant biomass production (Naeem *et al.* 1994), but it has never been explored theoretically. Here we present a simple model for a light-limited terrestrial ecosystem to assess the potential effects of light-use complementarity among plant species on plant biomass. We show that complementary resource use is not enough to increase total plant biomass in species-rich communities. Competitive imbalance among species also plays an important role and can counteract the complementarity effect, thus providing a potential explanation for negative selection effects in biodiversity experiments.

THE MODEL

The model is a spatially implicit, height-structured model of competition for light. Complex, quantitative physiological models that incorporate light interception, canopy structure and photosynthesis have recently been developed and applied to experimental data (Anten & Hirose 1999, 2003; Werger *et al.* 2002; see Anten 2005; Hirose 2005 for reviews). Here we present a simpler model that enables us to obtain analytical results for multispecies communities while taking into account the asymmetric effect of shading of small individuals by larger individuals. The model consists of the following three elements.

Size structure

Plant size structure (e.g. height and weight distribution) is an essential feature of the model because light competition is asymmetric among plants of different sizes (Hikosaka *et al.* 1999). We assume allometric relationships between different

measures of size for simplicity (Iwasa *et al.* 1984; Hara 1986, 1993; Kohyama 1989; Pacala *et al.* 1996; Anten & Hirose 1999):

$$y = A_i x^{\alpha_i}, \quad (1)$$

where x is height and y is, e.g. weight or leaf area. A_i and α_i are species-specific allometric parameters, and subscript i or j represents species i or j throughout the article (Table 1).

Relative growth rate

The relative growth rate (RGR) of an individual plant of height x , $\text{RGR}_i(x)$, consists of two terms, solitary growth and shading effect, as follows:

$$\text{RGR}_i(x) = (a_{0i} - a_{1i}x^{m_i}) - \sum_{j=1}^N k_{ij} \text{LAI}_j(x), \quad (2a)$$

$$\text{LAI}_j(x) \equiv \int_x^{x_{\max-j}} y^{\gamma_j} n_j(y, t) dy, \quad (2b)$$

where $\text{LAI}_j(x)$ is the leaf area index of species j above height x . The integration on the right-hand side of eqn 2b is taken from x to the maximal size of species j , $x_{\max-j}$; $n_j(y, t)$ is the height distribution of species j at time t ; a_{0i} , a_{1i} , m_i and γ_j are species-specific parameters (Table 1). The first term of

Table 1 Symbols used for basic parameters in the model

N :	number of species
d_0 :	total density of a culture
x, y :	size, e.g. height and weight, trunk diameter at breast height (dbh)
A_i :	coefficient of allometric relation for biomass
α_i, γ_j :	power constant of allometric relation for biomass and leaf area
a_{0i} :	potential growth rate
a_{1i} :	reduction rate
m_i :	power constant
k_{ij} :	competitive effect of species j on species i
k_{ij}^* (i, j):	element of the inverse matrix of the light-competition intensity matrix (k_{ij})
X_i :	converted light-competition intensity of species i
$f(\cdot)$:	biomass function
$(1/2 < \alpha, 0 < m - \gamma < 1)$	
$B = \frac{m A^2 a_1 \alpha}{m - \gamma + 2\alpha - 1} \left(\frac{a_0}{a_1} \right)^{[(m - \gamma + 2\alpha - 1)/m]}$	
$C = \frac{(m - \gamma) d_0}{m a_1} \left(\frac{a_0}{a_1} \right)^{(m - \gamma)/m}$	
$D = \frac{m - \gamma + 2\alpha - 1}{m - \gamma}$	
$\beta = \frac{BC^2 D(D - 1)}{2}$	
$B1 = \frac{m A^2 \alpha}{m - \gamma + 2\alpha - 1} \left(\frac{a_0}{a_1} \right)^{(m - \gamma + 2\alpha - 1)/m}$	
$C1 = \frac{(m - \gamma) d_0}{m} \left(\frac{a_1}{a_0} \right)^{(m - \gamma)/m}$	

eqn 2a represents solitary growth by Richard's function, which was derived to represent the RGR of an isolated plant's weight by Yokozawa & Hara (1992). The polynomial function form $a_0 - a_1 x^m$ can approximate over a wide range of isolated growth by tuning the parameters a_0 , a_1 and m , including Gompertz function derived based on field data to represent RGR of a solitary tree's trunk diameter at breast height (dbh) by Kohyama (1989). It accounts for the decline in growth as size increases and leads to an analytically tractable model. The second term represents a reduction in RGR due to shading by neighbours. The shading effect of species j on species i is the product of its leaf area index, $LAI_j(x)$, and the rate at which a unit of its leaf area reduces the RGR of species i , k_{ij} , which we call *light-competition intensity*. This is a natural extension of the forest dynamics model developed by Kohyama (1989, 1992, 1993).

