



Overyielding and species diversity: what should we expect?

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Summary

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- Recent empirical studies have found evidence of increased biomass production ('overyielding') in species mixtures relative to monoculture, but the interpretation of these results remains controversial, in part, because of the lack of a theoretical expectation.
- Here, we examined the expected frequency and stability of overyielding species mixtures using Lotka–Volterra models of species dynamics in two- and four-species systems in conjunction with community, population, and specific rate of biomass production (SRP) definitions of overyielding.
- Overyielding plant mixtures represented > 55% of potential species assemblages under community definitions and approximately 100% of species were either overyielding or underyielding under the population definition. Our species simulations approached their equilibria in 1–2 yr, supporting the relevancy of an equilibrium analysis. The range of parameter space that we explored produced realistic values of plot biomass, supporting their biological relevance.
- We show that overyielding is expected to be common under community definitions and population definitions. Overyielding, under community or population definitions, does not imply an actual increase in the specific rate of biomass production. In addition, assemblages of overyielding and underyielding species under all three definitions can be stable over time with underyielding species persisting in the presence of overyielding species.

Key words: biodiversity, overyielding, species diversity, productivity, Lotka–Volterra.

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Introduction

The impact of biodiversity on community and ecosystem processes such as productivity is a question of great significance given the current rates of species loss (Pimm *et al.*, 1995). Empirical evidence seems increasingly to support the occurrence of increased productivity ('overyielding') in species mixtures compared with monocultures (Tilman *et al.*, 1996, 2001; Hector *et al.*, 1999; Loreau & Hector, 2001; van Ruijven & Berendse, 2003), but others question these results (Hooper & Vitousek, 1997; Huston *et al.*, 2000). Interpreting the evidence of biodiversity effects on productivity can be difficult, however, because studies have employed different definitions of overyielding

and there is only a limited expectation of how common overyielding should be under the different definitions (i.e. a 'null' model) (Loreau, 1998; Fox, 2003). We characterize the various empirical definitions of overyielding as community (Loreau, 1998; Hector *et al.*, 2002), population (Hille Ris Lambers *et al.*, 2004) or specific rate of biomass production (SRP), such as an individual-based definition (van Ruijven & Berendse, 2003), based on the metric used, and then address the question: How common, or rare, should we expect overyielding to be in ecological communities using these definitions? Empirical studies of overyielding have also identified species that underyield when grown in mixture (Tilman *et al.*, 2002; van Ruijven & Berendse, 2003; Hille Ris Lambers *et al.*, 2004), leading to

speculation as to whether underyielding species can persist in mixtures with overyielding species (Hille Ris Lambers *et al.*, 2004). This leads us to a second question: Are species assemblages that are composed of overyielding and underyielding species stable over time? Will the underyielding species persist in the presence of overyielding species? We explored these questions using simple Lotka–Volterra models of species dynamics.

Description

We first present community, population and specific rate of productivity definitions of overyielding before describing our models. The community definition is based on the productivity of species mixtures compared to monocultures of the constituent species. Two types of community overyielding have been defined: transitive and nontransitive overyielding (Hector *et al.*, 2002). Transitive overyielding occurs when the yield of the mixture is greater than the yield of any of the component species in monoculture:

$$\sum_i S_i > \max(K_i)$$

S_i is the biomass per unit area of species i ; K_i is the species' yield in monoculture (e.g. its carrying capacity); the summation and maximum are over all i species. This is a stringent condition for overyielding and is equivalent to the D_{\max} overyielding metric defined by Loreau (1998). Nontransitive overyielding occurs when the yield of the mixture is greater than the weighted average of the species' yields in monoculture or

$$\sum_i S_i > \frac{\sum_i K_i}{n_{\text{species}}}$$

when plots are seeded with equal initial abundance, where n_{species} is the number of species in mixture. This definition is equivalent to the relative land output measure of Jolliffe (1997) or the overyielding metric D_T , defined by Loreau (1998), and is a less stringent criterion than transitive overyielding. Unlike the community-level definitions, the population definition identifies individual species that are overyielding or underyielding by comparing the yield of a given species grown in mixture to its yield in monoculture (Hille Ris Lambers *et al.*, 2004). Those species whose biomass in mixture is greater than their yield in monoculture, divided by the number of species present, are overyielders:

$$S_i > \frac{K_i}{n_{\text{species}}}$$

Underyielding species are those that meet the complementary condition

$$S_i < \frac{K_i}{n_{\text{species}}}$$

Finally, we consider a definition of overyielding or underyielding based on increased or reduced specific rates of biomass

production (SRP), respectively, in the presence of other species. We include this definition because it considers actual changes in the rate of biomass production per unit biomass by each species present in a mixture, and as such, does not include adjustments for the number of species growing in mixture. Under the SRP definition, an overyielding species would have an increased SRP while an underyielding species would have a decreased SRP, when comparing SRP in mixture to that in monoculture. We treat the SRP as an instantaneous rate (e.g. $dS_i/S_i dt$), although it would more likely take the form of a relative growth rate in empirical studies (Beckage & Clark, 2003; van Ruijven & Berendse, 2003), and compare the SRP definition with a related population-level metric (relative yield; van Ruijven & Berendse, 2003).

