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Summary

1. Grime's CSR and Tilman's resource-ratio theories are two major contributions to our understanding of plant community dynamics. They have both been corroborated empirically, whilst providing several contradictory predictions. Notably, contrary to Tilman, Grime predicts that competition for soil resources is unimportant on poor soils.

2. We show that Grime's CSR theory can be modelled with the same type of differential equations for resource and plant biomass dynamics used by Tilman in his resource-ratio theory.

3. Using this unified modelling framework, we demonstrate that both models predict intense competition for soil resources on poor soils, as long as biomass loss per unit mass is modelled as a size-independent process. When considering biomass loss per unit mass as a size-dependent process mimicking farming activities, both models predict a unimodal relationship between soil fertility and the intensity of soil resource competition, and a decreasing relationship between disturbance rate and resource competition.

4. *Synthesis.* Our modelling analysis reveals that the resource-ratio and CSR theories make different predictions regarding competition on poor soils, not because of their differing schemes of plant strategies, but because of the different disturbance types that they are considering. Tilman's predictions apply to little disturbed natural habitats, whilst Grime's predictions apply to disturbed ones.

Key-words: community modelling, disturbance, plant competition, plant population and community dynamics, plant strategy, resource competition, size dependence

Introduction

The nature and strength of plant interactions in community dynamics is a fertile background for debate. In regard to the role of plant–plant competition, two distinct theories prevail: the CSR theory (Grime 2001) and the resource-ratio theory (MacArthur 1969, 1972; Tilman 1982, 1988). They make different predictions about the intensity of competition along environmental gradients; however, both have been supported by experiments and field observations.

The resource-ratio theory of plant competition was originally proposed by MacArthur (1969, 1972) and subsequently developed by Tilman (1980, 1982, 1988). It models how plants grow and consume resources, leading to coupled dynamics of plants and resources (eqns 1 and 2 below). Competition between plants is assumed to happen through their consumption of resources. Hence, subsequent resource reduction leads to the exclusion of species which have the largest resource needs (R^*, Fig. 1a,b). This theory makes a number of predictions that have been supported in various natural systems (Tilman 1982, 1988; Miller *et al.* 2005). Among them, resource-ratio theory predicts that the intensity of plant competition is constant along productivity gradients (Tilman 1988, p. 21), but changes from below-ground competition on poor soils to above-ground competition on rich soils.

CSR theory was developed by Grime (1977, 2001). It recognizes three primary strategies for plants: to be a good Competitor for resources, to be a good Stress-tolerator in stressful environments or to have a Ruderal strategy to quickly reach newly available habitats through efficient colonization. According to CSR theory, competitors have an investment strategy with high rate of return per tissue mass and high tissue temporal turnover, whilst stress-tolerators conserve resources within their tissues over the long term. This conservation–exploitation trade-off has found support in the recent literature (Wright *et al.* 2004; Maire *et al.* 2009).

