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Size asymmetry of resource competition and the structure of plant communities

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Summary

1. Plant communities show two general responses to gradients of soil resources: a decrease in species richness at high levels of resource availability and an associated shift in species composition from small and slow-growing species to large and fast-growing species. Models attempting to explain these responses have usually focused on a single pattern and provided contradicting predictions concerning the underlying mechanisms.

2. We use an extension of Tilman's resource competition model to investigate the hypothesis that both patterns may originate from the size-asymmetric nature of light exploitation by competing plants. The only mechanism producing changes in species richness and species composition in our model is mortality due to competition.

3. Under the framework of the model, asymmetric light exploitation is a necessary and sufficient condition to obtain the empirically observed responses of species richness and species composition to soil resource gradients. This theoretical result is robust to relaxing the simplifying assumptions of the model.

4. Our model shows that the traits enhancing competitive superiority depend on the mode of resource exploitation: under symmetric exploitation, competitive superiority is achieved by tolerance of low resource levels, while under asymmetric exploitation, it is achieved by the ability to grow fast and attain a large size. This result indicates that a long-standing debate concerning the traits that enhance competitive superiority in plant communities (the 'Grime–Tilman debate') can be reduced into a single parameter of our model – the degree of asymmetry in resource competition.

5. The model also explains the observed shift from below-ground to above-ground competition with increasing productivity, the associated increase in the asymmetry of competitive interactions and the increasing likelihood of competitive exclusion under high levels of productivity. None of these patterns could be obtained under symmetric competition in our model.

6. *Synthesis*. The ability of the model to explain a wide range of observed patterns and the robustness of these predictions to its simplifying assumptions suggest that the size asymmetry of competition for light is a fundamental factor in determining the structure and diversity of plant communities.

Key-words: asymmetric light competition, coexistence, functional traits, Grime–Tilman debate, plant height, productivity–diversity relationship, resource availability, species richness

Introduction

Plant communities show remarkable variation in species richness, species composition and functional traits along natural and experimental gradients of resource availability. Two of the most general patterns are a decrease in species richness at high levels of soil resources (e.g. Al-Mufti *et al.* 1977; Huston 1994; Rajaniemi 2003; Laliberte *et al.* 2013; Borer *et al.* 2014; Fraser *et al.* 2015; but see, Adler *et al.* 2011) and a shift in species composition from relatively small and slow-growing species to fast-growing species of larger size (e.g. Grime & Hunt 1975; Lepš 1999; Osem, Perevolotsky & Kigel 2004; Laliberte *et al.* 2013). Understanding the mechanisms underlying these patterns has been a major challenge for plant

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ecologists, and several theories have been proposed as possible explanations for these two patterns (e.g. Grime 1977; Tilman 1982, 1988; Huston & DeAngelis 1994; Partel & Zobel 2007; Jabot & Pottier 2012; Rees 2013). Most of these theories focus on resource competition as the main driver of changes in both species richness and plant size. But contradictions among existing theories (e.g. Rajaniemi 2003; Craine 2005; Jabot & Pottier 2012) and a long-standing gap between models focusing on species richness (e.g. Huston 1994; Xiao *et al.* 2010) and models focusing on the size and growth rates of individual plants (e.g. Connolly & Wayne 1996; Coomes, Lines & Allen 2011; Farrior *et al.* 2013) still limit our understanding of the mechanisms underlying these responses.

Here, we attempt to bridge this gap by focusing on a fundamental aspect of competition that has been overlooked in most previous theories, namely asymmetry in resource exploitation in relation to plant size. The idea of size-asymmetric resource exploitation was proposed decades ago (Weiner 1985), and its implications have been investigated with respect to a wide range of phenomena including the size distribution in single-species populations (Weiner & Thomas 1986), plant growth rates (Coomes, Lines & Allen 2011), competitive effects and responses (Connolly & Wayne 1996), population growth rates (Schwinning & Fox 1995), coexistence (Onoda *et al.* 2014), succession (Rees & Bergelson 1997) and ecosystem functioning (Yachi & Loreau 2007). Still, we are not aware of any attempt to explicitly model the effects of asymmetric resource exploitation on the diversity and composition of multispecies communities along resource gradients. This is surprising, because the linkage between asymmetric light competition and species diversity has been a major focus of both experimental studies and conceptual models (e.g. Rajaniemi 2003; Hautier, Niklaus & Hector 2009; Lamb, Kembel & Cahill 2009). Incorporating asymmetric resource exploitation in modelling community responses to resource gradients can be expected to improve our understanding of the observed responses because such gradients are inherently associated with a shift from root competition, which is predominantly symmetric, to light competition which is strongly asymmetric (Newbery & Newman 1978; Weiner & Thomas 1986; Schwinning & Weiner 1998; Anten & Hirose 1999; Lamb, Kembel & Cahill 2009).

We define size-asymmetric resource exploitation as a situation in which larger individuals exploit disproportionally greater amounts of the available resources when competing with smaller individuals (Schwinning & Weiner 1998). This definition differs from studies in which asymmetric competition was defined with respect to the *outcome* of competition (e.g. Keddy & Shipley 1989), and allows us to causally link patterns observed at the community level to the fundamental processes of individual growth and survival. Another advantage of such an individual-level approach is that the key processes and variables (plant growth and plant size, respectively) can be measured and manipulated in small-scale and short-term experiments. This advantage promotes empirical tests of the relevant mechanisms and fits the typical scale of plant competition experiments (Rees 2013).

Our study has three main parts. In the first part, we develop a general model that describes the growth of individual plants competing for one or more resources through size-symmetric and/or size-asymmetric exploitation of those resources. In the second part, we use the simplest version of the model (competition between two species for a single resource) to highlight some of the model's basic properties and predictions. Size asymmetry, the key parameter in this single resource model, may operate similarly for any number of resources.

In the third part, we extend our analysis to the case of competition among individuals of many species for two resources and investigate how the asymmetry of light exploitation affects the response of plant communities to gradients of soil resources. Our overall results support previous assertions that the distinction between size-symmetric and size-asymmetric resource exploitation is critical for understanding the responses of plant communities to gradients of resource availability (e.g. Lepš 1999; Rajaniemi 2003; Hautier, Niklaus & Hector 2009; Lamb, Kembel & Cahill 2009; Laliberte *et al.* 2013). At the more general level, we show that such distinction can reconcile a long-standing debate concerning the traits that enhance competitive ability within plant communities.