In our first model, we consider overyielding and underyielding for a two species system using a Lotka–Volterra competition (LVC) model. In this model, each species is negatively affected by the presence of the other species (Kot, 2001). The dynamics of the two species, S_1 and S_2 , respectively, are described by two ordinary differential equations:

$$\frac{dS_1}{dt} = r_1 S_1 \left(1 - \frac{S_1}{K_1} - \alpha \frac{S_2}{K_1} \right) \quad \text{Eqn 1}$$

$$\frac{dS_2}{dt} = r_2 S_2 \left(1 - \frac{S_2}{K_2} - \beta \frac{S_1}{K_2} \right) \quad \text{Eqn 2}$$

The growth rate of S_1 , biomass of species 1 measured on a per unit area basis, is decreased by the presence of S_2 in Eqn 1 (with $\alpha > 0$), and the growth rate of S_2 is decreased by the presence of S_1 in Eqn 2 (with $\beta > 0$). Note that this implies that S_1 and S_2 are underyielding by the SRP definition, although not necessarily by the community or population definitions. The parameters α and β describe the strength of the interspecific interactions. The left sides of Eqns 1 and 2 represent the instantaneous rate of change of plant biomass (i.e. biomass per unit area per year), while the right sides of the equations describe growth in biomass: r_1 and r_2 are the intrinsic rates of increase in biomass (1/year) of the two species, and K_1 and K_2 are the maximum amounts of biomass per unit area that the species can attain when grown in monoculture. We assume that each species inhibits its own growth, resulting in logistically increasing biomass and that $r_1, r_2, K_1, K_2, \alpha, \beta > 0$.

We also consider a second model of species dynamics with coupled positive and negative interactions that allow for both increased and decreased specific rates of biomass production, which correspond to over- and underyielding under the SRP definition. The specific rate of production of the overyielding species is increased by the presence of the second species, while the specific rate of productivity of the underyielding species is decreased. We used a similar model to Eqns 1 and 2, but with coupled positive and negative interspecific interactions (CPNI model) rather than strictly negative interactions:

$$\frac{dS_1}{dt} = r_1 S_1 \left(1 - \frac{S_1}{K_1} + \alpha \frac{S_2}{K_1} \right) \quad \text{Eqn 3}$$

$$\frac{dS_2}{dt} = r_2 S_2 \left(1 - \frac{S_2}{K_2} - \beta \frac{S_1}{K_2} \right) \quad \text{Eqn 4}$$

The sign in front of α is now positive (compare with Eqn 1), while Eqn 4 is identical to Eqn 2. In this model, the first species S_1 benefits from the presence of the second species, S_2 , which is negatively affected by the presence of the first species. In other words, the SRP of S_1 is increased by the presence of S_2 , whereas the SRP of S_2 is decreased by the presence of S_1 , implying that S_1 is an overyielder and S_2 is an underyielder under the SRP definition. This model is similar to a predator–prey model in which the ‘predator’ (overyielding species) is an omnivore, capable of surviving in the absence of the ‘prey’ (underyielding species) through utilization of resources that are not explicitly included in this simple two-species model.

We analysed both the LVC and CPNI models to determine if the conditions for a positive, locally stable solution overlapped with the community and population definitions of overyielding. We then used numerical simulations to explore the range and percentage of four-dimensional parameter space for α , β , K_1 , and K_2 in which the stability and overyielding criteria were jointly satisfied. For the LVC model, we explored parameters in the range of $0 < \alpha < 40$ and $0 < \beta < 40$, which exceeded the range of stable solutions (for which α and β could not exceed 35 based on the carrying capacities used in our simulation and described below). In the case of the CPNI model, the range used in the simulation was $0 < \beta < 40$ (again exceeding the bounds of positive stable solutions), but the potential range for α over which a positive stable solution existed was $(0, \infty)$ and, in this case, we increased α until our simulation results reached an asymptote (i.e. 200). These simulations required values for K_1 and K_2 (i.e. species’ carrying capacities) in order to evaluate the equilibrium and overyielding conditions. We used the range of carrying capacities reported in the biodiversity experiment of Tilman *et al.* (2001) (i.e. approximately 10–350 g m⁻²) and randomly generated 1000 pairs of carrying capacities (e.g. K_1 and K_2) assuming a uniform distribution across this range.

We determined the location and stability of equilibrium solutions for the system of equations. The equilibria were found by setting $dS_i/dt = 0$ for all i species, and then solving for each S_i . We only considered equilibria where both species coexisted with positive densities. The local stability of the equilibria was determined by computing the eigenvalues of the Jacobian, \mathbf{J}^* , evaluated at the equilibrium (Kot, 2001). The eigenvalues were calculated by solving the characteristic equation corresponding to $\text{Det}(\mathbf{J}^* - \lambda_1) = 0$. The resulting eigenvalues indicate the stability of the equilibrium: an equilibrium solution is stable when the real component of both eigenvalues is < 0 . Analyses were performed using MATHEMATICA (Wolfram Research, Inc., Champaign, IL, USA) and R software (<http://www.r-project.org>).