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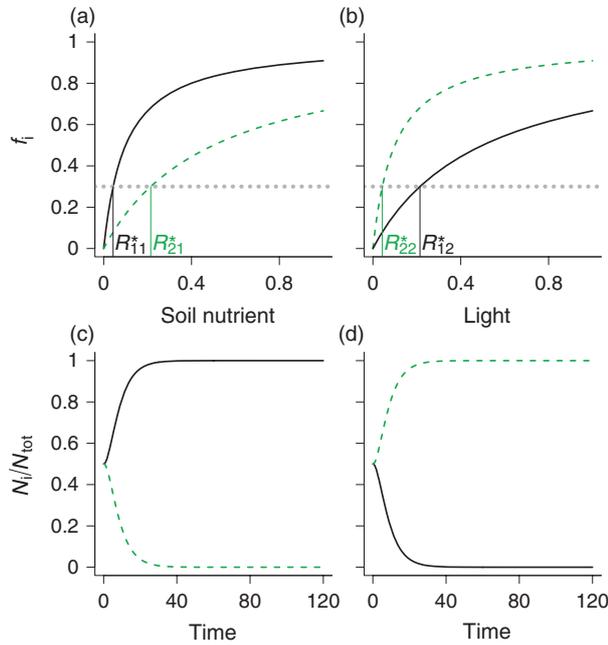
Fig. 1. Resource-ratio modelling with an allocation trade-off between above- and below-ground biomass: resource-ratio theory. Panel (a) represents species growth rate per unit mass $f_i(R_1)$ as a function of the soil resource, and assuming that light is not limiting $f_i(R_1) = f_i^{max} R_1/(K_{i1} + R_1)$. R_{i1}^* is the minimal soil resource level for species i to have a net positive growth rate (i.e. growth minus loss rates). Panel (b) represents species growth rate per unit mass $f_i(R_2)$ as a function of the light resource, assuming that soil nutrient is not limiting: $f_i(R_2) = f_i^{max} R_2/(K_{i2} + R_2)$. R_{i2}^* is the minimal light level for species i to have a net positive growth rate. Panel (c) represents relative biomass dynamics N_i/N_{tot} in a poor soil with high light availability: $a_1 = 1$, $a_2 = 10$, $R_{max,1} = R_{max,2} = 1$. Panel (d) represents relative biomass dynamics N_i/N_{tot} in a rich soil with low light availability: $a_1 = 10$, $a_2 = 1$, $R_{max,1} = R_{max,2} = 1$. Black lines stand for species 1 (a below-ground investor), green dashed lines stand for species 2 (an above-ground investor) and loss rates per unit mass are represented by the horizontal dotted grey lines in panels (a) and (b). $f_1^{max} = f_2^{max} = 1$, $K_{11} = K_{22} = 0.1$, $K_{12} = K_{21} = 0.5$, $m_1 = m_2 = 0.3$.

Contrary to Tilman, Grime argues that competition for soil resources is unimportant in unproductive habitats (Grime 2001; Craine 2005).

Strengths and weaknesses of both approaches have been highlighted (Craine 2005, 2007; Pierce, Vianelli & Ceraboini 2005; Grime 2007; Tilman 2007), mainly stressing their consistencies and inconsistencies with current knowledge in pedology and plant ecophysiology, and calling for a better integration of the ideas brought by these two theories. A major obstacle to better integration of both theories is the unavailability of a mathematical formulation of CSR ideas. Previous works have developed models of CSR ideas (e.g. Berendse 1985; Colasanti & Grime 1993; Aerts 1999), but using approaches that are not directly comparable with resource-ratio equations (but see Huisman 1994). In this contribution, we aim to demonstrate how CSR ideas can be modelled within the resource-ratio framework. We then use this unified modelling framework to understand the source of discrepancy between Grime's and Tilman's predictions on the

importance of nutrient competition on poor soils. This study identifies size dependence in biomass loss rates per unit mass as a key determinant of Grime's observations.

The resource-ratio modelling framework

Tilman's (1980) general model of resource competition can be written as

$$\frac{dN_i}{dt} = N_i f_i(R_1, \ldots, R_k) - N_i m_i \qquad \text{eqn 1}$$

$$\frac{dR_j}{dt} = a_j(R_j) - \sum_{i=1}^{n} N_i f_i(R_1, \ldots, R_k) u_{ij}(R_1, \ldots, R_k) \qquad \text{eqn 2}$$

where, N_i is the biomass of species i, $f_i(R_1,\ldots, R_k)$ is its intrinsic growth rate and m_i its loss rate per unit mass, R_j is the amount of the jth resource, $a_j(R_j)$ its supply rate and $u_{ij}(R_1,\ldots,R_k)$ is the consumption of the resource j per unit of biomass increase of species i. In numerical applications, we will consider (i) that growth rate functions are of a Monod type:

$$f_i(R_1, \ldots, R_k) = f_i^{max} \prod_j R_j / (K_{ij} + R_j),$$

with f_i^{max} being the maximum growth rate of species i and K_{ij} the value of the resource j at which the species i achieves half of its maximum growth rate, (ii) that supply rates follow an equable process (Tilman 1980): $a_j(R_j) = a_j \times (R_{max,j} - R_j)$ and (iii) that all $u_{ij}(R_1,\ldots, R_k) = 1$.