Dynamics of size distribution

The change in the density of a size class x is determined by immigration from the lower size class, $x - dx$, and emigration to the upper size class, $x + dx$. Death and new recruitment are set to zero to keep the total density of each plant species constant. Thus, the size distribution changes according to the transport equation as follows (Sinko & Streifer 1967; Takada & Iwasa 1986; Kohyama 1992, 1993; Hara 1993):

$$\frac{\partial n_i(x, t)}{\partial t} = -\frac{\partial}{\partial x} \{x \text{RGR}_i(x) n_i(x, t)\}. \tag{3}$$

The biomasses of mixtures and monocultures, B_{mix} and $B_{\text{mono}-i}$, are calculated at the positive equilibrium of eqn 3, $n_i^*(x)$. The net effect of biodiversity on biomass is evaluated by the index ΔB (Trenbath 1974; Vandermeer 1988; Garnier *et al.* 1997; Jolliffe 1997; Hector 1998; Loreau 1998a; Loreau & Hector 2001):

$$\Delta B \equiv B_{\text{mix}} - \frac{1}{N} \sum_{i=1}^N B_{\text{mono}-i}. \tag{4}$$

RESULTS

General results

When species differ only in their competition intensity, the net biodiversity effect on biomass, ΔB , is (Appendix S1):

$$\Delta B = \frac{1}{N} \sum_{i=1}^N f(X_i) - \frac{1}{N} \sum_{i=1}^N f(k_{ii}), \tag{5a}$$

$$X_i \equiv \frac{1}{N} \left(\sum_{j=1}^N \hat{k}_{ij} \right)^{-1}, \tag{5b}$$

where, \hat{k}_{ij} is the element (i, j) of the inverse of the competition intensity matrix (k_{ij}) , and $f(\cdot)$ is a decreasing, concave-up function. The biomass of species i in the mixture is $f(X_i)/N$. Equation 5 show that species i in the mixture is functionally equivalent to a species in a monoculture that has intraspecific competition intensity X_i . In this sense, we call X_i a *converted* competition intensity.

When the density of each culture is sufficiently low, the net biodiversity effect can be partitioned into two additive components as follows (Fig. 1):

$$\Delta B = \text{CR} + \text{CI}, \tag{6a}$$

$$\text{CR} \equiv \beta E_i [k_{ii} - E_j [k_{ij}]] = \beta \frac{1}{N} \sum_{i=1}^N \left(k_{ii} - \frac{1}{N} \sum_{j=1}^N k_{ij} \right), \tag{6b}$$

$$\text{CI} \equiv \beta E_i [E_j [k_{ij}] - X_i] = \beta \frac{1}{N} \sum_{i=1}^N \left(\frac{1}{N} \sum_{j=1}^N k_{ij} - X_i \right), \tag{6c}$$

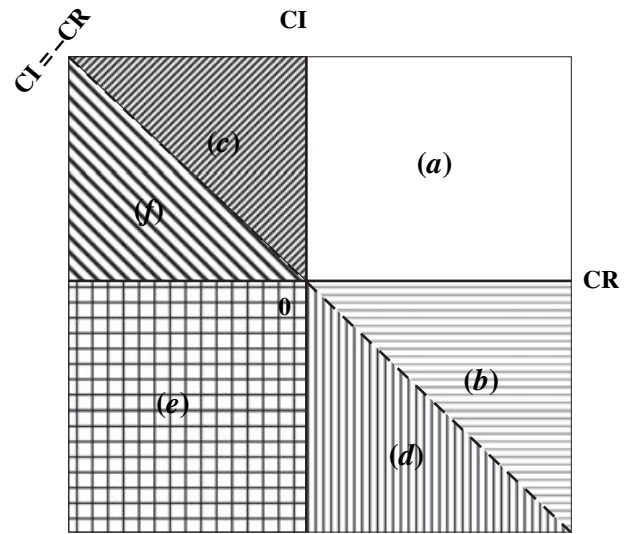


Figure 1 Contributions of competitive relaxation (CR) and competitive imbalance (CI) to the net biodiversity effect on total plant biomass, ΔB . The horizontal and vertical axes represent CR and CI respectively. Enhancement of total plant biomass in mixtures occurs in the region above the dotted line $\text{CI} = -\text{CR}$. This region is further divided into three subregions: in (a), both competitive relaxation and competitive imbalance work cooperatively to enhance total plant biomass; in regions (b) and (c), the two effects counteract each other. In region (d), the paradox of complementarity occurs, i.e. total plant biomass is reduced in mixtures despite the presence of complementary resource use. In region (e), there is neither complementarity nor enhancement of total plant biomass. In region (f), the opposite of the situation in region (d) occurs, i.e. negative competitive relaxation exceeds positive competitive imbalance.

where β is a constant derived from basic parameters (Table 1). From eqn 2a, $E_j[k_{ij}]$ represents the mean competitive effect experienced by species i per leaf area unit in the mixture, while k_{ij} is the competitive effect it experiences in monoculture. Thus, when CR is positive, it provides a measure of the average ‘competitive relaxation’ in the mixture compared with monocultures. Because a relaxation in light competition should be accompanied by an increase in light-interception efficiency, CR represents a measure of the potential increase in light use efficiency in the mixture.