Our analyses of species dynamics in the LVC and CPNI models were based on equilibrium conditions. An equilibrium analysis might not be relevant if long periods of time are required for the system to reach a steady state relative to other sources of variability, such as interannual variability in environmental conditions. We therefore examined the transient dynamics to determine the time to steady state using numerical simulations for both the LVC and CPNI models, which required values for r_1 , r_2 , K_1 , and K_2 , as well as α and β . We generated values for K_1 and K_2 as already described. Values of r were estimated by extrapolating daily growth rates for C3 grasses, C4 grasses, forbs and legumes given in Reich *et al.* (2003) for unfertilized treatments, over the growing season (c. 140 d). Seed biomasses were also reported in Reich *et al.* (2003) and were used as estimates of initial biomasses in our transient calculations. Seed biomass and species growth rates were reported together by species, allowing us to select these values in pairs, preserving their correlation structure. Both the Tilman *et al.* (2001) and Reich *et al.* (2003) studies were conducted in the same study area with overlapping suites of species, so that mixing parameters from both of these studies is reasonable. For each simulation, we randomly selected the seed biomass, as the species’ initial biomass, and growth rate r , and a value of K . Values of α and β were selected from the center of the region of stable equilibrium values: (α, β) of (0.1, 0.75) and (20, 1.5) were used for simulations of the LVC and CPNI models, respectively. We recorded the longest time required for both species (in each species pair) to reach 95% of its steady state biomass, beginning from seed, in each of 1000 simulations.

While we intentionally explored parameter space to assess the theoretical potential for overyielding and underyielding under our three definitions, we also assessed whether the presumed values of α and β were biologically relevant. This was difficult to directly address since few studies explicitly estimate competition coefficients in plant communities for comparison to our ranges of α and β . We therefore used an alternative approach to gauge the realism of the competition coefficients used in our simulations. We simulated the range of biomasses associated with a given set of α and β parameter values, randomly selecting carrying capacities from the range used in our previous simulations and described earlier, and compared this distribution with the distribution of biomass actually observed in two-species field plots, as reported in Tilman *et al.* (2001). We calculated the proportion of our simulated plot biomasses that intersected the reported plot biomasses, which ranged from near 0 to 400 g m⁻², as an indication of the realism of a specified set of α and β parameters.

We repeated our equilibrium analyses for a four species model to see if our results generalized to more species-rich systems. While the dynamics of such multispecies models can be quite complex, with no simple analytical results, we were able to investigate the dynamics of generalizations of both the LVC (Eqns 1 and 2) and the CPNI (Eqns 3 and 4) models to four species systems using numerical simulations. In the CPNI

model, we allowed overyielding species to benefit from the presence of all other species (not just underyielders) and underyielders to be negatively affected by all other species (not just overyielders). We generated values of r and K for each species as described above and explored the parameter space of α and β values, which was now 12-dimensional as opposed to two-dimensional in the two species model.

Results

The LVC model of Eqns 1 and 2 resulted in one equilibrium solution at which both species co-occurred:

$$S_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta} \quad \text{Eqn 5}$$

and

$$S_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta} \quad \text{Eqn 6}$$

This equilibrium solution was locally stable with positive values of S_1 and S_2 when

$$\alpha < \frac{K_1}{K_2} \quad \text{Eqn 7}$$

and

$$\beta < \frac{K_2}{K_1} \quad \text{Eqn 8}$$

implying that $\alpha < 1/\beta$. The community level definitions of overyielding require that

$$\frac{K_1(1 - \beta) + K_2(1 - \alpha)}{1 - \alpha\beta}$$

is greater than

$$\frac{K_1 + K_2}{-2}$$

for nontransitive overyielding and greater than $\max(K_1 + K_2)$ for transitive overyielding, in addition to conditions Eqns 7 and 8. Under the community definitions of overyielding, 75% of parameter space that supported a positive, locally stable equilibrium resulted in an overyielding species mixture: 47% (of total parameter space supporting a positive stable equilibrium) were transitively overyielding and 28% were nontransitively overyielding (Fig. 1a,c). The equilibrium conditions in Eqns 7 and 8 coincided with the population definition of overyielding or underyielding when

$$\alpha < \frac{K_1}{2K_2 - \beta K_1} \quad \text{(where species 1 is the overyielder)} \quad \text{Eqn 9}$$

or

$$\beta > \frac{K_1}{2K_1 - \alpha K_2} \quad \text{(where species 2 is the underyielder)} \quad \text{Eqn 10}$$

respectively. Reversing the inequalities in Eqns 9 and 10 leads to species 1 being the underyielder and species 2 being the overyielder. In our numerical simulations of the LVC model, both overyielding and underyielding species (by the population definition) occurred in 54% of the range of parameter space in which a stable, positive equilibrium existed (Fig. 1e). In the remaining 46% of parameter space, both coexisting species were overyielders. Our simulation did not result in any species other than overyielding or underyielders under the population level definition: only a species with an α exactly equal to the right hand side of Eqn 9 or a β equal to the right side of Eqn 10 would not be an overyielder or underyielder (e.g. Fig. 2a,c) – an exceedingly unlikely event. A representative phase space diagram is given for the LVC model in Fig. 2(e).