The model

Our model simulates the growth of n individual plants that compete for m shared resources. Each of the n individuals is characterized by a distinct growth strategy, determined by two parameters: maximal growth rate (μ, the growth rate per unit biomass [RGR] in the absence of any resource limitation) and maintenance cost (M, the amount of resource required for the maintenance of a unit biomass). The latter parameter is resource specific and may vary from one type of resource to another. Positive growth requires that, for all limiting resources, the amount of resource available per plant exceeds the amount required for maintenance. A resource can limit the growth of an individual plant either because its rate of supply is less than the maintenance cost, or because competing plants reduce its availability to levels that are lower than the maintenance cost.

A major simplifying assumption of our model is that each species is represented by a single individual. This approach provides the simplest possible framework for analysing the linkage between properties of the resources (symmetric vs. asymmetric exploitation), individuals (plant size), species (growth strategies) and the community (species richness and composition), while focusing on individual plants as the basic unit and plant growth as the basic process. Our results show that adding differences in abundance among species does not change the qualitative predictions of the model (see Supporting Information, Appendix S1.1).

In real communities, differences in growth rates among individuals lead to, or are associated with, differences in other processes (e.g. reproduction, dispersal, disturbance, herbivory, etc.) whose effects are beyond the scope of the current study. Our model is theoretical and designed to investigate the effect of a specific factor (asymmetric light competition) on a particular phenomenon (response of plant communities to soil resource gradients). It is not designed to be a realistic description of community dynamics.

The model simulates plant growth over time as a discrete process:

$$S_{i(t+1)} = S_{i(t)} + S_{i(t)} \cdot \mu_i \cdot p_{i(t)} \qquad \text{eqn 1}$$

where $S_{i(t+1)}$ and $S_{i(t)}$ are the biomass of an individual plant belonging to species i in time step (t) and (t+1), respectively; μ_i is its maximal growth rate; and $p_{i(t)}$ is a modifier of the growth rate expressing the effect of resource limitation.

We assume that a single resource j limits the growth of the plant at each time step. The identity of the limiting resource may change over time depending on the dynamics of the various resources (Farrior *et al.* 2013) and is determined by Liebig's law of the minimum (Huston & DeAngelis 1994).

$$p_{i(t)} = \min\left(\frac{r_{1i(t)}}{k + r_{1i(t)}}, \frac{r_{2i(t)}}{k + r_{2i(t)}}, \ldots \frac{r_{ji(t)}}{k + r_{ji(t)}}, \ldots, \frac{r_{mi(t)}}{k + r_{mi(t)}}\right) \qquad \text{eqn 2}$$

This equation is a Michaelis–Menten (Monod) type, where the value of p ranges from zero (no growth) to one (maximal growth), k is the half-saturation constant and $r_{ji(t)}$ is the *net* amount of resource j available *per unit biomass* of a plant belonging to species i at time (t), after taking into account the resource-specific maintenance cost:

$$r_{ji(t)} = \frac{R_{ji(t)}}{S_{i(t)}} - M_{ji} \qquad \text{eqn 3}$$

$R_{ji(t)}$ is the amount of resource j available *for the whole plant* at time (t) and M_{ji} is a parameter indicating the maintenance cost of resource j for species i. If maintenance cost (M) exceeds the amount of resource available per unit biomass (R/S), p is set to zero (i.e. no negative growth). The parameter of maintenance cost (M) is similar to R^* in Tilman's (1982) theory of resource competition in the sense that it depicts the lowest resource level at which a positive growth is possible. However, while Tilman's (1982) model focuses on population growth rate, our model focuses on individual growth rate.

We further assume that each resource is supplied at some constant rate to the system. The amount of resource j available for plant i at a given time step ($R_{ji(t)}$) is determined by the equation (Schwinning & Weiner 1998):

$$R_{ji(t)} = \bar{R}_j \cdot \frac{{S_{i(t)}}^{\theta}}{\sum_{i=1}^{n} {S_{i(t)}}^{\theta}} \qquad \text{eqn 4}$$

where R_j is the supply rate (total amount of resource j supplied to the system at each time step), and θ indicates the level of asymmetry in resource exploitation. When $\theta = 1$, resource exploitation is completely size symmetric (each plant gets the same amount of resource *per unit biomass*), whereas as θ increases, resource exploitation becomes more asymmetric and larger plants get larger amounts of resource per unit biomass than smaller plants. We further assume that unconsumed resources are lost, that is there is no accumulation of resources over time.

Results from a variety of studies suggest that the two parameters defining the growth strategy in our model (maximal growth rate and maintenance cost) cannot be considered independent because higher growth rates are inevitably associated with a greater loss of water and minerals from plant tissues, thereby increasing maintenance costs for below-ground resources (Poorter & Garnier 1999; Aerts & Chapin 2000; Gremer *et al.* 2013). Consistent with these studies, fast-growing species are usually less tolerant to low resource levels than slow-growing species (Shipley & Keddy 1988; Grime *et al.* 1997). To account for these empirically observed trade-offs in our model, we assume that maximal growth rate is positively correlated with the maintenance cost of below-ground resources. Specifically, we assume that for below-ground resource:

$$M_i = c \cdot \mu_i \qquad \text{eqn 5}$$

where c is the coefficient of maintenance. Maintenance costs of light are assumed to be constant among species, and for simplicity, we assume that they equal the average maintenance cost of below-ground resources (see Appendix S1.2 for relaxation of this assumption).

A general analysis of the model

Our model can be represented graphically by plotting the relative growth rate (growth per unit biomass) of a slow-growing (A) and a fast-growing species (B) under alternative scenarios of resource exploitation (symmetric vs. asymmetric), and with vs. without a trade-off between maximal growth rate and maintenance cost (Fig. 1). For simplicity, we focus here on competition for a single resource.