Tilman (1988) further proposed that plant communities may be modelled by considering two main limiting resources: light and soil nutrients (nitrogen in his case) and that plants face a fundamental trade-off between investing in below-ground biomass to harvest nutrients efficiently (Fig. 1a) and investing in above-ground biomass to harvest light efficiently (Fig. 1b). With this simplified model with two resources, Tilman (1988) predicted that plants investing below ground should dominate on poor soils where light is not limiting (Fig. 1c), whilst plants investing above ground should dominate on rich soils where competition for light becomes more important (Fig. 1d). In both cases, the dominant plant is the one with the lowest R^* for the limiting resource, where, R^* is the resource level at which a plant has a growth rate which is equal to its loss rate (Fig. 1a,b).

The realism of competitive exclusion through soil resource depletion has since been questioned. Indeed, different models of nutrient diffusion in the soil suggest that plant roots generally deplete soil resources very locally (Huston & DeAngelis 1994; Raynaud & Leadley 2004), so that spatial distances between plants is likely to be far larger than required for effective competitive exclusion. Little is known, however, on the root spatial distribution of coexisting species. Recent findings based on molecular techniques suggest a high level of mixing between the root systems of various species (Frank *et al.* 2010). Mycorrhizae associated with roots are likely to further increase this mixing of root systems (Selosse *et al.*

2006). And the predictions of the resource-ratio model can be in agreement with those of more complex models of nutrient diffusion in the soil, when competitive ability is primarily driven by root density (Raynaud & Leadley 2004). Other critics mention that resource supply occurs by pulses rather than continuously (Craine 2005), but a well-developed root system also increases the likelihood of capturing such pulses, and thus, will prevent other species from capturing them through subsequent root development. Overall, the resource-ratio modelling approach is simplistic, but this simplicity offers an adequate way of translating basic mechanisms of plant competition for soil resources into mathematical predictions (Tilman 2007). Hence, this framework is sufficiently flexible to simulate community dynamics based on other theoretical assumptions such as those characterizing CSR theory.

Applying the resource-ratio modelling framework to CSR theory

Grime (2001) argued that plants do not face a trade-off between above- and below-ground biomass investments, but rather face a conservation–exploitation trade-off linked to within organ allocations (Craine 2005). This conservation–exploitation trade-off can also be modelled using the differential equation framework of the resource-ratio model, provided that we appropriately change the model parameters.
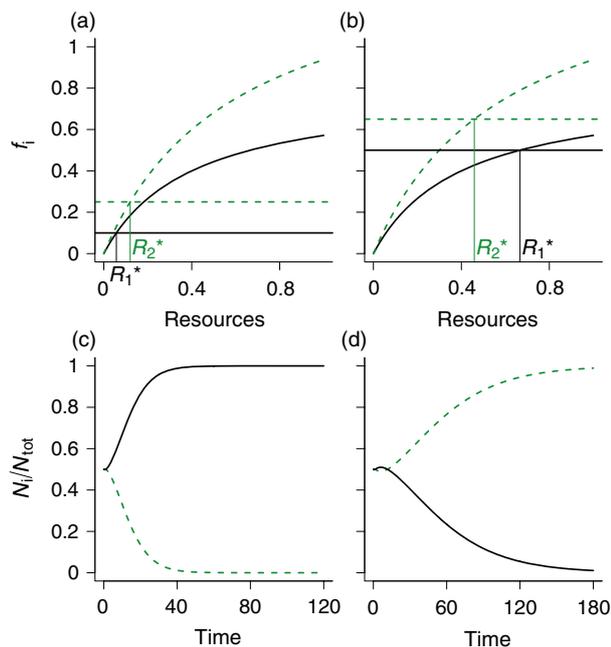
Fig. 2. Resource-ratio modelling with a conservation–exploitation trade-off: CSR theory. Same legends as for Fig. 1. Species 1 (solid black line) and species 2 (green dashed line) are respectively stress tolerant and competitive species sensu Grime (2001). The competitive species always has larger $f(R)$ and m values than the stress-tolerant species, whatever the resource considered. Panels (a) and (c) represent stressful conditions (e.g. poor soils with low loss rates per unit mass). Panels (b) and (d) represent productive but disturbed conditions (e.g. fertile soils with high loss rates per unit mass). $f_1^{max} = 0.8$, $f_2^{max} = 1.5$, $K_{11} = K_{12} = 0.4$, $K_{21} = K_{22} = 0.6$. $m_1 = 0.1$, $m_2 = 0.25$ in panels (a,c). $m_1 = 0.5$, $m_2 = 0.65$ in panels (b,d).