The second term, CI, vanishes when either: (i) there is no interspecific competition, i.e. $k_{ij}=0(j \neq i)$, or (ii) the variance of the converted competition intensities, $\text{var}_i[X_j]=0$ or, equivalently, $\text{var}_i[E_j[k_{ij}]] = 0$ (Appendix S1). Thus, CI is an effect generated by ‘competitive imbalance’ among species; it represents the deviation from a situation in which the converted competition intensities of the various species are in perfect balance, i.e. in which the competitive effect on each species is the same.

Equation 6a shows that the reduction in the average competition intensity due to competitive relaxation in the mixture ($CR > 0$) works to enhance the biomass of the mixture. The contribution of competitive imbalance, however, can be either negative or positive. These results still hold qualitatively when the density of each culture is high (Appendix S1).

An example: two-species mixtures

For two-species mixtures in which only interspecific competition intensities k_{12} and k_{21} differ, the competitive imbalance index CI proves to be always negative when the two species coexist at equilibrium, except in the limiting case when $\text{var}_i[E_j[k_{ij}]] = 0$, i.e. $k_{12} = k_{21}$ (Fig. 2a). This result also holds when only intraspecific competition intensities k_{11} and k_{22} differ (Fig. 2b). Thus, in two-species mixtures in which either interspecific or intraspecific competition intensities differ, competitive imbalance always acts to reduce total biomass for feasible equilibria (Fig. 2a,b). Although competitive relaxation due to reduced niche

