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IDEA AND PERSPECTIVE

Coexistence, niches and biodiversity effects on ecosystem functioning

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Abstract

General principles from coexistence theory are often invoked to explain how and why mixtures of species outperform monocultures. However, the complementarity and selection effects commonly measured in biodiversity experiments do not precisely quantify the niche and relative fitness differences that govern species coexistence. Given this lack of direct correspondence, how can we know whether species-rich mixtures are stable and that the benefits of diversity will therefore persist? We develop a resource-based included-niche model in which plant species have asymmetric access to a nested set of belowground resource pools. We use the model to show that positive complementarity effects arise from stabilising niche differences, but do not necessarily lead to stable coexistence and hence can be transient. In addition, these transient complementarity effects occur in the model when there is no complementary resource use among species. Including a trade-off between uptake rates and the size of the resource pool stabilised interactions and led to persistent complementarity coupled with weak or negative selection effects, consistent with results from the longest-running field biodiversity experiments. We suggest that future progress requires a greater mechanistic understanding of the links between ecosystem functions and their underlying biological processes.

Keywords

Additive partition, biodiversity, coexistence, complementarity effects, niches, selection effects, transient complementarity.

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INTRODUCTION

Current rates of biodiversity loss may be as high as those observed during the major extinction events known from the fossil record (Barnosky *et al.* 2011). Unfortunately, efforts during the last two decades to slow the decline of biodiversity have largely failed, and this general degradation of the environment is set to continue for the foreseeable future (Butchart *et al.* 2010; Perrings *et al.* 2011). This lack of success is disappointing and worrying not only because of the loss of diversity itself but also because of potentially negative consequences for the functioning and stability of ecosystem processes and the environmental services provided to humanity. Recent reviews and meta-analyses of research from the last 20 years have confirmed that when compared with depauperate versions, more diverse ecosystems appear to utilise resources more effectively and are consequently more productive and stable (Balvanera *et al.* 2006; Duffy 2009; Cardinale *et al.* 2011, 2012; Hooper *et al.* 2012; Naeem *et al.* 2012). There is therefore a general consensus that biodiversity loss will have undesirable consequences for ecosystem functioning.

While the empirical results are clear, the cause of the positive relationship between diversity and functioning has been rather more contentious. Over the last 20 years, biodiversity researchers have repeatedly drawn on the coexistence literature to help explain observed patterns, for example, suggesting that niche differences allow species to complement one another in mixture and hence better utilise the available resources (Gross *et al.* 2007; Northfield *et al.* 2010; Cardinale 2011). Coexistence theory is clearly relevant for biodiversity research, as only in stable communities can diversity persist and hence continue to deliver whatever benefits it confers. However, ecological niches and the coexistence they enable are notoriously slippery concepts, perhaps explaining why most references to niches within the biodiversity literature remain vague. Here, we first review past and current attempts to synthesise coexistence theory with the biodiversity literature and use a new model developed for plant communities to improve our interpretation of the complementarity and selection effects and how they relate to concepts from coexistence theory.

Conceptual development

A Darwinian synthesis?

The idea that the mechanisms underpinning species coexistence are the same as those that link biodiversity with ecosystem functioning can be traced all the way back to Darwin's principle of divergence (McNaughton 1993; Hector & Hooper 2002; Hector 2009) whereby natural selection drives the evolution of species into different and complementary niches. Darwin explicitly states that more diverse ecosystems should have higher rates of 'chemical composition and decomposition'. He even talks of the 'division of labour' arising from the divergence of species into different niches, using Adam

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Smith's 1776 phrase for the efficiencies gained by specialisation within manufacturing (pin making in Smith's industrial example). Although Darwin's emphasis was on evolution by natural selection as an explanation for diversity rather than the consequences of biological diversity for the functioning of ecosystems, it seems clear that he viewed one as an outcome of the other. The idea that these causes and consequences of diversity can be seen as two sides of the same coin therefore appears to have a long and illustrious pedigree. The dearth of more recent attempts to formally connect the two is partly because the coexistence literature appears messy and complicated, invoking an apparently endless variety of mechanisms to explain the coexistence of different groups of organisms. Only recently did a modern synthesis emerge that demonstrated how all coexistence mechanisms can be viewed as the interplay between two opposing forces.

The maintenance of diversity

From the seemingly disparate coexistence mechanisms, Chesson (2000) produced a unifying framework in which he grouped all mechanisms into either equalising or stabilising forces. Equalising forces are those that reduce fitness differences among species. In the limit, when fitness differences are zero, a neutral model can emerge in which drift is the only force influencing community dynamics (Hubbell 2001). However, because fitness equalisation among species exhibiting substantial trait variation is unlikely (Turnbull *et al.* 2008; Purves & Turnbull 2010) coexistence requires the operation of stabilising forces that induce frequency-dependent community dynamics, reflected in species having higher population growth rates when rare (Levine & HilleRisLambers 2009). Whether or not coexistence is observed depends on the relative strengths of these opposing forces: if fitness differences are large, then stabilising forces will have to be correspondingly large to prevent competitive exclusion (Adler *et al.* 2007). Stabilising forces result from what are commonly called niche differences, and cause species to limit themselves more than they limit others. Such stabilising niche differences can be due to a whole variety of biological mechanisms: for example, species might specialise on different resources (McKane *et al.* 2002) or take up the same resources at different times or from different spatial locations (Hooper & Vitousek 1998; Fargione & Tilman 2005). In addition, niche differences do not have to be resource based, but can include stabilising interactions with other trophic levels, such as soil pathogens (Bever 2003; Petermann *et al.* 2008), specialist herbivores (Grover 1994; Thebault & Loreau 2003) or mycorrhizas (Klironomos 2002). A key question for biodiversity-function researchers is whether stabilising niche differences, regardless of their form, can be identified using only monoculture and mixture yields, and perhaps more importantly, is it possible to know whether the mixture is stable and that the benefits of diversity will persist?

Biodiversity-ecosystem function experiments

In contrast to work on coexistence, research on the effect of biodiversity on ecosystem functioning began with less theoretical motivation and largely consisted of manipulating the numbers of species in experimental communities and measuring a variety of ecosystem processes, for example, productivity and nutrient cycling (Hooper & Vitousek 1997; Tilman *et al.* 1997a; Hector *et al.* 1999). Over the last 20 years, many such experiments have been carried out and the resulting relationships between diversity and ecosystem processes typically show a positive effect of diversity on ecosystem processes, although flat or negative relationships are found more rarely (Balvanera *et al.* 2006; Cardinale *et al.* 2007, 2011). These relationships also often show diminishing returns; in other words, while these regressions are typically positive, they quickly approach an asymptote, although relationships can become stronger over time (Reich *et al.* 2012) and analyses of multiple ecosystem functions generally show that different species are important for different functions (Duffy *et al.* 2003; Hector & Bagchi 2007; Gamfeldt *et al.* 2008; Zavaleta *et al.* 2010; Isbell *et al.* 2011). The data also show that transgressive overyielding, in which species mixtures outperform the best component monoculture, is neither widespread nor strong. For example, Cardinale *et al.* (2011) found that in 63% of cases, the mixture actually had lower yield than the best component monoculture and left more resources unused. This is perhaps surprising, given that complementary resource use by the component species is generally expected to yield a greater total biomass in mixture driven by more complete use of available resources (Tilman *et al.* 1997b; Fox 2003).