Concretely, CSR theory assumes that the superior competitor (exploitative strategy) shows the highest growth rates across soil nutrient and light gradients but at the same time the highest rate of biomass loss per unit mass (Fig. 2a,b). Doing so, however, we still obtain the result that the dominant species at equilibrium is the one with the lowest R^*. In this modelling framework, the sole possibility of explaining why different species dominate nutrient-poor and nutrient-rich habitats (Fig. 2c,d) is to require that per unit of biomass loss rates m_i are higher in nutrient-rich habitats than in nutrient-poor habitats, and that this increase is strong enough to cause an inversion of the R^* hierarchy (Fig. 2a,b). In this vein, Tilman argued that Grime's observations in British grasslands may confound the effects of soil fertility and disturbance intensity, since fertile grasslands are likely to be more intensely grazed than unfertile ones (Tilman 1988) inflating the rates of biomass loss per unit mass of the species. Importantly, this tentative modelling of CSR ideas predicts, as resource-ratio theory does, that plants strongly compete for soil nutrients on poor soils, since in this model, the plants with the highest R^* will be excluded by nutrient-level reduction in the soil (Fig. 2c).

An alternative modelling of biomass loss

In the resource-ratio modelling framework, the loss of biomass of species i is the product of its intrinsic per unit mass loss rate m_i, which is constant (i.e. independent of biomass or resource supply), and its biomass N_i. This is a reasonable starting point to model losses due to natural mortality (Tilman 1988). However, in managed grasslands where plants are exposed to mowing and/or livestock feeding, alternative modelling of biomass loss may be more appropriate.

Mowing of a given grassland plot consists in cutting all the biomass above a height threshold h_t. To capture this disturbance parsimoniously in the equation of biomass dynamics, we make two very simple assumptions: (i) that plants of species i occupy an area of size S_i and have equal height h_i and (ii) that they show a homogeneous distribution of their biomass along their height, so that $N_i = S_i \times h_i$. With these simple assumptions, plants will loose biomass if $h_i > h_t$, and this biomass loss will be equal to $S_i \times (h_i - h_t) = N_i - (S_i \times h_t)$ at each mowing event (Fig. 3a). Biomass dynamics can then be modelled by

$$\frac{dN_i}{dt} = N_i f_i(R_1, \ldots, R_k) - N_i m_i - \alpha [N_i - S_i h_t]_+ \qquad \text{eqn 3}$$

where, α is the rate of mowing, assumed to be constant through time hereafter, and the notation $[x]_+$ is equal to x if $x > 0$ and to 0 otherwise. The new term depicts the effect of mowing on plant biomass, whilst $N_i \times m_i$ stands for other loss causes such as senescence. Unlike in the original resource-ratio modelling, here the cutting-mediated per unit mass loss rate of species i increases with its own biomass.

Livestock feeding is, somehow, more complex. We will assume here for simplicity that it can be modelled with the same equation as mowing. A more refined modelling of the
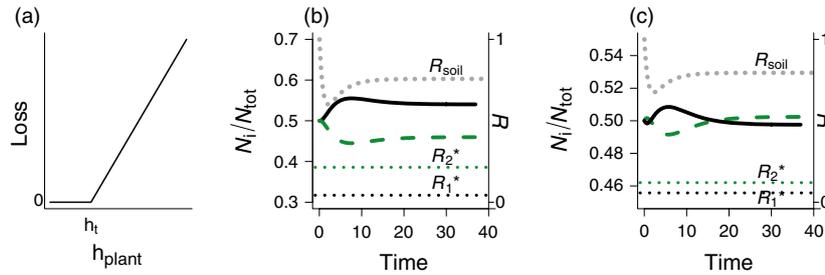
Fig. 3. Per biomass size-dependent loss rates modelling. Panel (a) illustrates the modelled relationship between plant height h_{plant} and loss rate mediated by farming activities (e.g. mowing and grazing). h_t stands for the height threshold above which biomass is cut at a rate α. Panel (b) and (c), respectively, depict biomass dynamics under eqn 3 with parameters representative of the allocation trade-off (resource-ratio theory; see Fig. 1c) and parameters representative of the conservation–exploitation trade-off (CSR theory; see Fig. 2c). Grey dotted lines represent the dynamics of the soil nutrient R_{soil}. Horizontal dotted lines represent the R^* values of the two species. Biomass dynamics are modelled under high light (low productivity) conditions: $a_1 = 1$, $a_2 = 10$, $R_{max,1} = R_{max,2} = 1$, $\alpha = 0.5$ and $S_i(0)h_t = 0.1$.