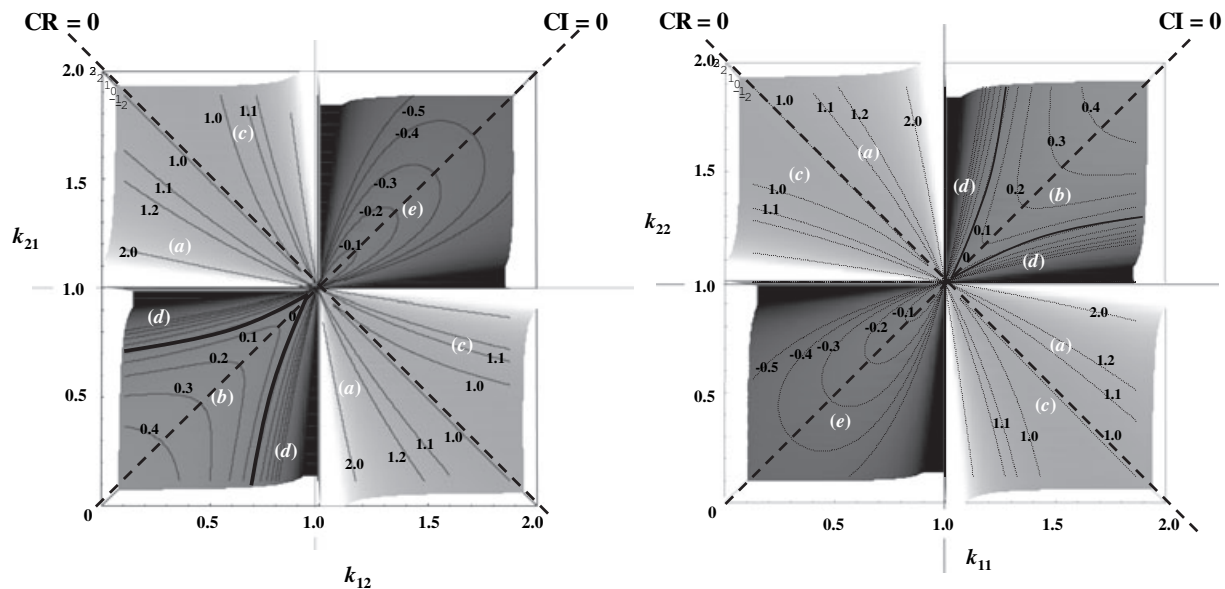


Figure 2 Three-dimensional representation of the effects of intra- and interspecific competition intensities on the net biodiversity effect on total plant biomass in a two-species mixture, ΔB . (a) Effects of interspecific competition intensities k_{12} and k_{21} . The x -, y - and z -axes represent k_{12} , k_{21} and ΔB respectively. Curves are ΔB isoclines. Intraspecific competition intensities are here set to be equal: $k_{11} = k_{22} = 1$. $CR = \beta \frac{1}{4} \{ (1 - k_{12}) + (1 - k_{21}) \}$, $CI = -\beta \{ (k_{12} - k_{21})^2 / 4(1 - k_{12})(1 - k_{21}) \}$. The size-distribution equilibria $n_1^*(x)$ and $n_2^*(x)$ are simultaneously feasible only in the two dark-grey regions $R_1 \equiv \{ (k_{12}, k_{21}) | 0 < k_{12} < 1, 0 < k_{21} < 1 \}$ and $R_2 \equiv \{ (k_{12}, k_{21}) | 1 < k_{12}, 1 < k_{21} \}$. They are not feasible in the two light-grey regions. The two dotted lines correspond to $CR = 0$ and $CI = 0$. Subregions (a–e) as in Fig. 1. (b) Effects of intraspecific competition intensities k_{11} and k_{22} . The x -, y - and z -axes represent k_{11} , k_{22} and ΔB respectively. Curves are ΔB isoclines. Interspecific competition intensities are here set to be equal: $k_{12} = k_{21} = 1$. $CR = \beta \frac{1}{4} \{ (k_{11} - 1) + (k_{22} - 1) \}$, $CI = -\beta \{ (k_{11} - k_{22})^2 / 4(k_{11} - 1)(k_{22} - 1) \}$. The size-distribution equilibria $n_1^*(x)$ and $n_2^*(x)$ are simultaneously feasible only in the two dark-grey regions $R_1 \equiv \{ (k_{11}, k_{22}) | 0 < k_{11} < 1, 0 < k_{22} < 1 \}$ and $R_2 \equiv \{ (k_{11}, k_{22}) | 1 < k_{11}, 1 < k_{22} \}$. They are not feasible in the two light-grey regions. The two dotted lines correspond to $CR = 0$ and $CI = 0$. Subregions (a–e) as in Fig. 1.

overlap contributes to enhance the total biomass of the mixture, this effect is counteracted by competitive imbalance among species. The net effect of biodiversity on biomass then depends on the relative strengths of these two effects.

TESTING THE LIGHT COMPLEMENTARITY HYPOTHESIS

Intuitively, complementarity is a concept that should satisfy the following two properties: (i) it should be a *relative* attribute of a mixture compared with the corresponding monocultures, hence it should be measured as a *difference* in some quantity between the mixture and the monocultures; and (ii) it should reflect a difference between species in some traits that determine their resource utilization, hence it should affect the *efficiency* of some process related to resource utilization. Complementarity is often defined as an increase in the resource-use efficiency of a mixture compared with the mean resource-use efficiency of the corresponding monocultures. The competitive relaxation index CR derived from the above mechanistic dynamical model satisfies this definition of complementarity. However, it is not straightforward to measure or estimate this index using field data. In this section, we derive another, more operational, mechanistic light complementarity index, LC, based on the measurement of the light absorption efficiency of cultures. We show that LC enhances the total light energy absorption of a mixture compared with the corresponding monocultures under the same conditions that CR enhances ΔB . This new index can easily be used to test the complementarity hypothesis using field data (Table 2).

Our index of 'light complementarity', LC, is defined as an increase in the 'light absorption efficiency' of a mixture, e_{mix} , compared with the mean light absorption efficiency of its N corresponding monocultures, $(1/N)\sum_{i=1}^N e_i$:

$$\text{LC} = e_{\text{mix}} - \left(\frac{1}{N}\right) \sum_{i=1}^N e_i. \quad (7)$$

This definition is practical in two senses: (i) light absorption is easy to measure by optical methods; and (ii) it is directly related to the growth rate of the cultures.

To obtain a measure of the light absorption efficiency of a culture that is independent of differences in leaf area (and hence biomass) among cultures, we define it as the light energy actually absorbed by the culture, ΔE , standardized by the theoretical maximum light energy absorption of that culture, ΔE_{max} :

$$e_i = \frac{\Delta E_i}{\Delta E_{i-\text{max}}}, \quad (8a)$$

$$e_{\text{mix}} = \frac{\Delta E_{\text{mix}}}{\Delta E_{\text{mix-max}}}. \quad (8b)$$

Because ΔE_{max} is always greater than or equal to the actual energy absorbed, ΔE , by definition we have:

$$0 \leq e_i \leq 1, \quad (9a)$$

$$0 \leq e_{\text{mix}} \leq 1. \quad (9b)$$

Thus, our index of 'light complementarity', LC, is independent of differences in leaf area and captures the effect of differences among species in their architecture or other traits related to light absorption.

Absorbed light energy, ΔE , is calculated by the law of energy conservation as the difference in the average light intensity above the culture, L_0 , and on the ground, L_G , the difference being due to the light absorption by the plants in the culture (reflection of light on the leaf surface and absorption by air are here ignored for simplicity):

$$\Delta E = L_0 - L_G. \quad (10)$$

The maximum light energy absorption of a culture, ΔE_{max} , would be realized if all the leaves in that culture were rearranged so that they have minimal overlap with each other and each leaf is perpendicular to the incoming light. In this ideal situation, assuming that a leaf of species i absorbs a fraction q_i of the incoming light, the maximum light energy absorption of monocultures and mixtures are respectively (Appendix S1):

$$\Delta E_{i-\text{max}} = L_0 g(q_i, \text{LAI}_{\text{mono-}i}), \quad (11a)$$

$$\Delta E_{\text{mix-max}} = L_0 g(\bar{q}, \text{LAI}_{\text{mix}}), \quad (11b)$$

where $g(q, \text{LAI})$ is an increasing function of q and LAI defined as:

Table 2 Symbols for light complementarity index and measurable field data

LC: light complementarity index
$e(e_i, e_{\text{mix}})$: light absorption efficiency
ΔE : light energy currently absorbed in the culture
ΔE_{max} : maximum light energy absorption
L_0 : light intensity above the culture
L_G : average light intensity on the ground
LAI_i : total leaf area of species i in the culture
δE : increase in total light energy absorption
q_i : species-specific light absorption rate per leaf
$g(\cdot, \cdot)$: light absorption function

$$g(q, \text{LAI}) = 1 - (1 - q)^k + q(1 - q)^k(\text{LAI} - k), \quad (12)$$

where k is the largest integer that is smaller than or equal to LAI ($k \leq \text{LAI} < k + 1$), $\text{LAI}_{\text{mono-}i}$ is the leaf area index of species i in monoculture, LAI_{mix} is the total leaf area index of the mixture, and \bar{q} is the average value of q among the species present in the mixture.

The increase in the total light energy absorption of the mixture compared with the monocultures, δE , can be defined as follows:

$$\delta E \equiv \Delta E_{\text{mix}} - \left(\frac{1}{N}\right) \sum_{i=1}^N \Delta E_{\text{mono-}i}. \quad (13)$$

By substituting eqns 10 and 11 into eqn 13, δE can be represented in terms of the light absorption rates, e , the total leaf areas, LAI, and the light complementarity index, LC, as follows:

$$\begin{aligned} \delta E &= L_0 \left\{ e_{\text{mix}} g(\bar{q}, \text{LAI}_{\text{mix}}) - \left(\frac{1}{N}\right) \sum_{i=1}^N e_i g(q_i, \text{LAI}_{\text{mono-}i}) \right\} \\ &= L_0 g(\bar{q}, \text{LAI}_{\text{mix}}) \left\{ \text{LC} + \left(\frac{1}{N}\right) \sum_{i=1}^N e_i \right. \\ &\quad \left. \left[\frac{1 - g(q_i, \text{LAI}_{\text{mono-}i})}{g(\bar{q}, \text{LAI}_{\text{mix}})} \right] \right\}. \quad (14) \end{aligned}$$

Although the net biodiversity effect on biomass, ΔB , is difficult to relate explicitly to LC, it should be positively related to δE because biomass ultimately results from light energy absorption. If the mixture, on average, absorbs more light energy than do monocultures ($\delta E > 0$), this extra energy will, in average, lead to a greater biomass production. Thus, analysing δE should provide indirect information on the effect of LC on ΔB .

Equation 14 shows that the net biodiversity effect, δE , can be partitioned into two additive components as in eqn 6a. Light absorption is enhanced by light complementarity ($\text{LC} > 0$), but δE can still be negative because of the second term in the parenthesis, i.e. if the total leaf area of the mixture, LAI_{mix} , is sufficiently reduced as a result of unbalanced growth. Thus, this second term corresponds to the competitive imbalance effect, CI in eqn 6a. On the other hand, if the growth of the various species in the culture is balanced by some tradeoff mechanism that suppresses severe interspecific competition, the effect of unbalanced growth can be neglected, and LC alone determines the sign of δE .

Thus, the theoretical results obtained above from our dynamical model can be restated using our operational approach in terms of parameters that are easily measurable in the field. In practice, our method only requires the measurement of the incoming light intensity, L_0 , the light intensity on the ground, L_G , the fractions of light absorbed by the leaves of the various species, q , and their leaf area indices, LAI.

DISCUSSION

Two effects that emerge from light competition in mixtures

Mixing species changes the conditions under which light competition takes place, and generates two qualitatively different effects on total plant biomass, competitive relaxation and competitive imbalance. Two indices, CR and CI, capture the magnitude of these two effects. Both effects can take positive, negative and zero values depending on the combination of species (Fig. 1). The sign and relative magnitude of these effects are not affected by any other parameters than the competition intensities k_{ij} as can be seen from eqn 6b,c and Table 1.

The competitive relaxation effect is a direct functional consequence of the changes in the mean competition intensity – i.e. in the mean light interception efficiency – that result from niche differences between species (Chesson's 2000 stabilizing mechanisms). Because competitive relaxation implicates an increase in the average light interception efficiency of the mixture, a positive CR effect ensures positive functional complementarity among species according to our definition of complementarity. On the other hand, the competitive imbalance effect appears at the level of total light interception as a cumulative result of the variance of competition intensity (it is a functional consequence of mechanisms that promote fitness inequalities, i.e. that oppose Chesson's 2000 equalizing mechanisms). Competitive imbalance causes unequal resource gains among species, which accumulate to generate unequal gains in biomass and leaf area. Small differences in these gains are amplified through growth by the positive feedback process of asymmetric light competition. As a result, the increase in the biomass of the competitively superior species can be overwhelmed by the loss of biomass of the inferior species. Thus, even when biodiversity enhances total biomass through complementarity, it may at the same time generate a negative competitive imbalance effect that exceeds the effect of competitive relaxation, leading to the paradoxical situation in which ecosystem functioning is impaired despite the presence of functional complementarity. The regions (d) in the two-species cases (Fig. 2a,b) correspond to this situation.