An argument over mechanism

Why are biodiversity effects generally positive? Perhaps, the simplest explanation for the enhanced performance of mixtures is via competitive dominance of high-yielding species. If we assume a zero-sum game of resource competition, then the dominance of productive species will come at a direct cost to their weaker opponents. Furthermore, if the productive species are competitively superior, then as they become dominant the mixture will tend to have similar characteristics to these high-yielding species. High-diversity mixtures that contain lots of species are also more likely to include a high-yielding species; hence, positive biodiversity effects might simply be due to this so-called sampling or selection effect (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b; Loreau 1998b). The second – and to ecologists more interesting – possibility for the enhanced average performance of mixtures is due to the niche differentiation hypothesised by Darwin. This allows deviations from the zero-sum game known as overyielding (Trenbath 1974), because if species have different niches, they can potentially achieve higher per-capita yields in mixture than they do in monoculture.

Additive partitioning of biodiversity effects

The main analytical approach used to distinguish between the effects of overyielding and competitive dominance on productivity (or surrogates like herbaceous biomass) is the additive partitioning of biodiversity effects (Box 1; Loreau & Hector 2001). The additive partitioning method works by defining a 'net biodiversity effect' that can then be partitioned into a 'selection effect' and a 'complementarity effect' (additive because NE = SE + CE). The net biodiversity effect, ΔY, is the difference between the observed yield of a mixture and its expected yield based on monocultures. The null expectation is that the yield of an even mixture involving n species is equivalent to harvesting $1/n$th of each of the component monocultures. The net effect is partitioned into two components. The selection effect is measured by the covariance between the monoculture yields of the species and the deviation from their expected relative yields in mixture. When species are sown at equal density, the expected relative yield in mixture is simply $1/n$, where n is the number of species; hence, the expected relative yield in a two-species mixture is 0.5 and the expected relative yield total is 1.0. Positive selection occurs when species with higher-than-average monoculture biomass have greater increases in their relative yields in mixture, while negative selection occurs when the same applies to species with lower-than-average monoculture yields. If only selection effects operate, then the relative yield total will be 1.0, despite the non-equivalence of competitors (i.e. their differences in monoculture biomass). In contrast, positive complementarity effects (overyielding) occur when increases in the relative yields of some species are not exactly compensated by decreases in others. In this case, the relative yield total is > 1.0. Such effects have often been interpreted as indicative of stabilising niche differences including complementary resource use. But in fact, the complementarity effect is influenced by the combined effects of all interactions within an ecological community (Loreau 1998b; Loreau & Hector 2001; Petchey 2003; Cardinale *et al.* 2011; Carroll *et al.* 2011; Loreau *et al.* 2012). The additive partitioning of biodiversity effects into complementarity and selection effects seems to offer a clear parallel with the niche and relative fitness differences identified by Chesson (2000). Thus, there was the tantalising prospect that these two influential frameworks could be unified.

Box1 Additive Partitioning of Biodiversity Effects

Define, for any mixture,

M_i = yield of species i in monoculture;

$Y_{O,i}$ = observed yield of species i in the mixture;

$Y_0 = \sum_i Y_{0,i}$ = total observed yield of the mixture;

$RY_{E,i}$ = expected relative yield of species i in the mixture, which is simply its proportion seeded or planted;

$RY_{O,i} = Y_{O,i}/M_i$ = observed relative yield of species i in the mixture;

$Y_{E,i} = RY_{E,i}M_i$ = expected yield of species i in the mixture;

$Y_E = \sum Y_{E,i}$ = total expected yield of the mixture;

$\Delta Y = Y_O - Y_E$ = deviation from total expected yield in the mixture;

$\Delta RY_i = RY_{O,i} - RY_{E,i}$ = deviation from expected relative yield of species i in the mixture;

N = number of species in the mixture.

It then follows:

$$\Delta Y = Y_0 - Y_E = \sum_i RY_{0,i}M_i - \sum_i RY_{E,i}M_i = \sum_i \Delta RY_i M_i$$
$$= N.\overline{\Delta RY}.\overline{M} + N.\text{cov}(\Delta RY, M)$$

In this equation, $N.\overline{\Delta RY}.\overline{M}$ measures the complementarity effect, and $N.\text{cov}(\Delta RY, M)$ measures the selection effect. Note that because the covariance applies to the whole population of species in each mixtures rather than a sample of species the calculation is done using N (the number of species) and not the more usual N-1 (the usual default for covariance functions in most software packages). This approach is a generalisation of the widely used relative yield total (*RYT*) approach in plant population biology and intercropping and, more recently, the proportional deviation from expected value (*D*) approach devised by Loreau 1998b. Fox (2005) extended the additive partition to a tripartite version in which the complementarity effect is renamed the trait-independent CE (CE = TICE) while the selection effect from Loreau and Hector is split into two covariance terms: trait-dependent complementarity effect (TDCE) and a dominance effect (DE). Here, we limit ourselves to using the original additive partition as it is more commonly used in published work to date.

Unifying the frameworks: early attempts

The first attempts to link coexistence mechanisms to ecosystem functioning occurred before the development of the additive partition. These studies generally presented models with different assumptions about resource uptake and competition and analysed whether they resulted in sampling effects or overyielding. Early models investigated the inclusion of resource-use complementarity (Tilman *et al.* 1997b; Loreau 1998a) and more specific coexistence models such as the competition-colonisation trade-off (Mouquet *et al.* 2002). Some even offered explanations for why in long-term experiments, sampling effects might be detected early on, with a later shift to overyielding as competition begins to dominate (Pacala & Tilman 2001). Most of these early models suggested that the presence of stabilising niche differences, in particular the inclusion of resource-use complementarity, should lead to transgressive overyielding (Tilman *et al.* 1997b), which was later confirmed by a study applying the additive partition to exactly such a model (Fox 2003).

Perhaps, the simplest analysis of the link between coexistence and biodiversity-ecosystem functioning is based on the Lotka–Volterra framework. Within this framework, each species has a carrying capacity, *K*, which can be equated with the species' yield in monoculture. The conditions for stable coexistence require that the average strength of interspecific competition is weaker than the average strength of intraspecific competition, i.e. that there are stabilising niche differences. Loreau (2004) showed that within the Lotka–Volterra framework a stable mixture would inevitably overyield; hence, the conditions for stable coexistence are consistent with the existence of complementarity. Loreau was careful to point out that the existence of niche differences does not necessarily guarantee stable coexistence. Therefore, it is not clear from this analysis how often overyielding would be observed in transient mixtures that would not be stable. However, these analyses of Lotka–Volterra models did not attempt to establish whether there were precise parallels between complementarity and selection effects and niche and fitness differences, which was the focus of the next attempt.