effect of grazing would require considering spatial effects (Cid & Brizuela 1998; Adler, Raff & Lauenroth 2001; Rossignol *et al.* 2011), but this is out of the scope of the present contribution.

Alternative modelling of biomass loss leads to Grime's predictions

To analytically solve eqn 3, we will make two supplementary assumptions: (i) that light is not limiting (i.e. $R_2 \gg K_{i2}$), so that the unique resource considered is the limiting nutrient in the soil (annotated R hereafter) and (ii) that $S_i(t) = S_i(0)$ is constant, which means that plants grow only in height. We will also consider an alternative to assumption (ii), namely that plants grow homothetically in the three dimensions, so that $S_i(t) = \beta N_i(t)^{2/3}$. Alternative allometric relationships are imaginable as well as alternative plant spatial strategies (e.g. Bolker & Pacala 1999). We here only consider these two simple assumptions, which are useful to make our point. Since the homothetic case provides qualitatively the same results as the constant surface case, we report the results for the homothetic case in Appendix S1 (see Supporting Information).

This new way of modelling biomass loss leads to new equilibrium solutions. If the rate of mowing α is high enough to keep plant biomass small, nutrient concentration in the soil is not reduced to a point where species exclusion occurs. A new equilibrium (Appendix S1, Fig. 3b,c) is then given by

$$R = R^{eq} \qquad \text{eqn 4}$$

$$N_i^{eq} = \frac{\alpha S_i(0)h_t}{\alpha + m_i - f_i(R^{eq})} \qquad \text{eqn 5}$$

At equilibrium, the nutrient concentration in the soil is a constant R^{eq}, which can be computed numerically (Appendix S1), and the biomass of species i, N_i^{eq}, increases with growth rate $f_i(R^{eq})$ and/or decreases with loss rate per unit mass m_i. Grime (2001) has noted that in resource-ratio formulas, slow-growing plants [low $f_i(R^{eq})$] with low loss rates per unit mass (low m_i) could be as competitive as fast-growing plants with high loss rates per unit mass. What is new with our formulation is that it is not necessary to invoke an ad hoc increase of

species loss rates per unit mass in rich soils compared with poor soils to explain changes in species dominance when plants face a conservation–exploitation trade-off (as in Fig. 2). Indeed, in poor soils (low R^{eq}), $f_i(R^{eq})$ is likely to be low for all species, so that slow-growing species with low loss rates per unit mass are likely to dominate. In contrast, in rich soils (large R^{eq}), fast-growing species are likely to overcompensate for their larger loss rates per unit mass (Aerts 1999). These contrasted dynamics between poor and rich soils are possible in this model, since resources can be prevented from progressively decreasing down to the smallest R^* as in resource-ratio models, due to non-linear loss rates (eqn 3, Fig. 3a). Size-dependent growth or loss rates per unit mass have already been shown to prevent competitive exclusion in consumer-resource models (Lobry, Rapaport & Mazenc 2006; Ruan *et al.* 2007). We will further show here that they are key to theoretically recovering Grime's observations on the intensity of competition along a soil fertility gradient.