The CPNI model (Eqns 3 and 4) also resulted in a single positive equilibrium with both over- and underyielding species coexisting:

$$S_1 = \frac{K_1 - \alpha K_2}{1 + \alpha\beta} \quad \text{Eqn 11}$$

and

$$S_2 = \frac{K_2 - \beta K_1}{1 + \alpha\beta} \quad \text{Eqn 12}$$

This equilibrium solution was locally stable with positive values of S_1 and S_2 when

$$\beta < \frac{K_1}{K_1} \quad \text{Eqn 13}$$

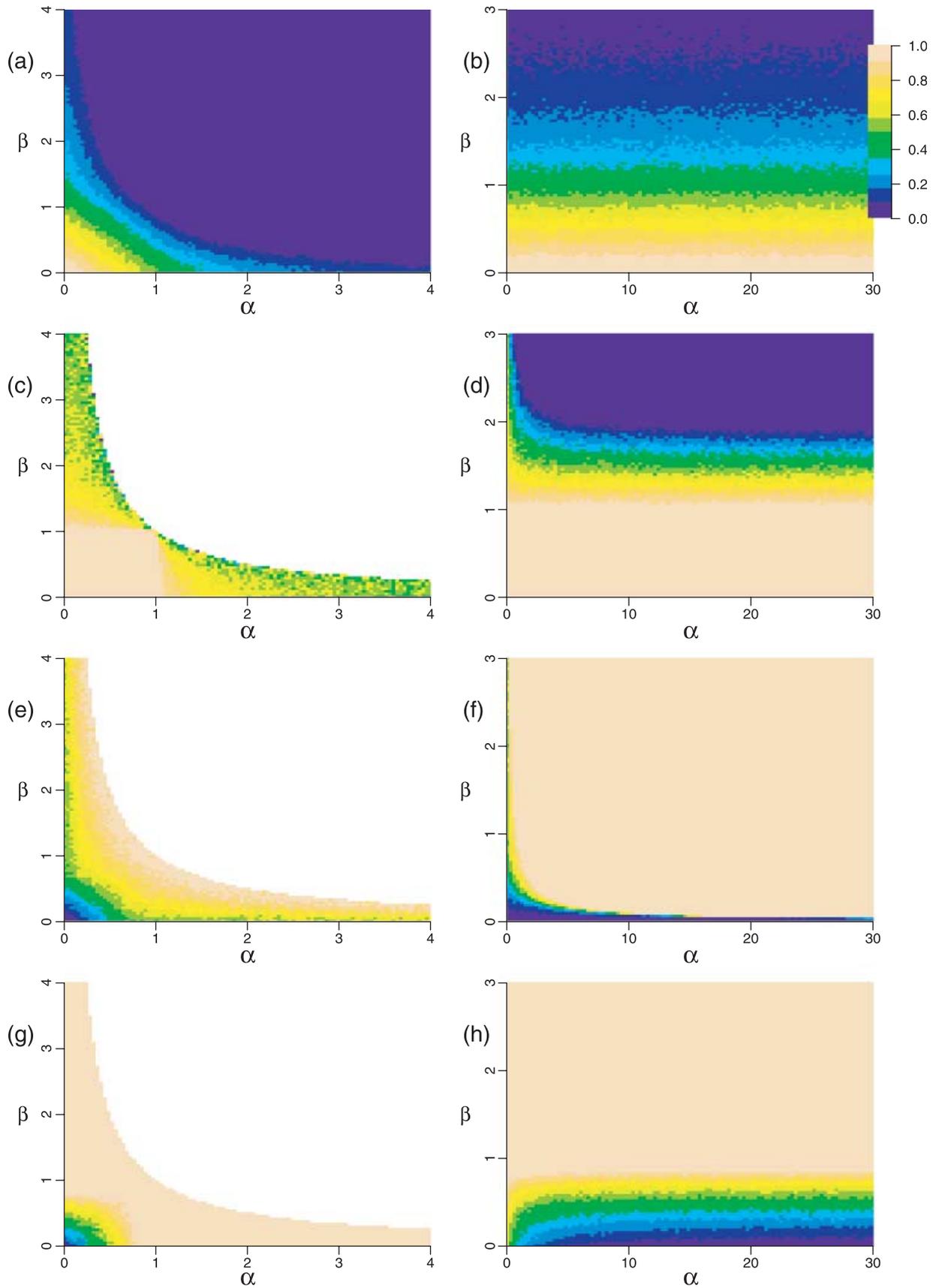
and was, in this case, globally stable for any initial condition with positive biomasses of both species (the Bendixson–Dulac criterion implies there is no limit cycle; see Kot, 2001). The condition Eqn 13 is a subset of the conditions required for the LVC model (identical to Eqn 8) indicating a broader parameter region of species coexistence, which is apparent in Fig. 1b compared with Fig. 1a. The criteria for transitive and nontransitive overyielding in the CPNI model were identical to those for the LVC model, except that the sign in front of the terms with α was positive in the CPNI model. Under the community definitions of overyielding, 55% of parameter space with a locally stable, positive equilibrium resulted in an overyielding species mixture (Fig. 1d): 47% was transitively overyielding and 8% was nontransitively overyielding. The equilibrium condition (Eqn 13) overlapped with the population definition of overyielding and underyielding when