Unifying the frameworks: a more detailed analysis

Carroll *et al.* (2011, 2012) analysed MacArthur's consumer-resource model to investigate more precisely how coexistence theory maps onto biodiversity effects. In the MacArthur model, stabilising niche differences come about through specialisation on different resources. However, Carroll *et al.* were more concerned with how the fitness differences and stabilising niche differences from Chesson's conceptual framework relate to the selection and complementarity effects measured in biodiversity research. Carroll *et al.* showed that while these concepts were broadly related, there was no direct correspondence. Instead, although complementarity always occurred in the coexistence region, its magnitude was also influenced by the size of the relative fitness differences, a result that they did not expect. Moreover, the strength of the selection effect depended on both niche and fitness differences. Their analysis raises a very important question: despite the desirability of such a connection, should ecologists ever in fact have expected a one-to-one correspondence between niche and fitness differences on the one hand and complementarity and selection effects on the other?

An imperfect marriage

In fact, both the selection and complementarity effect inevitably include a combination of niche and fitness differences (Carroll *et al.* 2011, 2012; Loreau *et al.* 2012). We begin by examining the complementarity effect. In the long term, stabilising niche differences are clearly necessary for stable coexistence, so without niche differentiation, there can be no long-term maintenance of diversity nor long-term complementarity. Even in the shorter term, complementarity arises through reductions in interspecific competition that are the outcome of stabilising niche differences. But why should fitness differences also contribute to complementarity? The magnitude of complementarity depends not just on how much better species perform in mixture than in monoculture (an effect of stabilising niche differences), but also on the relative abundance of the competitors in mixture; for example, little overyielding is possible if the mixture is 99% composed of one species. Fitness differences, along with niche differences, regulate this relative abundance, and thereby influence complementarity. In the extreme, an overwhelming fitness difference can altogether prevent complementarity, even between species with large stabilising niche differences, by causing the elimination of the species with lower fitness. In sum, stabilising niche differences are a necessary, but insufficient condition for both coexistence and complementarity. It therefore appears that evidence for complementarity is evidence for stabilising niche differences between competitors, but certainly not evidence that the species will coexist.

For reasons also related to the controls over relative abundance, we should expect stabilising niche differences to affect the strength of selection effects. Even when relative fitness differences are positively correlated with monoculture performance (and would generate a positive selection effect), niche differences should still influence the relative abundance of species in mixture. Stronger niche differences will favour more even relative abundances, reducing the strength of the selection effect. At the opposite extreme, without any niche differences, the best competitor will win in mixture generating a pure selection effect. We therefore hypothesise that selection effects are indicative of the presence of relative fitness differences, but not their strength.

Where next?

If we do not expect a direct correspondence between the two schemes, is there any point in pursuing these connections further? We believe that establishing whether diverse mixtures are likely to be stable in the long term is an important part of biodiversity research, and is therefore still a goal worth pursuing. One important task that remains unaddressed is to clarify the interpretation of the widespread presence of complementarity in biodiversity experiments. For example, when positive complementarity effects are detected, it is rarely considered that this might only be a transient phenomenon (but see Weis *et al.* 2007) and positive complementarity effects are often assumed to result from complementary resource use by species in mixtures (Eisenhauer 2012; Roscher *et al.* 2012). But are such conclusions justified? Here, we develop a model that allows us to address whether the presence of complementarity can be reasonably interpreted: (1) as evidence for species coexistence, (2) as evidence for stabilising niche differences that might, however, be insufficient to give coexistence and (3) as evidence for complementary or more complete resource use by species in mixtures.

An included-niche model

Justification and assumptions

To address these questions, we need a model appropriate for plant communities, as most biodiversity manipulation experiments are carried out with plants. Most of these experiments comprise just a few

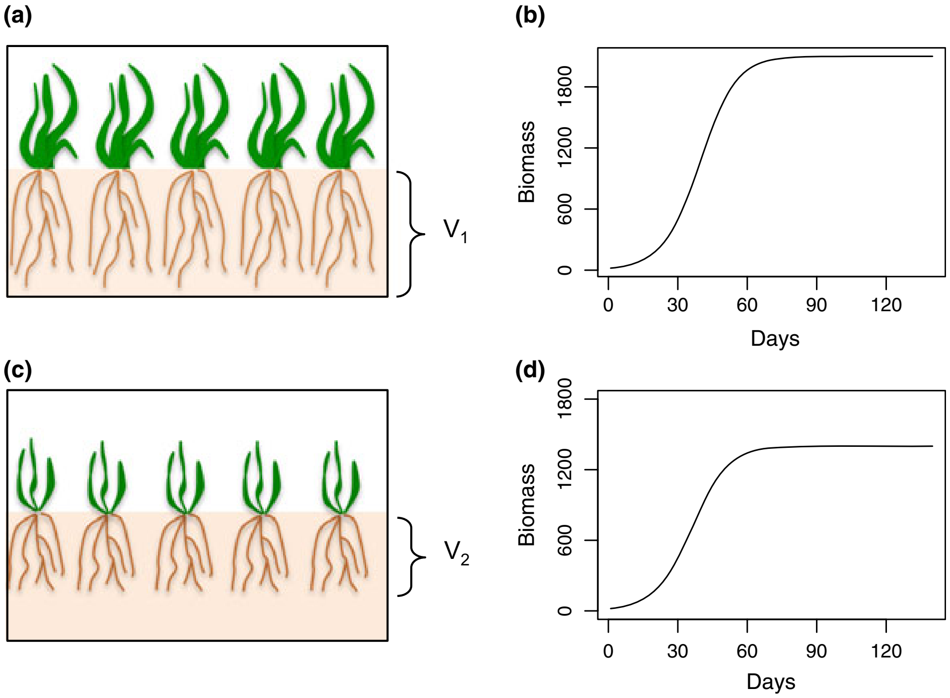

Figure 1 An illustrative example of an included niche based on soil depth. (a) Species 1 can access a larger resource pool and hence reach a higher yield (b) than species 2. (c) In turn, species 2 has shallower roots and can hence achieve a lower monoculture biomass (d) than species 1.

generations or even a single season of growth in which there is little or no population turnover (e.g. Fridley 2002). We therefore develop a model that includes an explicit representation of plant growth over each season, and which therefore yields predictions for the biomass of both monocultures and mixtures after a single season of growth. We use an included-niche model, in which the 'included' species only have access to a nested subset of the available resources. The species with access to the largest resource pool will have the highest monoculture yield, and mixtures containing more than one species can never yield higher than the best monoculture; hence, transgressive overyielding is impossible. In this version of the model, there is also no true complementary resource use among the species, as each species can only use a subset of the resources available to the others. Additional trade-offs between the size of the resource pool (a measure of niche breadth) and the efficiency with which resources are extracted can also allow for stable coexistence (Levins 1968; Berendse 1979). We therefore have the opportunity to explore more deeply the relationship between complementarity, stabilising niche differences, resource-use patterns and coexistence.