Several key features of the model can be seen this way. First, under competition for a single resource, the growth strategy of a species is fully described by a function relating its relative growth rate ($\mu \cdot p$) to the amount of resource available per unit biomass ($R_{i(t)}/S_{i(t)}$). The asymptote of this 'growth function' indicates the maximal growth rate (μ) obtainable under unlimited amount of the resource, and its intercept with the abscissa determines the minimum level of resource required for maintaining positive growth (M, the maintenance cost). The trade-off between maximal growth rate and maintenance cost is expressed by the condition that a fast-growing species has a higher relative growth rate at high resource levels, but requires a higher amount of resource to maintain a positive growth (upper panels in Fig. 1). In the absence of such a trade-off, the two functions differ in their slope and asymptote but not in their intercept with the abscissa (lower panels in Fig. 1).

Secondly, the shapes of the growth functions are not influenced by the mode of resource exploitation (symmetric or asymmetric); the former is a property of the species (defined by μ and M), while the latter is an independent property of the resource (Connolly & Wayne 1996; Schwinning & Weiner 1998). It is the interaction between these two elements that determines the dynamics of growth, and therefore the outcome of competition.

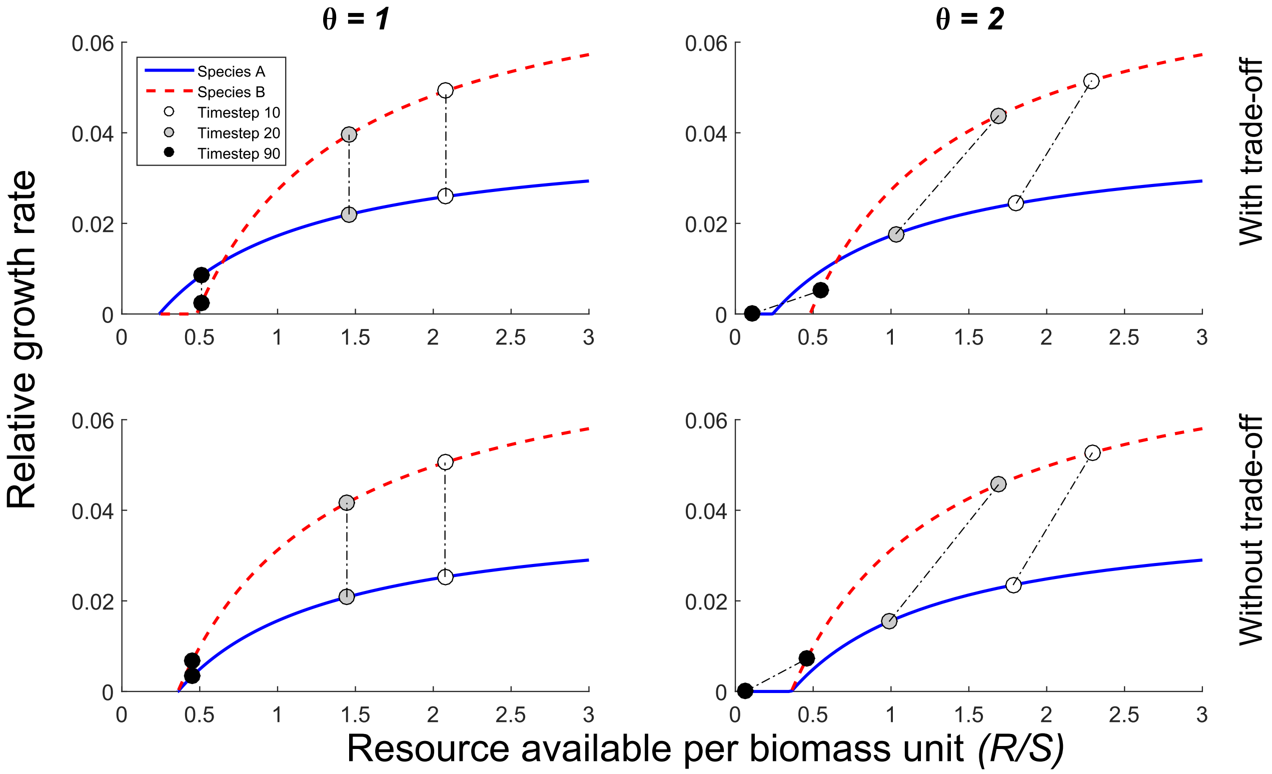

Fig. 1. Summary of growth trajectories of a slow-growing species (A, μ = 0.04) and a fast-growing species (B, μ = 0.08) illustrated by plotting the relative growth rates (RGR) as a function of the resource available per unit biomass. In the upper panels, there is a trade-off between RGR and maintenance ($M = 0.24$ and 0.48, respectively) while in the lower panels maintenance is equal ($M = 0.36$). Circles connected by dashed lines indicate RGR values of the two species at different steps in a simulation where the two species were competing for the same resource under symmetric ($\theta = 1$) vs. asymmetric ($\theta = 2$) resource exploitation. The mode of resource exploitation does not affect the growth strategies, but it does affect the rate of decrease in the amount of resource available per unit biomass during the growth process and the resulting relative growth rate. Other parameters are as follows: resource supply rate ($\bar{R}$) = 3, half-saturation constant (k) = 1 and initial size (S_0) = 0.5.

Thirdly, while the mode of resource exploitation (symmetric or asymmetric) does not affect the *shape* of the growth functions, it does affect the *rate*s with which the amounts of resource available per unit biomass of the two species (and therefore their realized growth rates) shift along the respective growth functions during the growth process. If resource exploitation is symmetric (left panels), each biomass unit gets the same amount of resource at each time step independently of the growth strategy, and the amounts of resource available per unit biomass of the two species decrease at the same rate during the growth process. This scenario is expressed by the vertical dashed lines in Fig. 1, which indicate different time steps during growth. There are two potential outcomes for this mode of resource exploitation. If there is a trade-off between maximal growth rate and maintenance cost (upper left panel), the slow-growing species always out-competes the fast-growing species by reducing the amount of limiting resource to levels at which the fast-growing species cannot maintain positive growth (time step 90 in Fig. 1). This result is equivalent to Tilman's (1982) resource competition model in which the species capable of maintaining a positive population growth under the lowest level of resource (i.e. the species with the lowest R^*) out-competes its competitors. If, on the other hand, there is no trade-off between maximal growth rate and maintenance cost (lower left panel), neither species can outcompete the other, and the two species continue to grow in an asymptotically diminishing rate towards the point at which they cannot maintain positive growth. This scenario is equivalent to competition between two species with the same R^* in Tilman's (1982) model.