Our size-dependent loss rate model shows that in disturbed habitats (high α), competition for soil resources may not be intense, as predicted by Grime (1977, 2001) and observed in experiments (e.g. Olofsson, Moen & Oksanen 2002; Carlyle, Fraser & Turkington 2010). To demonstrate this, we used a measure of competition intensity experienced by species i: $IC_i = 1 - (N_i^{competition}/N_i^{alone})$, where, N_i^{alone} stands for the equilibrium biomass of species i grown in monoculture predicted by eqn 5, and $N_i^{competition}$ stands for its predicted equilibrium biomass when grown with another species. This index is equal to 1 minus the competitive response index, also known as relative yield (Carlyle, Fraser & Turkington 2010), so that it increases when competition has a stronger impact on the biomass of species i at equilibrium. By varying the disturbance rate α and the nutrient carrying capacity of the soil R_{max}, we numerically show that for both CSR and resource-ratio theory-inspired models, competition intensity for soil resources decrease in highly disturbed habitats (large α, Fig. 4–c–f) and has a unimodal relationship (U-shape) with soil fertility (R_{max}, Fig. 4a,b,e,f). Note that if R_{max} or α are below a threshold (i.e. black dotted lines in Fig. 4), so that R^{eq} is below the largest R^* of the two species, the species with the largest R^* disappears (Fig. 4 and Appendix S1).

RRT−inspired model

(a)

CSR−inspired model

(b)
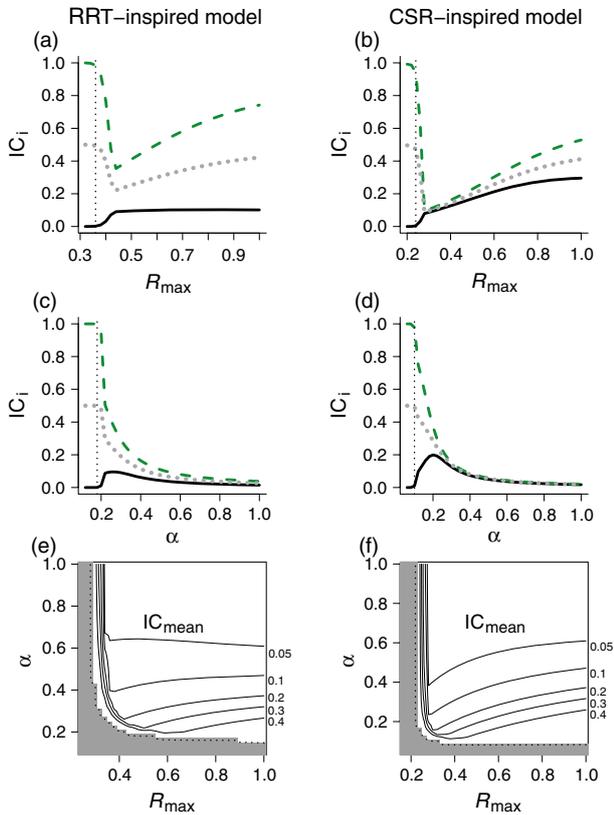
Fig. 4. Intensity of competition as a function of soil fertility (R_{max}) and disturbance (α). Competition intensity is measured by the index IC_i (see main text) and $IC_{mean} = (IC_1 + IC_2)/2$. Panels (a) and (c) refer to a model with a resource-ratio theory-inspired allocation trade-off using $\alpha = 0.25$ in panel (a), $R_{max} = 0.5$ in panel (c) and the other parameter values of Fig. 3b. The green dashed line represents IC for the weakest competitor for soil nutrients (species 2 in Fig. 1) and the black solid line the best competitor for soil nutrients (species 1 in Fig. 1). Grey dotted lines represent IC_{mean} and vertical black dotted lines highlight condition thresholds below which competitive exclusion takes place as in Figs 1 and 2. Panels (b) and (d) refer to a model with a CSR theory-inspired conservation–exploitation trade-off using $\alpha = 0.25$ in panel (b), $R_{max} = 0.5$ in panel (d) and the other parameter values of Fig. 3c. The green dashed line represents IC for the competitor species sensu Grime (species 2 in Fig. 2) and the black solid line the stress-tolerator species (species 1 in Fig. 2). Panels (e) and (f) portray the variations of IC_{mean} as a function of R_{max} and α. Panel (e) refers to a model with an allocation trade-off (resource-ratio theory) using the model parameters of Fig. 3b. Panel (f) refers to a model with a conservation–exploitation trade-off (CSR theory) using the model parameters of Fig. 3c. Variations of IC_{mean} are represented by isoclines. The grey areas delimited by the black dotted lines represent conditions where competitive exclusion takes place. Black lines are isoclines of IC_{mean} values equal to 0.05, 0.1, 0.2, 0.3 and 0.4 from top to bottom.