Inspired by the work by Berendse (1979, 1981), we develop a simple included-niche model in which each species has access to a nested set of belowground resource pools (Fig. 1). We believe that an included-niche model is justified because many biodiversity experiments begin with a rather homogenised environment, leaving few niche axes prominent. Perhaps because of this, most explanations for the complementarity effects in empirical work with plants emphasise rooting depth differences (Berendse 1979; Dimitrakopoulos & Schmid 2004; von Felten *et al.* 2012) or differences in the seasonal timing of growth (Hooper & Vitousek 1998). Yet, deep rooting plants also have shallow roots (Frank *et al.* 2010), and late phenology species often still emerge coincident with their competitors, matching some of the assumptions of included-niche models.

The model also includes an explicit representation of plant growth within a single growing season. Thus, it provides an expected end-of-season biomass from a known starting point. Such a model is particularly appropriate for a terrestrial plant biodiversity experiment carried out in a simplified environment in a seasonal climate. In biodiversity experiments, species are usually sown at high density and generally remain there; hence, we make the simplifying assumption that density remains constant throughout the growing season and from year to year. Species are normally sown into bare soil where nutrients are initially plentiful and plants grow and compete for the nutrients that they can access. Because most biodiversity experiments are harvested at the end of the growing season and there is substantial tissue loss over the winter, we further assume that plots begin each year from low biomass from which they regrow during the season. The model can be run over multiple generations by assuming that the proportion of each species in next year's initial mass is determined by the relative biomass of each species at the end of the previous growing season. Furthermore, we restore the nutrient concentration at the beginning of each year to its initial value. At the end of a season, the total biomass of each species in monoculture and in mixture can be used to calculate biodiversity effects.

Monocultures

The growth of all species within a growing season is limited by the availability of a single belowground resource, which for simplicity we call nitrogen. We further assume that nitrogen is evenly distributed throughout the soil and that species i takes up nitrogen at some rate per unit plant biomass (θ_i) from a given volume of soil (V_i). The total nitrogen pool available to species i (K_i) is thus the product of the initial nitrogen concentration in the soil at the beginning of the growing season (N_0) and the maximum soil volume that species i can exploit (V_i); hence $K_i = N_0 V_i$, and can be viewed as a carrying capacity within a season. Given the carrying capacity, K_i, and assuming that we sow n seeds of size M_0, then the growth increment of an individual in a monoculture of species i in each time step ($I_{i,t}$) is given by a discrete-time logistic equation:

$$I_{i,t} = \rho\theta_i M_{i,t-1} N_0 \left[\frac{N_0 V_i - n_i M_{i,t-1}}{N_0 V_i}\right] \tag{1}$$

where $M_{i,t}$ is the mass of an individual of species i at time t. The multiplier ρ is equivalent to the C : N ratio and converts grams of nitrogen into grams of carbon. If all species have the same value of the C : N ratio (ρ) and values of the nitrogen uptake rate are high enough to allow species to achieve their carrying capacity within a single growing season, then monoculture yields are solely determined by the volume of soil that species can access.

Mixtures

An include niche means that when two species are grown in competition, species 1 can access a resource pool ($N_0 V_1$) that is completely nested within the resource pool available to its competitor, species 2 ($N_0 V_2$, where $V_2 > V_1$). This means that the growth increment for species 1 would become negative once the combined mass of species 1 and 2 exceeds the carrying capacity of species 1. Instead, we assumed that nitrogen locked into plant tissue during a growing season cannot be recycled until the following year. To prevent species 2 from extracting resources directly from the tissues of species 1, we set the growth increment for species 1 to zero whenever the growth rate of species 1 is expected to be negative. Species 2 is unaffected by this and continues to grow until it reaches its carrying capacity. Hence, the growth increment of species 1 in mixture is given by

$$I_{1,t} = \begin{cases} \rho\theta_1 M_{1,t-1} N_0 \left[\frac{N_0 V_1 - (n_1 M_{1,t-1} + n_2 M_{2,t-1})}{N_0 V_1}\right] & if I_{1,t} > 0 \\ 0 & if I_{1,t} < 0 \end{cases} \tag{2a}$$

And the growth of species 2 by

$$I_{2,t} = \rho\theta_2 M_{2,t-1} N_0 \left[\frac{N_0 V_2 - (n_1 M_{1,t-1} + n_2 M_{2,t-1})}{N_0 V_2}\right] \tag{2b}$$

Under these assumptions, individual-level plant competition is not completely biomass symmetric even if all species share identical nitrogen uptake rates (θ_i). This is because the realised growth increment at a given plant size is the product of the current mass of the plant and the amount of nitrogen remaining in the soil, which is greater for species with access to a larger nitrogen pool. However, this effect is very small early in the growing season when plants are small.

Assessing coexistence

The equations given so far simulate the growth of monocultures and mixtures during a single growing season from an initial seed inoculum. However, to understand the dynamics of the community, we need to run the system over multiple generations. To do this, we assume that at the end of the growing season, the existing biomass is removed and the plants begin again from the same total ini-