A different scenario results if resource exploitation is asymmetric (right panels in Fig. 1). Under such circumstances, the fast-growing species obtains a larger amount of resource per unit biomass than the slow-growing species, and this difference increases with time due to a positive feedback between differences in size and differences in the amount of resource available per unit biomass. This feedback is expressed by the inclination of the dashed lines representing successive time steps in plots of asymmetric resource exploitation (right panels in Fig. 1). Under this scenario, the fast-growing species may out-compete the slow-growing species by reducing the amount of resource available per unit biomass to a level lower than that required for its maintenance (time step 90 in Fig. 1). This latter outcome is in contrast to the prediction of Tilman's (1982) model, which implicitly assumes that resource exploitation is symmetric, and therefore predicts that the species capable of maintaining a positive growth under the lowest amount of resource will always out-compete its competitors (Fig. 1, upper left panel). As shown here, asymmetric competition may reverse this result.

The model also makes predictions concerning the factors determining the likelihood that a fast-growing species will out-compete a slow-growing species under asymmetric resource exploitation. According to the model, this probability increases with increasing asymmetry of resource exploitation, as higher asymmetry allows the fast-growing species to reduce the amount of resource available for the slow-growing species to lower levels (i.e. it increases the slope of the lines representing similar time steps along the growth functions). Decreasing resource availability has the opposite effect, because it increases the likelihood that the growth rate per unit biomass of the slow-growing species would be higher than that of the fast-growing species from the beginning (i.e. that competition would start to the left of the point at which the two growth functions cross in Fig. 1). Finally, increasing the coefficient of maintenance (*c* in eqn 5) increases the difference between the y-intercepts of the two functions, thus extending the range of resource under which the slow-growing species is expected to out-compete the fast-growing one.

The above predictions of the model are general in the sense that they do not refer to any particular resource (Table 1), but they are limited to the case of competition between two species for a single resource. In the next section, we extend the model to address competition among several species for two resources and use the model to investigate the mechanisms determining the response of plant communities to gradients of soil resources.

Community responses to soil resource gradients

Our working hypothesis is that the asymmetric nature of competition for light may explain the observed responses of plant size, species richness and species composition to gradients of soil resources. We explore this hypothesis by simulating competition among multiple species representing different growth strategies under two scenarios: competition for two resources where both resources are exploited symmetrically, and competition for two resources where one resource (representing a soil resource) is exploited symmetrically and the other (representing light) is exploited asymmetrically. The former scenario can be considered as our 'null model'. These simulations are performed under different levels of the soil resource. A comparison of the results obtained from the two scenarios allows us to ask whether asymmetric competition for light can affect the response of the modelled communities to gradients of soil resources.

Table 1. Predicted outcomes of competition between two species with different growth strategies (a fast-growing species and a slow-growing species) competing for a single resource, under different scenarios of resource exploitation (symmetric vs. asymmetric) and a trade-off (with vs. without trade-off between maximal growth rate and maintenance cost)

	Resource exploitation	
	Symmetric	Asymmetric
Trade-off		
With	Slow-growing species wins	Winner depends on model parameters*
Without	Neither species wins	Fast-growing species wins

*Fast-growing species are more likely to win under larger differences in maximal growth rate (μ), higher asymmetry of resource exploitation (θ), higher resource level ($\bar{R}$), lower coefficient of maintenance (*c*) and smaller initial size (S_0)

Each 'community' in the simulations consists of 100 individual plants that vary in their maximal growth rates (and, therefore, in their position along the trade-off between fast growth and low maintenance cost). Initial size (S_0) was the same for all species (although we relax this assumption later). Values of maximal growth rates were randomly derived from a normal distribution (see Table 2 for parameters used in the simulations). Each simulation was run for 1000 time steps, which was sufficient to reach the asymptotic biomass of most species. Longer simulations did not affect any of the patterns (Appendix S1.3).

An important difference between competition for a single resource (Fig. 1) and competition for two resources is that, in the latter case, consumption of one resource affects the availability of the second resource in a complex, nonlinear manner that depends on the parameters of the growth strategies.

EFFECT OF SOIL RESOURCE AVAILABILITY ON PLANT SIZE

Our results indicate that the level of soil resource interacts with the mode of light exploitation (symmetric vs. asymmetric) in determining the distribution of species' sizes (Fig. 2). Under a low level of the soil resource, growth rates of all species are limited by this resource, and the mode of light exploitation does not have any effect on the distribution of plant sizes (upper panels in Fig. 2). As fast-growing species have a higher maintenance cost for the soil resource, actual growth rates of fast-growing species are lower than those of

Table 2. Parameters used in the model and the values used in simulations of community responses to variation in soil resource availability. We used similar units ('Abstract Resource Units', ARU) for both soil resources and light, to simplify the construction and interpretation of the model

Symbol	Description (units)	Value
μ (mean)	Average maximal relative growth rate (fraction)	0.05
μ (SD)	Standard deviation of maximal relative growth rate (fraction)	0.01
c	Coefficient of maintenance (ARU/mass)	3
k	Half-saturation growth constant (ARU/mass)	1
S_0	Initial size (mass)	0.5
θ	Asymmetry of resource exploitation (dimensionless number)	1, 1.001, 1.01, 2
$\bar{R}$ (soil resource)	Soil resource availability (supply rate) (ARU)	1, 2, 3,…, 300
$\bar{R}$ (light)	Light availability (supply rate) (ARU)	150