As light is a directional resource, competition for light is highly asymmetrical and is generally thought to provide fewer opportunities for niche differentiation than is competition for other resources such as nutrients. The asymmetrical nature of light competition does strongly constrain species coexistence and might exacerbate the competitive imbalance effect in our model. However, competitive imbalance is unlikely to be specific to light competition. Competition for nutrients leads to competitive exclusion in well-mixed media. Implicit or explicit spatial or temporal heterogeneity is

usually responsible for species coexistence in models based on nutrient competition (Grover 1997; Tilman *et al.* 1997b; Loreau 1998a). Differences in the competitive abilities of different species, however, should generate a similar competitive imbalance effect in nutrient competition as in light competition. More theoretical work on the dynamics of nutrient competition would be needed to explore the potential for resource-use complementarity and competitive imbalance in nutrient-limited multispecies communities under realistic conditions.

Relaxing the assumption of an absence of mortality and recruitment in our model would only enhance this competitive imbalance effect because the density and frequency of each species in mixture would not be conserved any more. In the limiting case when there is no complementarity in light use, the mixture would be dominated by the most competitive species whose biomass would coincide with its monoculture biomass. The selection effect, *sensu* Loreau & Hector (2001) would be the statistical manifestation of this competitive imbalance effect. As competitive imbalance can be positive, zero or negative, the selection effect can take on different signs depending on the correlation between competitive dominance and monoculture biomass (Loreau & Hector 2001). Our analysis of two-species communities, however, suggests that competitive imbalance might often be negative under conditions that lead to species coexistence, which may explain why negative selection effects have often been found in recent biodiversity experiments.

Similarly, there is a close relationship between our measure of competitive relaxation and the complementarity effect of Loreau & Hector (2001). The Loreau–Hector complementarity effect is positive whenever there is stable coexistence in simple two-species Lotka–Volterra competitive systems, i.e. whenever the geometric mean of the interspecific competition coefficients is smaller than the geometric mean of the intraspecific competition coefficients (Loreau 2004). In our mechanistic approach devised for light competition among an arbitrary number of species, the competitive relaxation index CR is positive when the arithmetic mean of the interspecific competition coefficients is smaller than the arithmetic mean of the intraspecific competition coefficients. In most cases the two approaches should deliver congruent results, except when the average intensities of interspecific and intraspecific competition are close to each other but there is a large variance in competition intensity among species (in which case the arithmetic and geometric mean values diverge significantly).

An extension of the competitive relaxation index

So far, we have discussed the case when only competition intensity, k_{ij} , differs. More generally, when other

species-specific traits (e.g. allometric parameters) differ, analytical results are hard to obtain and the results may not be robust to variation in the several parameters. This is an issue to be developed in future work. However, the following analytically tractable case suggests insight into more general cases. When two characteristics, competition intensity k_{ij} and potential growth rate a_{0i} , differ among species, it can be shown analytically that the two parameters affect total plant biomass simultaneously through their impact on the RGR. The following quantity is then proportional to the competitive relaxation index in this case (Appendix S1):

$$E_i \left[\frac{k_{ij}}{a_{0i}} - \frac{E_j[k_{ij}]}{a_{0i}} \right] = \frac{1}{N} \sum_{i=1}^N \left\{ \frac{k_{ij}}{a_{0i}} - \frac{1}{a_{0i}} \left(\frac{1}{N} \sum_{j=1}^N k_{ij} \right) \right\}. \quad (15)$$

This means that the efficiency measure that contributes to total plant biomass is competition intensity standardized by the potential growth rate, which is a natural extension of eqn 6b. Thus, the competitive relaxation and imbalance effects are derived similarly as in the case when species differ only in competition intensity.

A possible scenario for light-use complementarity in action

The competitive imbalance effect, whether positive or negative, can be reduced by decreasing the variance among species in their average competition intensity, $\text{var}_j[E_j[k_{ij}]]$. When more than one trait differs among species, balanced growth can be achieved by a tradeoff between these traits, which tends to suppress competitive imbalance while maintaining the species-specific trait differences that are required for niche partitioning. For example, if potential growth rate, a_{0i} , and competition intensity, k_{ij} , differ, the tradeoff can be represented as follows (Appendix S1):

$$\frac{E_j[k_{ij}]}{a_{0i}} \approx \text{const.} \quad (16)$$

Such a tradeoff provides a greater potential for balanced growth by allowing two traits to co-vary and compensate for each other. It also better matches the reality of nature, which contains a diversity of lifestyles. If it is accompanied by other tradeoffs, niche complementarity should generally lead to an enhancement of total biomass. This qualitative conclusion should not be restricted to light competition or terrestrial ecosystems, but it should be valid for competitive systems in general.