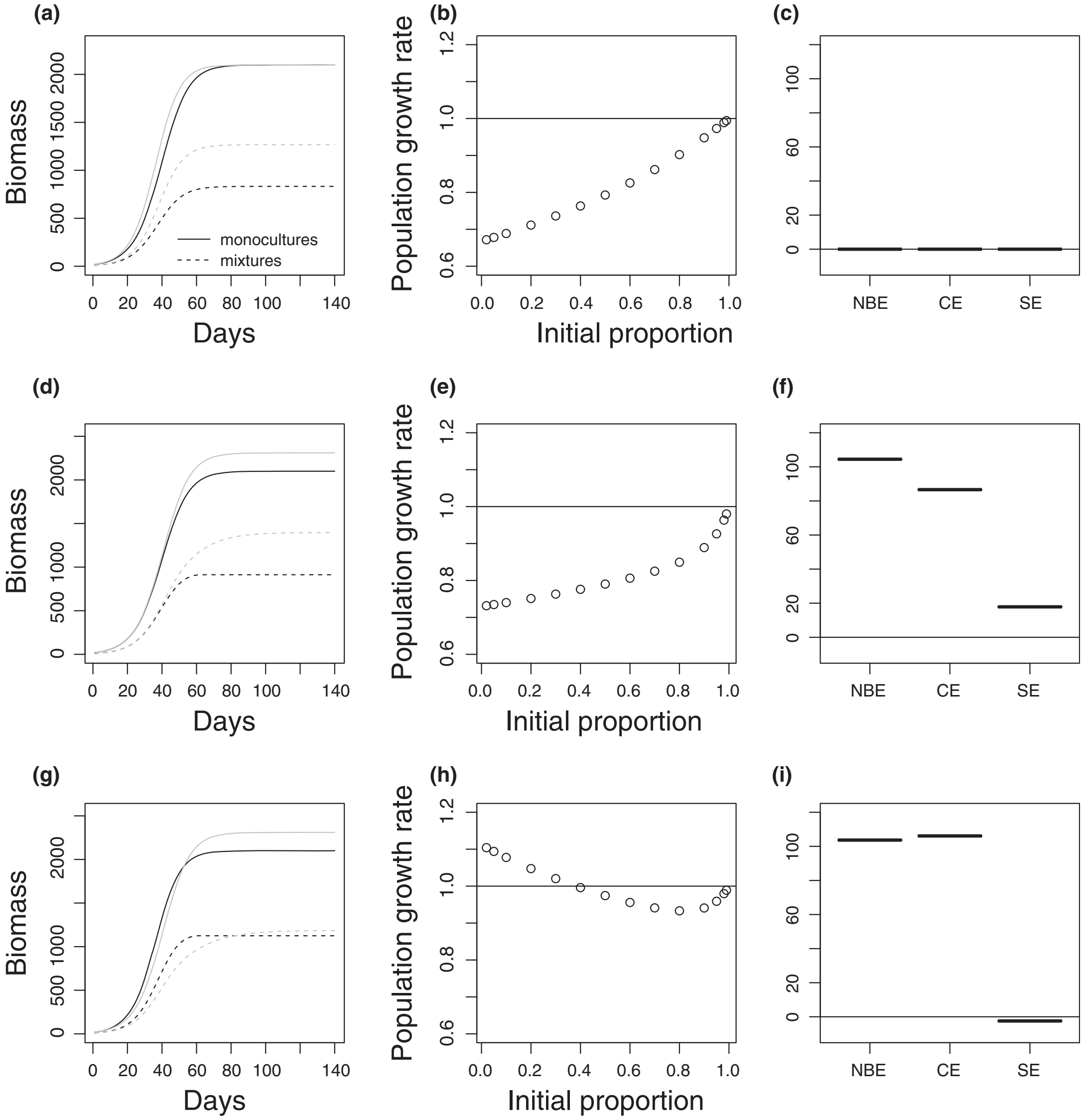

Figure 2 Top row (a) growth over a single growing season for two species that differ by 10% in their resource uptake rates (θ_i); (b) the population growth rate of the slower growing species in mixture from different initial proportions and (c) the associated net biodiversity effect (NBE), complementarity effect (CE) and selection effect (SE) for the 50:50 mixture at the end of a single growing season. Middle row (d–f): the same except that the two species now differ by 10% in the total soil volume that they are able to exploit (V_i). Bottom row (g–i): the same except species 1 (black) now has a resource uptake rate that is 10% higher than species 2 (grey), but species 2 can exploit a soil volume that is 10% higher than species 1. Parameter values: $N_0 = 0.07$; sowing density = 1000; seed mass = 0.002; $\rho = 10$. Top row: $\theta_1 = 1.80$, $\theta_2 = 1.98$, $V_1 = 3000$, $V_2 = 3000$; Middle row: $\theta_1 = 1.80$, $\theta_2 = 1.80$, $V_1 = 3000$, $V_2 = 3300$; Bottom row: $\theta_1 = 1.98$, $\theta_2 = 1.80$, $V_1 = 3000$, $V_2 = 3300$.

tial mass as in year 1. For simplicity, we call these seeds, but after year one, it is more likely that these would be the surviving parts of adult plants. The fraction of the seeds belonging to species i in generation g+1 ($F_{i,g+1}$) is given by the fraction of the total biomass that species i had at the end of the gth generation. Hence,

$$F1, g + 1 = M1, g/(M1, g + M2, g) \qquad (3)$$

and a species ending the year with a higher fraction of the total plant biomass will start the following year with a higher fraction of the total seeds. The initial soil nitrogen concentration (N_0) is returned to the same value each year. To determine whether a given two-species mixture is stable, we can continue this process for multiple generations and assess whether one species drives the other to extinction. We can also test for stability of the mixture by comparing the start-of-season seed mass ratio to the end-of-season biomass ratio. If a stable equilibrium exists, then the two ratios should be equal at the equilibrium point.

Choosing parameter values

We first carried out simple simulations of two-species mixtures and their component monocultures to determine the relationships between biodiversity metrics and coexistence. We used a substitutive design, with constant sowing density of 1000 seeds each with an initial mass of 0.002. The value for the initial nitrogen concentration in the soil, N_0, was set to 0.07. The volume over which species 1 extracted resources (V_1) was allowed to vary tenfold over the range 1000–10000, reflecting the tenfold range of biomass often seen among monocultures in biodiversity experiments with plants. The value of species 1's uptake rate (θ_1) was allowed to vary threefold over the range 1.5–4.5. The narrower range on the uptake rate reflects the maximum range measured for plants with similar life histories (Turnbull *et al.* 2012), while the minimum values still allowed monocultures to achieve a mass close to their asymptotic mass by the end of the growing season. Values for the soil volume and uptake rate of species 2 (V_2 and θ_2) were constrained to be 10% larger or smaller than the respective values for species 1 (V_1 and θ_1). The growing season was 140 days, equivalent to roughly 4.5 months, which seems reasonable for Northern temperate climates.

In the results that follow, we highlight three cases: (1) species differ in their uptake rates (θ_i) but not in the soil volume exploited (V_i), (2) species differ in the soil volume exploited, but not in their uptake rates, and (3) species differ in both the soil volume exploited and in their uptake rates in a manner consistent with a trade-off. We simulated 500 species-pairs in each case.

Results 1: species differ only in their uptake rates

As expected, if species varied only in the nitrogen uptake rate but not in the volume of soil that they could exploit (Fig. 2a), then no stable equilibrium was possible. The absence of a stable equilibrium can be visualised by plotting the population growth rate of the weaker competitor (species 2) for different initial seed fractions. The population growth rate is calculated as the proportion of species 2 in the end-of-season biomass divided by the proportion of species 2 in the start-of-season seed inoculum. Because $\theta_1 > \theta_2$, the population growth rate of species 2 is < 1 for all initial conditions, hence its rapid exclusion (Fig. 2b). Exclusion occurs because there are fitness differences between the species: in this case, species 1 can extract resources faster from the common resource pool. Because species do not differ in their monoculture yields and there is no coexistence, there is no potential for biodiversity effects, which are all zero (Fig. 2c).

Results 2: species differ only in the soil volume exploited

If species differed by 10% in the volume of soil that they could exploit but not in their nitrogen uptake rates (Fig. 2d), there was also no stable coexistence, as indicated by the lack of a stable equilibrium (Fig. 2e). However, the biomass of the mixture was the same as the best component monoculture, which is why we see a positive net biodiversity effect after one growing season (Fig. 2f). The additive partition reveals that the positive net effect is due to both a positive selection effect and a positive complementarity effect (Fig. 2f). The positive selection effect arises because the high-yielding monoculture has a greater relative yield, indicating its competitive dominance. The positive complementarity effect occurs because although the high-yielding monoculture species begins in mixture at half the monoculture density, it is able to exploit most of the additional resources that are available to it alone by producing bigger individuals. This gain in relative yield comes at a lower cost to the second species than expected, as the second species does not compete for this additional pool. Thus, the relative yield total is > 1, as also noted by Berendse (1979). Therefore, if species differ only in the total amount of resources that they can exploit, we can expect to observe transient complementarity effects, even when there is no stable coexistence. Following traditional usage, because this mixture overyields (RYT > 1), it would be defined as 'complementary'. However, because the subordinate's resource pool is a perfectly nested subset of the dominants, there is no complementarity in the sense of its original and usual usage in which each species supplies something that the other does not (Woodhead 1906).