$$\alpha < \frac{K_1}{\beta K_1 - 2K_1} \quad \text{(where species 1 is the overyielder)} \quad \text{Eqn 14}$$

and

$$\beta > \frac{K_2}{2K_1 - \alpha K_2} \quad \text{(where species 2 is the underyielder)} \quad \text{Eqn 15}$$

respectively. In our numerical simulations, 80% of the parameter space with a locally stable, positive equilibrium coincided with



the population definition of overyielding and underyielding species (Fig. 1f). In the remaining 20% of the simulations, both coexisting species were overyielders. This result was similar to the LVC model results: species were either overyielding or underyielding by the population definition (Fig. 2b,d). The region with an equilibrium defined by Eqns 11–13 (e.g. the region indicated in Fig. 1b) necessarily refers to overyielding based on the SRP definition, since the form of the model insures an increased specific rate of productivity for the first species in the presence of the second species. A representative phase space diagram for the CPNI model is given in Fig. 2f. Note that the equilibrium biomass is greater than the carrying capacity, K_1 . This is not the case for the LVC model (Fig. 2e).

We note that the SRP definition of overyielding corresponds to a relative yield (RY) population definition of over- and underyielding when the species' yield in mixture is compared to its yield in monoculture: If overyielding is defined to occur when $S_i/K_i > 1$ and underyielding occurs when $S_i/K_i < 1$, then this RY definition of overyielding and underyielding coincides with the stability criteria for both the LVC and CPNI models. The species in the LVC model are underyielders under the RY definition when stability conditions in Eqns 7 and 8 are met. In the CPNI model, species 1 is an overyielder and species 2 is an underyielder when the stability condition in Eqn 13 is met. Both species in the LVC model therefore are underyielding under both the SRP and RY definitions. Similarly, species 1 in the CPNI model is always overyielding while species 2 is always underyielding under both the SRP and RY definitions.

Species in our models generally approached their equilibria in 1–2 yr. The mean time to steady state for the LVC model was 1.86 yr (median 1.33 yr) and the 95th quantile was 4.1 yr, while for the CPNI model, the mean was 0.84 yr (median 0.75) and the 95th quantile was 1.4 yr. These results support the relevancy of an equilibrium analysis in general, and specifically to the 7-yr-old plots reported in Tilman *et al.* (2001), from which we have taken model parameters and with which we compare our simulation results.

The range of α and β parameter space that we explored produced realistic values of plot biomass for both the LVC and CPNI models (Fig. 1g,h), supporting their biological relevance. For the LVC model, the entire range of parameter space where stable, positive equilibria occurred coincided with