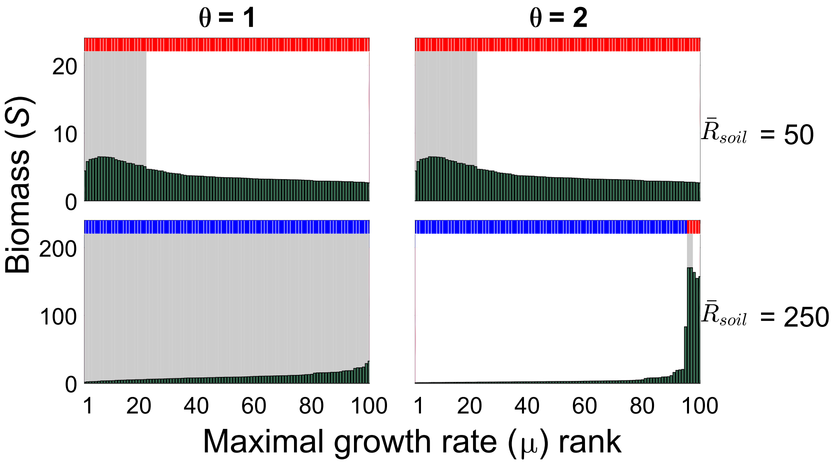

Fig. 2. Individual biomass of 100 competing species (green bars) under different levels of the soil resource ($\bar{R}_{\mathrm{soil}}$) and asymmetry of light exploitation (θ). Species are ranked by their maximal growth rate (μ) from lowest (1) to highest (100). Note the different scales of the y-axes under the different resource levels. Red and blue marks at the top of a panel represent limitations by soil vs. light, respectively. A grey background represents persistence (i.e. maintaining a positive growth rate throughout the simulation), and a white background represents species that did not persist (a negative balance between resource supply and demand).

slow-growing species, resulting in a negative correlation between maximal growth rate and plant size (upper panels in Fig. 2).

Under a high level of soil resource (bottom panels of Fig. 2), the above pattern is reversed. Competition is predominantly for light, and as the maintenance cost of light is not correlated with maximal growth rate, fast-growing species attain larger sizes than slow-growing species, independently of the mode of competition for light. As a consequence, plant size is positively correlated with maximal growth rate (lower panels in Fig. 2). The mode of light competition still has a profound effect on the *magnitude* of the differences in size between fast- and slow-growing species. Under symmetric exploitation, these differences are relatively small, resulting in a gradual increase in plant size with increasing maximal growth rate (lower left panel in Fig. 2). This pattern occurs because, under symmetric resource competition, fast-growing species get the same amount of resource per unit biomass as slow-growing species do, and the only mechanism that increases their size relative to slow-growing species is their higher growth rates per unit of resource.

In contrast, under asymmetric light competition, the size differences between fast- and slow-growing species are intensified by differences in the amount of light exploited per unit biomass. This positive feedback leads to a highly skewed distribution of species sizes, with a few fast-growing species comprising most of the community. Soil resources limit these fast-growing species, as they are able to monopolize most of the light flux (lower right panel in Fig. 2). Among these soil resource-limited species, species with the least maintenance cost for soil resource (and inevitably lower maximal growth rate) achieve the highest biomass.

EFFECT OF SOIL RESOURCE AVAILABILITY ON SPECIES RICHNESS AND COMPOSITION

Our second analysis focused on the responses of species richness and composition to variation in soil resource availability. This covered a wide range of soil resource availability (1, 2, 3,…, 300) to simulate a series of local communities at different positions along a gradient of soil resources. To evaluate the sensitivity of the observed responses to the magnitude of asymmetry in light exploitation, simulations of asymmetric light exploitation were run under both very low (θ = 1.001) and very high (θ = 2) levels of asymmetry.

Analysing the effect of competition on species richness and species composition requires adding a criterion for individual mortality, as mortality of individuals is the only process that may cause changes in species composition (and therefore the number of species) in our model. The criterion we chose was based on energetic considerations: a plant dies if it does not obtain the minimum amount of resources required for its maintenance (Aikman & Watkinson 1980). As a single individual represents each species, mortality of an individual plant is equivalent to extinction of a species from the community.

The results show that asymmetric competition for light changes the relationship between resource availability and species richness from monotonically positive pattern to unimodal (dotted lines in upper panels of Fig. 3). Even an extremely small level of asymmetry (θ = 1.001) is sufficient to cause this qualitative change. Higher levels of asymmetry reduce overall species richness and shift the level of soil resource that maximizes richness into lower levels (Fig. 3).

Asymmetric competition for light also changes the pattern of species composition along the soil resource gradient from a nested pattern, in which any increase in soil resource adds species with faster growth rates to the community, into a 'turnover' pattern, where the gain of fast-growing species at high levels of the soil resource is associated with a loss of slow-growing species from the community (Fig. 3, upper panels). The magnitude of this turnover increases with an increasing level of asymmetry.

We attribute the above results to the interaction between the mode of resource competition and the growth strategies of fast- vs. slow-growing species. Under symmetric resource competition, fast-growing species obtain a similar amount of resources per unit biomass as slow-growing species do, but pay a larger cost for maintenance. As a result, a fast-growing species always requires a higher level of soil resource to persist in the community than a slow-growing species. This effect results in the observation that the minimum level of soil resource at which a species is able to persist in the community increases with increasing maximal growth rate (upper left panel in Fig. 3). As competition at high levels of soil resources is predominantly for light, all species get the same amount of light per unit area under symmetric light competition, and as there are no differences in the maintenance cost of light among species, no species is able to exclude another species.

In contrast, asymmetric light competition enables fast-growing species to reduce the amount of light available for slow-growing species to levels that are insufficient for their maintenance, thereby excluding slow-growing species from the community (upper panels with $\theta > 1$ in Fig. 3). The magnitude of this effect depends on the degree of asymmetry as higher asymmetry increases the differences in size between fast- and slow-growing species. As expected for asymmetric light competition, competitive exclusion always starts with the slowest growing species, and increasing asymmetry results in the exclusion of species with higher growth rates (upper panels in Fig. 3).

EFFECTS OF DIFFERENCES IN INITIAL SIZE

Previous studies have pointed out that size-asymmetric resource competition means that differences in initial plant size (size at the start of growth) are important in determining the outcome of competition (Schwinning & Fox 1995; Rees & Bergelson 1997). We therefore performed an additional series of simulations in which we tested the consequences of such differences for the predictions of our model. These simulations were identical to the original simulations except that the constant values of initial plant sizes were replaced by heterogeneous, species-specific values (randomly drown from a normal distribution with a mean equal to the original value), representing, for example, differences in initial size among species (e.g. due to differences in seed size) and/or stochastic variation due to differences in microhabitat conditions. The results (Fig. 3 lower panels) were qualitatively similar to those obtained from simulations with fixed initial sizes: asymmetric light exploitation modified the response of species richness from a positive to a unimodal pattern, and increasing the level of asymmetry increased the magnitude of species turnover along the gradient (bottom panels in Fig. 3). Particularly notable is the robustness of the productivity–diversity relationship to these differences (Fig. 3). The species occurring at a specific position along the gradient was not always the same as in simulations without variation in initial size (compare upper and lower panels in Fig. 3). In many cases, species that were able to persist in a community when initial size was fixed were excluded from the community when initial size differed among species. In other cases, species that did not persist under the deterministic initial size scenario did persist when initial size was stochastic. Such changes in species composition were limited to communities occurring at relatively high levels of the soil resource (Fig. 3). Under lower levels, growth is limited by the soil resource, and as this is exploited symmetrically, differences in initial size did not affect the outcome of competition.