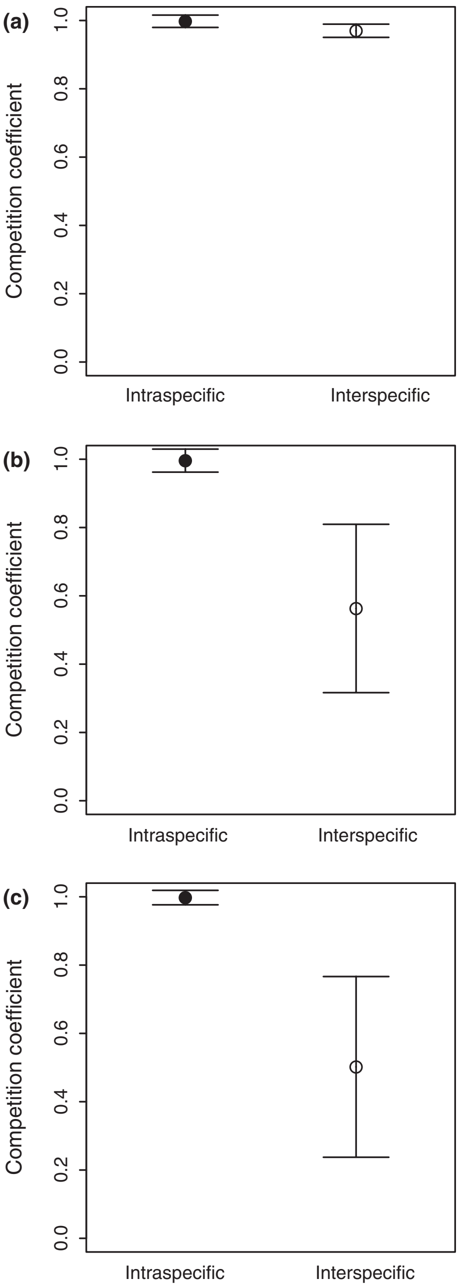

Figure 3 The strength of intra- and interspecific competition when (a) there are 10% differences in the nitrogen uptake rate (θ_i); (b) there are 10% differences in the total size of the resource pool (V_i) and (c) when there is a trade-off between the two parameters. (b) Parameter values as in Fig. 2 but V_1 varies over the range 1000–10000 and θ_1 varies over the range 1.5–4.5. V_2 and are θ_2 constrained to be 10% smaller or larger than V_1 and θ_1. The variation in the interspecific competition coefficients is due to variation in model parameters, which were sampled over a wide range. The mean and 95% confidence intervals from 500 simulated pairs are shown.

Results 3: a trade-off between uptake rates and soil volumes

When there was a trade-off between the uptake rate (θ_i) and the soil volume (V_i), such that species 1 could exploit a soil volume 10%

larger than species 2 but had an uptake rate that was 10% lower (e.g. Fig. 2g), species stably coexisted (Fig. 2h). The two-species equilibrium is indicated by the intersection of the population growth rate curve with the line $\lambda = 1$. Hence, the population growth rate of species 2 is > 1 when rare and < 1 when common (Fig. 2h). Biodiversity metrics after one growing season once again yield positive net biodiversity effects of similar magnitude to the case with no trade-off. Complementarity effects are still large and positive, while selection effects are smaller and often negative (Fig. 2i). The reduced selection effect indicates that the species are more equal competitors because the low-yielding species is now a better competitor for the shared resource pool. Note that despite the negative selection effect, the low-yielding species does not necessarily dominate the mixture biomass in absolute terms; it simply has a greater relative yield.

Evidence for niches

To see whether a positive complementarity effect in our model was consistent with the presence of stabilising niche differences, we quantified the relative strength of intraspecific and interspecific interactions. Stabilising niche differences are often defined by their ability to cause intraspecific effects to exceed interspecific effects. We therefore estimated the individual-level pairwise competition coefficients: α_{11}, α_{12}, α_{21}, α_{22}. To estimate these coefficients, we simulated the growth of a single individual of each species with no neighbours and then with varying numbers of both conspecific and heterospecific neighbours. As in annual plant models, the end-of-season biomass of the focal individual ($M_{i,t}$) declines as the number of neighbours increases and a Beverton–Holt model generally provided a good fit to the resulting data:

$$M_{i,t} = \frac{M_{i,max}}{1 + \propto n} \qquad (4)$$

where $M_{i,\max}$ is the biomass of a plant with no neighbours and n is the number of neighbours (not counting the focal plant). By taking reciprocals, we can then estimate the resulting competition coefficients using linear modelling. Model fits were good for the rather modest 10% differences in uptake rates (θ_i) or soil volumes (V_i) that we explored. We therefore estimated the alpha values for all the 1500 pairs of species above.

For all pairs, the value of the intraspecific competition coefficients was extremely close to the expected value of 1.0 (an individual with one conspecific neighbour should achieve exactly half the biomass of an individual growing alone; Fig. 3a). For pairs that differed only in resource uptake rates (θ_i), the average strength of interspecific competition (0.970) was very similar to the average strength of intraspecific competition (0.998) indicating little potential for niche differentiation (Fig. 3b). However, when species differed in the size of the resource pool that they could access (V_i), the average strength of interspecific competition was much lower than unity (Fig. 3b), indicating the likely presence of stabilising niche differences. However, in the absence of other trade-offs, these stabilising niche differences are not enough to lead to stable coexistence. Introducing a trade-off between uptake rates (θ_i) and soil volumes (V_i) did not significantly change the average strength of interspecific competition (nor intraspecific competition), which suggests that the trade-off primarily acts to reduce relative fitness differences (Fig. 3b), which is reflected in the reduced size of the selection effect. This result confirms that complementarity only occurs in the presence of stabilising niche differences, as is the case