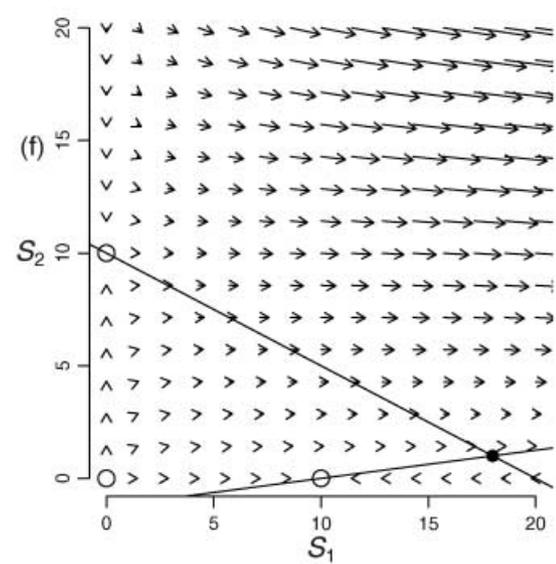
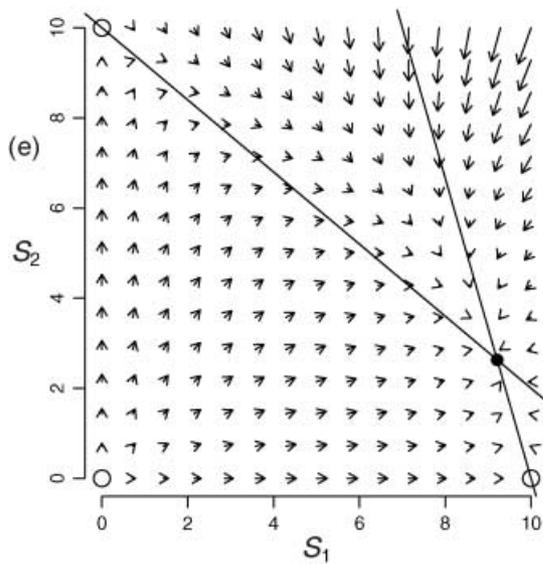
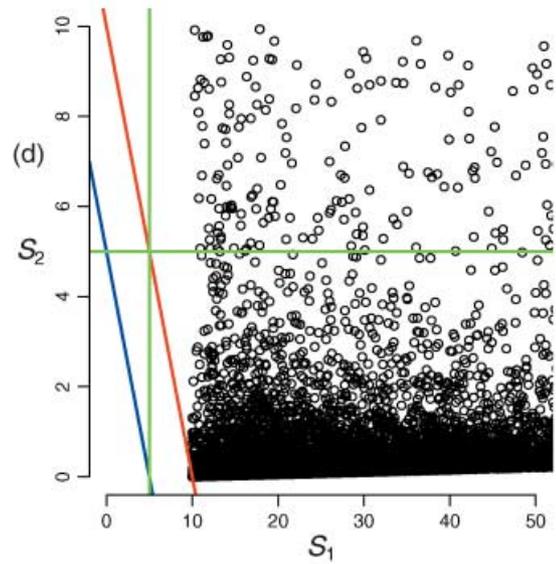
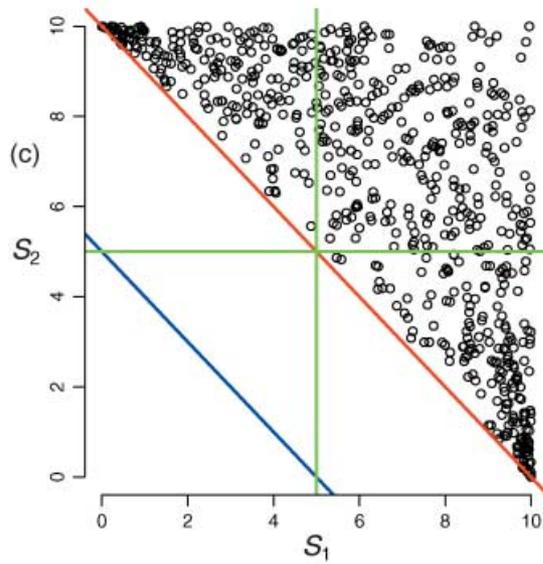
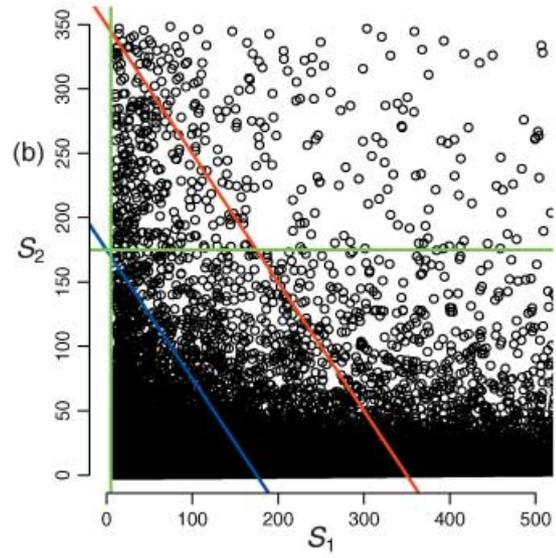
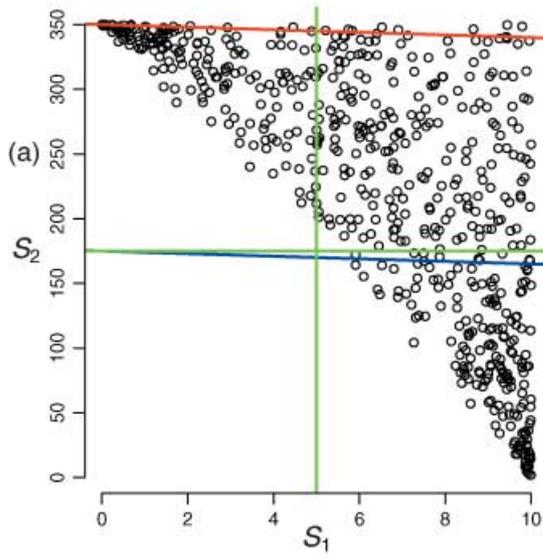
realistic values of plot biomass: the central 95% of the distribution of biomasses for each combination of α and β , over the range of parameter space explored, overlapped with the biomasses reported in Tilman *et al.* (2001). In the case of the CPNI model, most (*c.* 98%) of the range of parameter space examined in the CPNI model similarly resulted in realistic values of plot biomasses. The exception was the combination of large α and small β values (Fig. 1h), which led to unrealistically high biomasses.