The combination of maximal growth rate and initial size that enables a species to persist in a community depends on the mode of light competition (symmetric vs. asymmetric) and the level of the soil resource (Fig. 4). Under low levels of the soil resource, species composition is limited to slow-

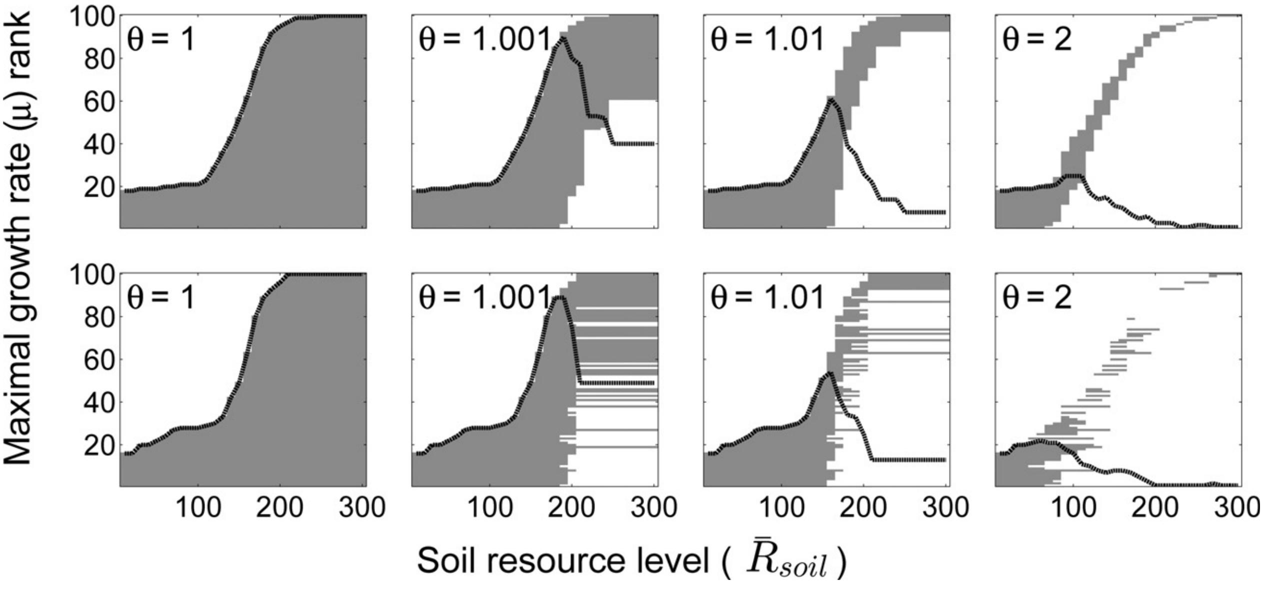

Fig. 3. Effect of soil resource availability on species richness (dotted lines) and species composition (grey marks) under different levels of asymmetry of light competition (θ). Species are ranked from lowest (1) to highest (100) maximal growth rate along the y-axes. Grey colour indicates that the relevant species is capable of persisting (maintaining a positive growth) at the relevant level of soil resource; white areas indicate species that were not able to persist. The upper panels represent simulations in which initial size was equal among all species. The lower panels represent simulations in which initial size was drawn randomly from a normal distribution with mean equal to the simulations with fixed initial sizes.

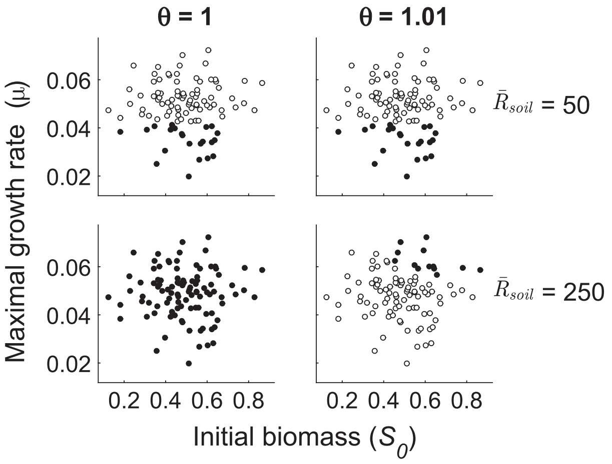

Fig. 4. Effect of initial size (S_0) and maximal growth rate (μ) on species composition under different levels of the soil resource ($\bar{R}_{\text{soil}}$) and asymmetry of light acquisition (θ). Black circles indicate species capable of persisting (maintaining positive growth) at the relevant level of soil resource and asymmetry; white circles indicate species that were not able to persist.

growing species independently of the mode of light exploitation (upper panels in Fig. 4). This pattern is attributed to the trade-off between maximum growth rate and the ability to tolerate low levels of the soil resource. As competition is predominantly for the soil resource, the mode of light exploitation does not have any effect on species composition under this scenario (upper panels in Fig. 4).

In contrast, under high levels of the soil resource, species composition is strongly influenced by the asymmetry of light competition (lower panels in Fig. 4). Under symmetric light exploitation, no species is capable of excluding other species, and therefore, all species persist in the community independently of their growth rates or initial sizes (lower left panel in Fig. 4). Under asymmetric light exploitation, fast-growing species are capable of excluding slow-growing species from the community, and a large initial size increases their competitive advantage. As a result, species composition is limited to a subset of species characterizing by relatively high growth rates and/or large initial sizes (lower right panel in Fig. 4).