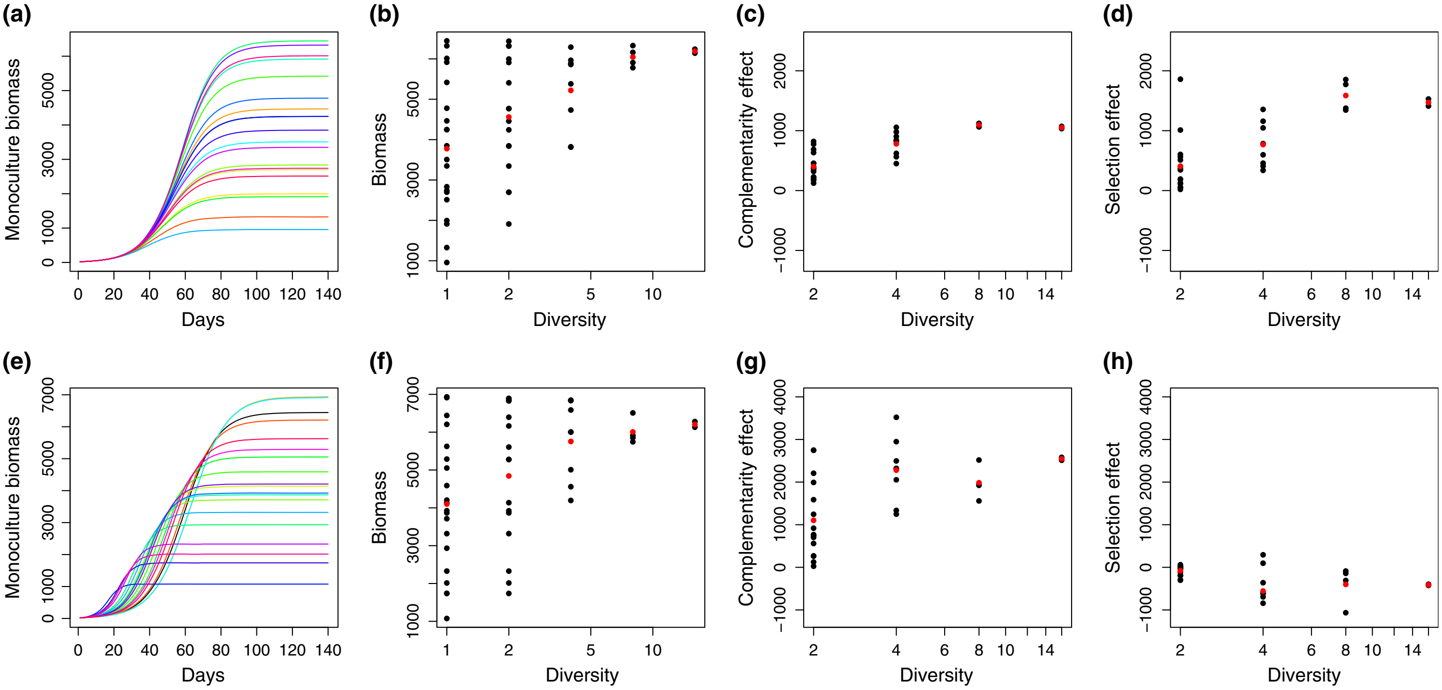

Figure 4 Typical results from simulated biodiversity experiments over a single growing season in which species vary in the size of the resource pools they can access but share a single uptake rate (Top row) and where there is a trade-off between the size of the resource pool and the uptake rate (Bottom row). (a) and (e) Monoculture yields of the 20 species in the pool; (b) and (f) mixture yields of randomly selected combinations; (c) and (g) complementarity effects; (d) and (h) selection effects. Values for particular mixtures are plotted in black and the average value for each diversity level in red.

for the Lotka–Volterra analysis above (Loreau 2004). However, the presence of transient complementarity clearly does not guarantee stable coexistence.

Simulations of higher diversity mixtures

In some of the larger biodiversity experiments carried out in grasslands, the strength of complementarity increases with species diversity (e.g. Spehn *et al.* 2005; Fargione *et al.* 2007; van Ruijven & Berendse 2009; Reich *et al.* 2012). To test whether this could also arise within an included-niche framework that lacked true complementary resource use (i.e. included niches with no trade-off), we used the model to recreate a typical biodiversity experiment. We simulated a single generation with 1, 2, 4, 8 or 16 species from a potential pool of 20 species. From the pool, we grew all monocultures: sixteen 2-species mixtures, eight 4-species mixtures, four 8-species mixtures and two 16-species mixtures. The composition of each mixture was drawn at random from the full 20-species pool. For each species, the size of the resource pool was drawn independently from a random uniform distribution with range 1000–10000. We compared results from 100 simulations where all species shared a single common value of the nitrogen uptake rate (θ) drawn from a random uniform distribution with range 1.5–4.5 and 100 simulations where there was a single common trade-off between the uptake rate (θ_i) and the soil volume (V_i) across the entire species pool. We wanted to use a trade-off that would at least ensure the stable coexistence of two-species mixtures, and hence, we explored the coexistence region more thoroughly with the soil volume (V_i) in the range 1000–10000 and the uptake rate (θ_i) in the range 1.5–4.5 (see Appendix S1). It was relatively easy to achieve the coexistence of two species as long as the relative advantage in the soil volume (V_i) was offset by a sufficiently large disadvantage in the uptake rate θ_i (see Fig. S1). For the simulations, we used a single trade-off of the form: $\theta_i = (18000/(V_i+3000))$ which for soil volumes in the range 1000–10000 constrains the uptake rate to the range 1.38–4.5 and keeps most of the possible pairs within the coexistence region. In each simulation, values of the soil volume (V_i) were sampled from a random uniform distribution as above. We did not assess whether higher diversity mixtures were also stable. In all mixtures, each of the component species received an equal share of the initial 1024 seeds and we ran the simulations for a single growing season only.

After one growing season when species differed in the soil volumes but shared the same uptake rate (Fig. 4a), average yield increased with species richness (Fig. 4b). The relationship was flat-topped because transgressive overyielding is impossible within our included-niche framework. The net biodiversity effect was always positive and is attributable to both positive complementarity effects (Fig. 4c) and positive selection effects (Fig. 4d) which generally increase in magnitude with species diversity. Selection effects were always positive, leading to a positive intercept in all cases and a positive slope against diversity in 79 of 100 cases. The intercept and slope of the relationship between the complementarity effect and diversity were positive in all cases. However, all these complementarity effects are transient because none of the mixtures are stable. Simulations of two-species mixtures revealed that the mean time to extinction for non-coexisting pairs was around 4.5 generations (range 2–22); hence, transient complementarity effects might persist for several generations.

After one growing season when there was a trade-off between the soil volumes and the uptake rates (Fig. 4e), the average yield also increased with species richness (Fig. 4f). As above, there was the same flat-topped shape, although the mixtures did not always perform quite as well as the best component monoculture. This is because the highest-yielding species now have the lowest resource uptake rates. In a high-diversity mixture, all species begin from rather low density; thus, the species with the slower uptake rates cannot fully exploit their additional resources by the end of a single growing season. Hence, a monoculture of the highest-yielding component species can actually outperform the mixture (Fig. 4f). The net biodiversity effect was again always positive although this time it was almost entirely due to complementarity effects which increased with species diversity (Fig. 4g) in 98 of 100 cases. However, the selection effect was on average negative although in 79 of 100 cases it was not significantly different from zero. The average slope of the selection effect was positive, but it was not significantly different from zero in 85 of 100 cases (Fig. 4h).

Note that the patterns observed in both cases are rather consistent with those documented in the most recent meta-analysis of biodiversity experiments with primary producers (Cardinale *et al.* 2011): the best mixture does not yield better than the best component monoculture and indeed might underperform due to the lower density of the high-yielding species in mixture compared to monoculture. The same effect would be seen for resource-use patterns (unused resources are here inversely related to biomass): although the resource use is better *on average* in higher diversity mixtures, resource use by mixtures never exceeds the best component monoculture, and indeed can be slightly worse, in agreement with the results of the meta-analysis.