Numerical simulations indicated that our results apply to systems with multiple species. In four species simulations, we readily obtained regions in multidimensional parameter space with stable coexistence of multiple overyielding and underyielding species using the community, population and SRP definitions for the CPNI model and the community and population definitions for the LVC model. As expected by the less restrictive stability criteria for the CPNI model, the region of coexistence was much broader for the CPNI model than for the LVC model: we sampled more than four times as many stable equilibrium points (where all four species coexist) in the CPNI compared with the LVC model. All simulated equilibria in the CPNI model were transitively overyielding (community definition) with either overyielding species (53%) or overyielding and underyielding species occurring together (47%) under the population definition. Under the LVC model, 100% of simulated communities were overyielding with 86% transitively overyielding and 14% nontransitively overyielding under the community definition. Overyielding species, as defined by the population definition, comprised 40% of these communities, while overyielding and underyielding species together made up the remaining 60%. These simulations are consistent with results from the two species models, suggesting that overyielding in mixtures is prevalent in multispecies models of this type.

Discussion

We used a simple model of species dynamics to show that overyielding of species mixtures, based on widely used community and population definitions, is expected to be prevalent in ecological communities. Furthermore, overyielding, under these definitions, does not imply an increase in the specific rate of biomass production (SRP). We have no reason to expect that our results are reliant upon the particular Lotka–Volterra

Fig. 1 Simulation results for our two-species models. (a) The color image represents the proportion of 1000 Lotka–Volterra competition (LVC) model simulations, carried out for each point in parameter space, that yielded a locally stable, positive equilibrium. (b) As (a), but for the coupled positive and negative interspecific interactions (CPNI) model. The range of stable, positive solutions for the CPNI model implies overyielding under the SRP definition. (c) Community definition of overyielding: the proportion of 1000 LVC model simulations that supported either a transitively or nontransitively overyielding equilibrium solution. Regions that do not provide stable, positive equilibria for both species are left uncolored. (d) As (c), but for the CPNI model. (e) Population definition of overyielding: The proportion of 1000 LVC simulations that supported both an over- and underyielding species. The complement to these contours is the proportion of species that were both overyielding. Regions that do not provide stable, positive equilibria for both species are left uncolored. (f) As (e), but for the CPNI model. (g) Reasonableness of α and β values used in LVC simulations: a plot showing the proportion of simulated biomasses for a given pair of α and β that intersected the range of biomasses reported in Tilman *et al.* (2001). Regions that do not provide stable, positive equilibria for both species are left uncolored. (h) As (g), but for the CPNI model.



form of the models, but the robustness of our conclusions with other community models, such as those with an Allee effect, will require further analysis. The use of other definitions of overyielding, however, may produce different results: the relative yield total (RYT) metric, for example, leads to all stable species mixtures solutions being nontransitively overyielding in a two-species system (Fox, 2003), but the RYT has shortcomings that argue against its use (Loreau, 1998). In our two-species CPNI and LVC models, 55% and 75% of the parameter space with a positive, stable equilibrium met the community definition of transitive or nontransitive overyielding, while nearly 100% of our simulated mixtures in the four-species models had an overyielding species assemblage. The higher proportion of overyielding in the four-species model may be the result of the difficulty in sampling the 12-dimensional range of parameter space for the four species model as thoroughly as for the two-dimensional two species model owing to computational limitations. Similarly, all species were either overyielders or underyielders under the population definition. The message is consistent across these simulations: overyielding, based on the community and population definitions commonly used in the literature, should be common. Finally, our model separates the effect of species performance in monoculture from that in mixture (through the K and the α and β values), so that a species that is a high yielder in monoculture may be a poor performer in mixture. While this decoupling of relationships between yield in monoculture and mixture might be contrary to the expectation that high yielders in monoculture should dominate in mixture, it is consistent with observations that species' yield in monoculture is not a good predictor of species dominance in mixture (Hector *et al.*, 2002; van Ruijven & Berendse, 2003).

Our model results indicate that nearly all species, as opposed to mixtures, should be over- or underyielders by the population definition, independent of the model used. In the LVC model, 53% of species (coexisting in a positive, stable equilibrium) consisted of a mixture of over- and underyielding species. The remaining 47% were overyielders. In the CPNI model, 80% of the species were coupled overyielders and underyielders with the remaining 20% comprised of overyielders only. The overwhelming preponderance of overyielding or

underyielding species in our simulations results from the population definition of overyielding or underyielding; for a species not to be an overyielding or underyielder, S must precisely equal K/n_{species} , which is highly improbable (see Fig. 2a–d). The failure to detect more species meeting the conditions for overyielding or underyielding species in empirical studies (Hille Ris Lambers *et al.*, 2004) may result from the nature of conventional hypothesis testing, in which a failure to reject the statistical null hypothesis, e.g. that S equals K/n_{species} , is mistakenly taken as evidence supporting the null hypothesis (Royall, 1997). For example, field studies require increasing levels of sampling to reject the null hypothesis as S approaches K/n_{species} using conventional hypothesis testing. Our simulations indicate that the null hypothesis is most likely untrue in mixtures (100% of our simulations), and that a failure to reject the null hypothesis in empirical studies most likely reflects the amount of sampling performed.