Discussion

In the framework of our model, size-asymmetric competition for a limiting resource (light) is a necessary and sufficient condition for predicting a wide range of empirically observed patterns, including the unimodal response of species richness to gradients of soil resources, the disappearance of slow-growing species in richer soils when competition for light is asymmetric, and the corresponding shift into dominance by larger species. Additional patterns predicted by the model are the shift from below-ground to above-ground competition with increasing productivity, the associated increase in the asymmetry of competitive interactions, the increasing likelihood of competitive exclusion under high levels of productivity, the effect of initial size on the outcome of competitive interactions and the resulting potential for a founder effect. None of the above patterns could be obtained under symmetric competition in our model.

Below, we discuss our main findings and their consequences for ongoing debates about the response of plant communities to resource gradients. We then discuss our model assumptions and their consequences for the results. We end with suggestions for empirical tests of the model.

SPECIES RICHNESS

A decrease in species richness at high levels of soil resources due to light competition was commonly attributed to the asymmetric nature of light exploitation (e.g. Hautier, Niklaus & Hector 2009; Lamb, Kembel & Cahill 2009). Our results provide theoretical support for this assertion. According to our results, even a small degree of asymmetry in light exploitation is sufficient to change the relationship between soil resource availability and species richness from positive to unimodal (Fig. 3). Still, the extreme sensitivity to asymmetry decreases when the simplifying assumption of equal maintenance costs for light is relaxed (Fig S2 in the Appendix S1). A variety of previous models have been proposed as possible explanations for the unimodal response of species richness to resource gradients (e.g. Huston 1994; Xiao *et al.* 2010), but most previous models are based on mechanisms involving reproduction and/or dispersal. Our model does not include reproduction or dispersal, and the only pattern-generating process is differential mortality. This difference is important because empirical studies show that a decrease in species richness at high levels of productivity is usually caused by competitive mortality rather than by dispersal limitations (e.g. Foster 2001; Stevens *et al.* 2004; but see Partel & Zobel 2007 for a different view).

The only previous model on which we are aware that incorporated light competition as a factor affecting the response of species richness to a soil resource gradient is Huston & DeAngelis's (1994) ‘resource transport model’. Their model generated a unimodal relationship between nutrient availability and species richness, despite the fact that light exploitation was assumed to be symmetric (as opposed to some citations of the model, e.g. Rajaniemi 2003). The increase in species richness at intermediate levels of nutrient availability resulted from the assumption that the effect of individual plants on nutrient availability was limited to their immediate neighbourhoods. In contrast, light exploitation by individual plants reduced the amount of light available for all other species, resulting in extinction of most species except for the most shade-tolerant ones, as predicted by conventional R^* theory (Tilman 1982).

FUNCTIONAL TRAITS

The finding that asymmetric resource exploitation may reverse the outcome of competitive interactions between slow-growing and fast-growing species (Fig. 1) sheds new light on the debate regarding the traits that enhance competitive ability in plant communities. One view, originally proposed by Grime (1977), holds that high rates of resource uptake and fast growth are the key characteristics underlying competitive superiority in plant communities (see also Gaudet & Keddy 1988). A different view, originally proposed by Tilman (1982), asserts that the ability to tolerate low resource levels is the main characteristic that enhances competitive ability (Dybzinski & Tilman 2007). Empirical studies have found evidence consistent with both views, and reconciling this debate (commonly referred to as the 'Grime–Tilman debate') has been a long-standing challenge in plant ecology (Grace 1991; Craine 2005; Jabot & Pottier 2012; Rees 2013).

Our results demonstrate that the Grime–Tilman debate can be reconciled by distinguishing between symmetric and asymmetric resource exploitation (Fig. 1): under symmetric resource exploitation, competitive superiority is achieved by tolerance of low resource levels (as predicted by Tilman 1982), while under asymmetric exploitation, it is achieved by the ability to grow fast and attain a large size (as predicted by Grime 1977). This simple pattern is consistent with empirical findings (e.g. Dybzinski & Tilman 2007) and fits the characteristics of the systems studied by Tilman (nutrient-limited communities) and Grime (light-limited communities). The simple version of our model integrates these two views within a unified framework and shows that this long-standing debate can be reduced into a single parameter of the model – the degree of asymmetry in light exploitation.

The multiple species version of our model (Figs 2–4) is similar to Tilman's 'ALLOCATE' model (Tilman 1988) in that both models focus on competition along a gradient of soil resource availability, assuming that soil resources are exploited symmetrically and light is exploited asymmetrically. Yet, the main trade-off applied in our model is between low maintenance cost for soil resources and maximal growth rate, while Tilman's (1988) model assumes a trade-off between low R^* for soil vs. light resources. For this reason, our prediction concerning the traits that maximize competitive ability under high levels of soil resources is more similar to Grime's (1977) view (high growth rates) than to Tilman's (1988) view (low R^* for light). Other advantage of our model is its greater simplicity, and the fact that the degree of asymmetry is expressed by a free parameter, thereby allowing explicit analysis of the manner by which asymmetric resource exploitation affects community-level patterns.

It is interesting to compare our model with a recent model proposed by Jabot & Pottier (2012). These authors have shown that the Grime–Tilman debate can be reconciled by adding a component of size-dependent biomass loss to Tilman's model. This was an attempt to express the effect of mowing and/or grazing, which are assumed to be more intense in the systems studied by Grime. Under high levels of size-dependent biomass loss, their model predicted weak competition in poor soils (as predicted by Grime) while under low levels of size-dependent biomass loss, their model predicted high competition intensity in poor soils (as predicted by Tilman). There are two important differences between the model proposed by Jabot & Pottier (2012) and the present model. First, their extension of Tilman's model requires an external source of biomass reduction such as mowing or grazing. Secondly, and more importantly, Jabot & Pottier (2012) ignored light competition, and assumed that plants compete only for soil resources. As a result, their model cannot explain the competitive superiority of large (or fast-growing) species over small species under high levels of resource availability.

POTENTIAL EFFECTS OF DIFFERENCES IN INITIAL SIZE

Our model supports previous theoretical (Schwinning & Fox 1995) and empirical (Newbery & Newman 1978; Gurevitch *et al.* 1990) evidence showing that differences in initial size can influence the outcome of interspecific competition. According to our model, such effects may operate in two directions: they allow slow-growing species to exist under conditions of high levels of soil resources, but may also exclude fast-growing species from the community (Fig. 3). The important point is that both effects are only possible if the limiting resource is light and light competition is asymmetric (Fig. 3). This result may explain inconsistencies among previous studies testing the consequences of size differences for competitive interactions (Ben-Hur & Kadmon 2015). Unfortunately, testing the prediction that such differences are only important under asymmetric competition is difficult as most experiments investigating the effects of initial size on competitive interactions have not explicitly distinguished between the two modes of competition (though see Newbery & Newman 1978; Wilson 1988 for indirect support of this prediction). One exception is a study by Gerry & Wilson (1995). They found that competition in their system was primarily below-ground and that differences in initial size had no effect on the outcome of competition, as predicted by our model.