Insights and interpretations

Within the relative yield framework, positive complementarity effects correspond to overyielding. In our simulations, such overyielding only occurs when there are stabilising niche differences between species. However, while our results suggest that positive complementarity does indicate the presence of stabilising niche differences, it does not demonstrate that these niche differences are strong enough to overcome fitness differences and hence bring about stable coexistence, nor does it quantify the strength of the niche differences. It has also been clear for a long time that the complementarity effect cannot reveal the detail of the underlying biological processes (Loreau 1998b; Loreau & Hector 2001; Petchey 2003; Cardinale *et al.* 2011; Carroll *et al.* 2011; Loreau *et al.* 2012).

Transient complementarity can occur in unstable mixtures

Our results reveal the existence of transient complementarity, how it can come about and how it relates to coexistence theory. These short-term transient complementarity effects occur when stabilising niche differences among species are not large enough to overcome fitness differences and exclusion is the inevitable outcome (hence the mixtures are unstable in the sense that they have no stable equilibrium). A naive expectation might suppose that selection effects will largely govern the transient behaviour of mixtures of species that will not stably coexist. However, in our model this was not the case, as some unstable mixtures had appreciable transient complementarity effects. The existence of transient complementarity raises the possibility that the effects seen in biodiversity experiments may be temporary and hence give a misleading impression of the benefits of diversity. However, two points should be noted: (1) although the mixture cannot outperform the best monoculture, it generally does not underperform by very much either; hence, given that it might be difficult to identify the highest-yielding species in advance, growing a low-diversity mixture that stabilises yields among years could still be a good insurance policy (Yachi & Loreau 1999; Cottingham *et al.* 2001; Isbell *et al.* 2009; Hector *et al.* 2010); (2) more sophisticated work with roots in natural settings does not generally support the idea that rooting depth zones are so clearly defined, and there is evidence that rooting behaviour can change dramatically in mixture compared to monocultures (e.g. Berendse 1981; Jumpponen *et al.* 2002; Dornbush & Wilsey 2010; de Kroon *et al.* 2012). However, included niches could come about in other ways, for example, species might differ in their abilities to extract limiting resources from a given soil volume. We therefore suggest that caution should be exercised when interpreting complementarity effects obtained in short-term experiments especially in highly simplified environments without additional data on the underlying biological processes. One possibility, which we did not try here, would also be to make more use of the tripartite partition (Fox 2005) which breaks down the complementarity effect into two separate components and which could be more revealing about the mechanisms underlying complementarity effects (see Box 1).

The importance of long-term biodiversity experiments

The most recent meta-analysis of biodiversity experiments with primary producers shows that complementarity and selection contribute roughly equally to the overall biodiversity effect (Cardinale *et al.* 2011). However, while these meta-analyses are essential for summarising the literature, they are of limited use for coexistence related questions as they combine experiments and conditions in which species will likely coexist stably with those where they will not. Instead, we concentrate on the development of patterns in the longest-running semi-natural grassland studies at Cedar Creek, Wageningen and Jena. A common feature of these studies is the lack of extinctions from high-diversity mixtures (suggesting that mixtures are stable) and the enhancement of positive complementarity over time in combination with selection effects that are often zero or negative, particularly at high diversity (Fargione *et al.* 2007; van Ruijven & Berendse 2009; Reich *et al.* 2012; Roscher *et al.* 2012). While it is not definitive, these observations suggest that these effects are not transient. Negative selection effects also indicate that species with lower-than-average monoculture biomasses have higher relative yields in mixtures. This implies that they have a mechanism of competitive advantage inversely related to their monoculture yields and in our model this led to coexistence rather than exclusion.

What is the link between complementarity and stabilising niche differences?

Consistent with Carroll *et al.* (2011), our modelling results suggest that the presence of stabilising niche differences, a driver of coexistence, rather than stable coexistence *per se* is a precondition for complementarity. But if stabilising niche differences can generate positive complementarity, is it safe to assume that this will always be the case? Although there is no substitute for analysing many different models of interacting species, here, we lay out a verbal argument that future studies might aim to disprove.

Stabilising niche differences increase per-capita population growth rates as relative abundance declines (Chesson 2000; Adler *et al.* 2007) and species in mixtures are, by definition, at lower relative abundance than in their respective monocultures. Averaging across species, stabilising niche difference should therefore cause greater population growth per unit sown seed in mixtures than would be expected from monocultures, and this generates a positive complementarity effect. Of course, fitness differences, if strong enough, can change the response of individual species in ways that oppose positive complementarity. Weaker competitors (the fitness inferiors), for example, may perform better in monoculture because here they do not encounter the better competitors. Nonetheless, short of competitive exclusion, these fitness difference effects should not entirely erase the average benefits species gain at lower relative abundance, and hence, the positive complementarity effect arising from stabilising niche differences. Indeed, this is exactly what we observed in our included-niche model in the absence of the trade-off.

One obvious case where this logic might fail is when there is no relationship between per-capita population growth rate (the currency of stabilising niche differences) and yield. This arises in models with zero-sum games (Hubbell 2001), but this assumption is made for mathematical convenience and was never meant to be an accurate representation of nature. More realistically, species might interact via shared consumers that assimilate the biomass of the measured competitors (Fox 2003). In this case, the yield benefits in mixture might not be visible at the level of the primary producers; but accounting for the production in the consumer might recover the predictions of the prior paragraph.

Can we turn this question around and instead ask whether positive complementarity effects necessarily reflect stabilising niche differences? This is inevitably trickier, because here we are attempting to relate a statistic back to a model. The logic above, and our specific model results, might suggest that in many cases positive complementarity does indeed result from stabilising niche differences, but that logic does not preclude other ways of allowing complementarity effects to be positive, especially in the transient phase. Although we do not see this as likely, rigorous tests require further model-level analyses, as Carroll *et al.* (2011) do for the MacArthur consumer resource model.

SUMMARY

In general, the results of our simulation models suggest a qualitative rather than a quantitative correspondence between the frameworks for coexistence and the additive partitioning of biodiversity effects. Our resource-based included-niche models show that the presence of complementarity effects arises from the presence of stabilising niche differences, but it does not demonstrate that these are strong enough to overcome fitness differences and generate stable coexistence. As a consequence, transient complementarity effects can occur in unstable mixtures where a weaker competitor can only access a completely nested subset of the dominant's resources and there is no true complementary resource use. Similarly, selection effects appear to be indicative of relative fitness differences, but not their strength. Taken together, our results urge greater caution in the interpretation of complementarity effects for resource-use patterns and community dynamics in short-term experiments. Finally, we call for a closer combination of modelling and experiments to better link the ecosystem functions of interest with the underlying biological processes.

AUTHORSHIP

Idea conceived by LAT and AH with input from JML and ML. Modelling and analyses carried out by LAT. LAT and AH wrote the first draft of the paper with substantial inputs from JML and ML.

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