As discussed above, positive competitive relaxation occurs when species in a mixture experience less severe competition on average than in monoculture, and thus the conditions under which functional complementarity takes place should greatly overlap with the conditions under which stable coexistence occurs (Loreau 2004).

Furthermore, tradeoffs are a key mechanism for multispecies coexistence (Kohyama 1993; Tilman & Pacala 1993; Anten & Hirose 1999; Werger *et al.* 2002; Anten 2005). Thus, it seems highly probable that in natural ecosystems, in which one or more coexistence mechanisms operate, the competitive imbalance effect, and hence the corresponding selection effect, tends to be suppressed, and the complementarity effect dominates. This conjecture is supported by several recent grassland experiments, which show that functional complementarity is responsible for the increase in plant biomass production with species diversity (Loreau & Hector 2001; Tilman *et al.* 2001; Hector *et al.* 2002; van Ruijven & Berendse 2003; Hooper & Dukes 2004). Our operational light complementarity index, LC, may then provide a useful method to test the mechanistic basis of this phenomenological complementarity.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Mathematical proof.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.00994.x>

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Appendix S1

Derivation of equation [5]

The equilibrium size distribution $n_i^*(x)$ ($i = 1, 2, \dots, N$) satisfies the equation $RGR_i(x) = 0$ for any x :

$$(a_0 - a_1 x^m) - \sum_{j=1}^N k_{ij} \int_x^{x_{\max-j}} y^\gamma n_j^*(y, t) dy = 0. \quad [\mathbf{A1}]$$

Differentiating both sides of **[A1]** with respect to x gives the following linear algebraic equations **[A2]**, from which $n_i^*(x)$ are obtained **[A3]**:

$$\sum_{j=1}^N k_{ij} n_j^*(x) = m a_1 x^{m-\gamma-1} \quad (i = 1, 2, \dots, N), \quad [\mathbf{A2}]$$

$$n_i^*(x) = \frac{m a_1}{N X_i} x^{m-\gamma-1}. \quad [\mathbf{A3}]$$

Maximum plant sizes, $x_{\max i}$, are calculated from the following linear algebraic equations **[A4]** obtained by substituting **[A3]** into **[A1]**:

$$\sum_{j=1}^N k_{ij} \sum_{l=1}^N \hat{k}_{jl} (x_{\max-j})^m = a_0 / a_1, \quad [\mathbf{A4}]$$

$$x_{\max-i} = (a_0 / a_1)^{1/m}. \quad [\text{A5}]$$

Minimum sizes, $x_{\min-i}$, are calculated from the conservation equations of total density

[A6] with [A5]:

$$\int_{x_{\min-i}}^{x_{\max-i}} n_i^*(x) dx = \frac{d_0}{N}, \quad [\text{A6}]$$

$$x_{\min-i}^{m-\gamma} = (x_{\max-i})^{m-\gamma} - \frac{(m-\gamma)d_0}{ma_1 \sum_{j=1}^N k_{ij}}. \quad [\text{A7}]$$

Finally, $B_{\text{mix-}i}$ is calculated by substitution integral as follows:

$$B_{\text{mix-}i} = \int_{x_{\min-i}}^{x_{\max-i}} Ax^\alpha \cdot \frac{d}{dx} \{Ax^\alpha\} n_i^*(x) dx = \frac{1}{N} f(X_i) \quad [\text{A8a}]$$

$$f(X_i) \equiv \frac{B}{X_i} \{1 - (1 - CX_i)^D\} \quad (0 < X_i < 1/C) \quad [\text{A8b}]$$

$$\equiv BCD - \frac{BC^2D(D-1)}{2} X_i \quad (0 < d_0 \ll 1). \quad [\text{A8c}]$$

B , C , D are constants calculated from the basic parameters (**Table 1**). Equation [A8b]

shows that $f(X_i)$ is a decreasing, concave-up function as long as $D > 1$. Monoculture

biomass $B_{\text{mono-}i}$ is obtained from [A8] by putting $N = 1$.

Proof of equation [6]

$$(1) k_{ij} = 0 \ (j \neq i) \Rightarrow CI = 0$$

Because the competition intensity matrix (k_{ij}) is diagonal, its inverse (\hat{k}_{ij}) is also diagonal with $\hat{k}_{ii} = 1/k_{ii}$. Thus, $X_i = k_{ii}/N$, which coincides with $E_j[k_{ij}] = k_{ii}/N$.

$$(2) \text{Var}_i[X_i] = 0 \Leftrightarrow \text{Var}_i[E_j[k_{ij}]] = 0 \Rightarrow CI = 0$$

Let us denote $Z_i = 1/(NX_i)$. If the inverse matrix of (k_{ij}) , (\hat{k}_{ij}) , exists, the following relation follows:

$$Z_i = \sum_{j=1}^N \hat{k}_{ij} \Leftrightarrow \sum_{j=1}^N k_{ij} Z_j = 1 \ (i = 1, 2, \dots, N). \quad [\text{A9}]$$

If $\text{Var}_i[X_i] = 0$ holds, it follows that $\text{Var}_i[Z_i] = 0$, i.e., $Z_i = c$ for any i . Thus, from [A9],

$\sum_{j=1}^N k_{ij} = 1/c$ holds for any i , i.e., $\text{Var}_i[E_j[k_{ij}]] = 0$. Because of the symmetry of $\sum_{j=1}^N k_{ij}$

and $\sum_{j=1}^N \hat{k}_{ij}$, the reverse is also true, and the first proposition follows. The second

proposition is evident from the above proof.