EVALUATION OF SIMPLIFYING MODEL ASSUMPTIONS

There are two types of simplifying assumptions in our model: basic assumptions of the model itself and assumptions limited to our specific implementation of the model. The most important assumptions of the model itself are that a single individual represents each species in the community and that the trade-off between maximal growth rate and maintenance cost is limited to soil resources. Relaxing these assumptions does not affect the qualitative patterns predicted by the model (Appendix S1.1, 1.2).

Another implicit assumption of the model that could have influenced our results is that plants with a negative balance between resource availability and maintenance cost ($R_{ji(t)}/S_{i(t)} - M_{ji} < 0$, see eqn 3) do not differ from plants with a positive balance in their rates of resource consumption. To evaluate the potential consequences of such differences, we repeated our simulations under an extreme scenario where plants with a negative balance between resource availability and maintenance cost do not consume any resources. This alternative assumption did not change the qualitative patterns predicted by the model (Appendix S1.4).

Among the assumptions made in our specific implementation of the model, the most significant are the reduction of overall resource competition into two types of resources and the description of asymmetry in resource exploitation by a single parameter (θ). Clearly, plants can compete for more than two resources and various soil resources may have different effects on community structure (Craine & Dybzinski 2013). We also acknowledge that under some circumstances light competition might be symmetric (Schwinning & Weiner 1998) and soil resource competition might be asymmetric (Schwinning & Weiner 1998; Rajaniemi 2002). Both scenarios can be easily incorporated by increasing the number of limiting resources (eqn 2) and/or varying the degree of asymmetry in the exploitation of those resources (eqn 4).

The use of a single parameter for quantifying the degree of asymmetry in our model (θ) is a compromise between a total ignorance of the asymmetric nature of light exploitation and an explicit description of light partitioning among species, which requires a much larger number of parameters (Schwinning & Weiner 1998). The assumption that the degree of asymmetry is a property of the resource is also a simplification. In some cases, plants themselves can influence the degree of asymmetry in resource exploitation (Weiner 1990). For example, increasing productivity may lead to an increase in population densities, thereby increasing the asymmetry of light exploitation (Schwinning & Weiner 1998). Our model can be considered conservative in the sense that even without changes in density, species richness decreases with increasing soil resource availability due to underlying increase in individual plant biomass. We expect that adding a density response to the model would increase the magnitude of the reduction in species richness at high levels of productivity.

Unlike other models of resource competition (e.g. Tilman 1988), resources that are not consumed in a given time step are lost in our model. This was done to represent light and soil resources in the same way, thereby making size asymmetry the only difference between them. While this assumption is realistic in the case of light exploitation, it is less realistic in the case of soil resources, where at least part of the unconsumed resources is usually available for future use. Still, the fact that both Tilman's (1988) model and our model predict that competitive ability results solely from R^* under symmetric competition and from R^* and size traits (e.g. seed mass) under asymmetric competition suggests that this result is robust, although further research is needed to assess this.

It should also be noted that our model does not include any mechanism that allows coexistence of plants with different growth strategies under asymmetric light competition. A variety of mechanisms may allow small species to coexist with larger species under asymmetric light competition (e.g. Aarssen, Schamp & Pither 2006; Onoda *et al.* 2014). Incorporating such mechanisms in the model would extend its realism and predictive power.

TESTING THE MODEL

The strongest prediction of our model, which distinguishes it from previous theories and models of plant competition, is that it is the *asymmetry* of resource exploitation, rather than the *kind* of resource (Tilman 1982) or the *intensity* of competition (Grime 1977), which causes the decline of species richness at high levels of soil resources. This theoretical result may explain a variety of apparently conflicting results in previous studies of plant competition. For example, while several experiments demonstrate that light is the main cause of decrease in species richness following fertilization (Hautier, Niklaus & Hector 2009; Lamb, Kembel & Cahill 2009), other studies show that below-ground competition may be important as well (e.g. Rajaniemi 2002). According to our model, asymmetry may still explain these findings, as increasing the availability of one soil resource may increase the competition for another resource that might be exploited more asymmetrically (e.g. in dry communities fertilization may increase competition for water).

We therefore suggest that research on plant competition pay more attention to the degree of asymmetry in resource exploitation as a factor affecting individual, population and community responses to competition. Progress can be achieved by developing experimental approaches that would allow the manipulation of asymmetry of resource exploitation as well as the absolute amount of resource within the framework of factorial experiments (e.g. manipulating the overall amount of light supplied to an experimental system (Hautier, Niklaus & Hector 2009) and the direction from which the light is supplied (bottom to top vs. top to bottom). Such experiments could distinguish between the mechanisms highlighted in the present model and those on which Huston & DeAngelis (1994) focussed.

Field studies should also pay more attention to the asymmetry of resource exploitation. For example, integrating measurements of light availability at different heights of the canopy with corresponding height measurements of the component species (e.g. Anten & Hirose 1999) may provide quantitative information on the potential for asymmetry in light partitioning among species in the community. Although numerous field experiments have quantified variation in competition intensity and/or species richness along productivity gradients, we are not aware of any study that has incorporated such measurements. Our results suggest that such data might explain much of the observed variation in the responses of plant communities to productivity gradients.

Conclusions

We explored the mechanisms by which asymmetric resource competition affects the response of plant communities to soil resource gradients using a minimalistic model of interspecific plant competition. The model explains a wide range of observed patterns in species richness, species composition, biomass distribution and individual plant traits. While some of these patterns have previously been attributed to other mechanisms, the ability of our model to explain such a wide range of patterns and the robustness of its predictions to many of its simplifying assumptions suggest that asymmetric competition for light is fundamental for understanding the structure and diversity of plant communities.

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Data accessibility

This study does not use data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Robustness of the results to model assumptions.

Appendix S2. Competition between two species for two resources.