Species that underyield by the population definition can persist in species mixtures that include overyielding species. Species mixtures with overyielders and underyielders formed stable communities both in the standard Lotka–Volterra competition (LVC) model as well as in a model with coupled positive and negative interactions between species (CPNI model). This result is consistent with empirical observations of population level overyielding and underyielding species co-occurring in apparently stable communities (Hille Ris Lambers *et al.*, 2004). While it has been known that strictly negative or positive species interactions (e.g. competition or mutualism) can result in stable assemblages of coexisting species (Kot, 2001), we have shown that coupled positive and negative interspecific interactions can also stabilize community diversity.

Our results are derived from models of species dynamics that are phenomenological in that interspecific interactions are described by simple parameters (e.g. α and β values). We do not address the biological mechanisms implicit in these parameters or the mechanisms that lead to coupled positive and negative species interactions (but see Callaway, 1995, for examples). Multiple mechanisms may be present in different systems that can lead to the growth rate assumptions in the general formulations that we have given. For illustration, we

Fig. 2 Range of over- and underyielding for two-species simulations with fixed carrying capacities. We repeatedly selected random values and plotted biomass of species 1 vs 2 given a positive, stable equilibrium. (a) Lotka–Volterra competition (LVC) model for $\alpha \in (0, 40)$ and $\beta \in (0, 40)$, and $(K_1, K_2) = (10 \text{ g m}^{-2}, 350 \text{ g m}^{-2})$. Overyielding under the community definitions: points above (or to the right of) the red line are transitively overyielding, while points above (or to the right of) the blue line are nontransitively overyielding. Overyielding under the population definition: points above (to the right of) the green line are overyielding realizations of species 2 (species 1), while points below (to the left of) are underyielding. Points precisely on either green line are not overyielding or underyielding. Note that the horizontal green line and the blue line nearly overlap. (b) As (a), but for the coupled positive and negative interspecific interactions (CPNI) model with $\alpha \in (0, 200)$ and $\beta \in (0, 40)$. The simulated biomass of species 1, an overyielder under the SRP definition, extended to a maximum of 68909 g m^{-2} . (c, d). As (a and b), except for $(K_1, K_2) = (10 \text{ g m}^{-2}, 10 \text{ g m}^{-2})$. For the LVC model (c), all realizations are now transitively overyielding under the community definition. The simulated biomass of species 1, an overyielder under the SRP definition, in the CPNI model (d) extended to a maximum of 1887 g m^{-2} . (e) A phase plane plot for a typical stable solution in the LVC model. S_1 and S_2 represent the biomasses of species 1 and 2 (g m^{-2}). Parameters were $K_1 = 10$, $K_2 = 10$, $\alpha = 8$, $\beta = 0.5$, and $r_2 = r_1 = 10$. The open circles represent unstable equilibria at $(0, 0)$, $(0, K_2)$ and $(K_1, 0)$, while the closed circle indicates the locally stable equilibrium. (f). As (e) except for the CPNI model, with $\alpha = 0.3$, $\beta = 0.8$. Note that the overyielding species S_1 has an equilibrium biomass greater than K_1 , which is not the case for (e).

mention one possible scenario of coupled positive and negative interactions between a nitrogen-fixing and a nonnitrogen-fixing species: The nitrogen-fixing species is negatively affected by the presence of the second species through competition for light and other resources, while the nonnitrogen-fixing species benefits from the increased availability of soil nitrogen in the presence of the nitrogen-fixing species (Hector *et al.*, 1999; Tilman *et al.*, 2001). We emphasize, however, that overyielding and underyielding and a positive diversity–productivity gradient are not limited to systems with nitrogen-fixing legumes (van Ruijven & Berendse, 2003). This observation is certainly consistent with our model results, since overyielding, under both community and population definitions, was also common in models without facilitation.

In conclusion, while the identification of overyielding in species and species mixtures depends strongly on the definition used (Fig. 2a–d), overyielding is expected to be a widespread phenomenon under commonly used population and community-level definitions. Furthermore, population and community definitions of overyielding do not necessarily imply an increase in the rate of production per unit biomass: species identified as underyielding through actual decreases in their specific rate of biomass production in mixture (SRP definition) can still be classified as overyielding using community or population definitions of overyielding. Finally, species and species mixtures identified as overyielding using all three definitions can form stable assemblages, with underyielding species persisting in the presence of overyielding species.

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