Proof of the general case

Just as in the case of low plant density, equation [5] can be partitioned into two additive components as follows:

$$\Delta B = E_i[f(E_j[k_{ij}]) - f(k_{ii})] + E_i[f(X_i) - f(E_j[k_{ij}])]. \quad [\mathbf{A10}]$$

As proof of [6], the second term of [A10] vanishes when $k_{ij} = 0$ ($j \neq i$) or $\text{Var}_i[X_i] = 0$ (or equivalently, $\text{Var}_i[E_j[k_{ij}]] = 0$). Thus, this term represents the competitive imbalance effect when it exists. Because $f(\cdot)$ is a decreasing function, $CR > 0$ is equivalent to $f(E_i[E_j[k_{ij}]]) > f(E_i[k_{ii}])$, and the difference $f(E_i[E_j[k_{ij}]]) - f(E_i[k_{ii}])$ increases as CR increases. Thus, $f(E_i[E_j[k_{ij}]]) - E_i[f(k_{ii})]$ also increases with CR because k_{ii} is fixed. The concaveness of $f(\cdot)$ ensures that $E_i[f(E_j[k_{ij}])] > f(E_i[E_j[k_{ij}]])$. Thus, $E_i[f(E_j[k_{ij}])] - E_i[f(k_{ii})]$, i.e., the first term of [A10], increases as CR increase and becomes positive if CR is sufficiently large. This means that the first term corresponds to the complementarity effect and CR approximately represents its magnitude. Similarly, CI approximately represents the magnitude of the competitive imbalance effect.

Derivation of condition [11]

ΔE_{i-max} ($k \leq LAI_i < k + 1$), which is attained if all the leaves are piled as layer so as not to make any overlap nor holes, is calculated by summing all the energy absorbed at each layer j where fraction q_i of injecting light intensity $L_0(1-q)^{j-1}$ ($1 \leq j \leq k$) and $(LAI_i - k)(1 - q_i)^k$ ($j = k$), is absorbed :

$$\begin{aligned}
\Delta E_{i-\max} &= L_0 q_i + L_0 (1 - q_i) q_i + L_0 (1 - q_i)^2 q_i + \cdots + L_0 (1 - q_i)^{k-1} q_i \\
&+ L_0 (LAI_i - k) (1 - q_i)^k q_i \\
&= L_0 \left\{ - (1 - q_i)^k + (LAI_i - k) (1 - q_i)^k q_i \right\}
\end{aligned}$$

[A11]

$\Delta E_{mix-\max}$ is approximated as $\Delta E_{i-\max}$ with LAI_{mix} ($k \leq LAI_{mix} < k + 1$), averaged

absorption rate of the mixture \bar{q} as :

$$\Delta E_{mix-\max} \approx L_0 \left\{ - (1 - \bar{q})^k + (LAI_{mix} - k) (1 - \bar{q})^k \bar{q} \right\} = L_0 g(\bar{q}, LAI_{mix}) \quad [A12]$$

Derivation of condition [14]

When a_{1i} is proportional to a_{0i} (say, $a_{1i} = ha_{0i}$), RGR is:

$$RGR_i(x) = a_{0i} (1 - hx^m) - \sum_{j=1}^N k_{ij} \int_x^{x^{\max-j}} y^\gamma n_j(y, t) dy. \quad [A13]$$

ΔB is calculated as a function of light-competition intensity and basic growth rates

following the same procedures as in the previous section:

$$\Delta B = \frac{1}{N} \sum_{i=1}^N F(Y_i) - \frac{1}{N} \sum_{i=1}^N F\left(\frac{k_{ii}}{a_{0i}}\right), \quad [A14]$$

$$Y_i \equiv \frac{1}{N} \left(\sum_{j=1}^N \hat{k}_{ij} \cdot a_{0j} \right)^{-1}. \quad [A15]$$

$F(Y_i)$ in [A14] is a decreasing, concave-up function which has the same functional form as [A8] upon substitution of B for B_1 and C for C_1 (Table 1).

The sufficient conditions for $CI = 0$ is similarly obtained as [A16], from which equation [15] follows.

$$\text{Var}[Y_i] = 0 \Leftrightarrow \text{Var}\left[\frac{E_j[k_{ij}]}{a_{0i}}\right] = 0. \quad \text{[A16]}$$