Consequently, our modified resource-ratio model recovers Grime's predictions on the decreasing importance of competition in poor soils, as long as sufficiently fertile and disturbed habitats are examined (on the right of the curve minimum in Fig. 4a,b). On very poor soils and/or undisturbed habitats, our model predicts that species may fail to persist either because of abiotic conditions (if $R_{max} < R*$) or because of competition for resources as argued by Tilman (if $R_{max} > R* > R^{eq}$). In the first case ($R_{max} < R*$), our model does not differ from the

resource-ratio original model. A species is unable to persist in the harsh abiotic conditions because it has a too large $R*$ value. As already noted by Grime (2001), the predictions of resource-ratio equations are not necessarily different from the predictions of the CSR theory in such a case. $R*$ depends on the balance between per unit mass growth (at rate f_i) and loss (at rate m_i), so that a competitor may fail to thrive in a harsh environment, where a stress-tolerator with a low loss rate per unit mass may persist. Consequently, both theories predict the survival of the species with the lowest $R*$, even if they postulate different mechanisms for a species to have a low $R*$ (resource pre-emption in the resource-ratio theory, and resource conservation in the CSR theory). Consequently, in such cases, the relevance of one or the other theory should be assessed with regards to the mechanisms themselves rather than their implications in terms of outcome of between-species competition (Grime 2001). These results were qualitatively robust to variations in model parameter values (data not shown).

Discussion

Previous research has primarily investigated the differences between resource-ratio and CSR theories in terms of allocation trade-offs (Craine 2005) and the nature of stress (i.e. resource limitation versus metabolic injury, Pierce, Vianelli & Cerabolini 2005) that plants face. Researchers have also investigated the potential role of nutrient cycling (Daufresne & Hedin 2005) and diffusion (Raynaud & Leadley 2004) and the potentially differing effects of various types of resource gradients on plant competition (Goldberg & Novoplansky 1997; Liancourt, Corcket & Michalet 2005). Our theoretical study shows that the contradictory predictions of resource-ratio and CSR theories regarding the intensity of competition on poor soils can also be explained by the different disturbance regimes considered. The predictions of resource-ratio theory rely on size-independent rates of biomass loss per unit mass, whilst the predictions of CSR theory can be recovered when such loss rates vary with species biomass, as often occurs in managed habitats where disturbance takes the form of partial destruction of above-ground biomass through mowing or grazing (Fig. 3a). Whilst Tilman forged his theory in the nitrogen poor natural prairies of Cedar Creek which are relatively unmanaged, Grime studied the British semi-natural grasslands which are significantly impacted upon by recurrent farming activities. It is, thus, not surprising that different loss rate models may be best adapted to these two contrasting situations. Importantly, our theoretical explanation for the discrepancy between Grime's and Tilman's predictions already finds support from field experiments (Olofsson, Moen & Oksanen 2002), where plant competition has been reported to be intense at various levels of fertility but reduced in unproductive habitats impacted by herbivores.

The idea that disturbance affects species interaction has a long history in ecology (Sousa 1984). The idea that ecological communities are not at equilibrium but rather at a dynamic equilibrium punctuated by recurrent disturbances dates back

at least to the work of Jones (1945), Watt (1947) and Tansley (1949, cited in Wilkinson 1999). Grime (1973) and Connell (1978) postulated that species diversity should be maximal in communities experiencing intermediate disturbance frequencies and intensities. Huston (1979) further pointed out that the time scale of disturbance had to be gauged against the rate of competitive displacement, so that environmental conditions favourable to organism growth (e.g. soil fertility) generally reduce community diversity. Our work builds on such general understanding of the role of disturbance on community structure. It highlights that, on top of its intensity and frequency, the kind of disturbance experienced by plant communities (size dependent versus size independent) can have a profound impact on interspecies competition (see also Gaujour *et al.* 2012). We show that farming activities can release the competition between plants by causing size-dependent loss rates, in the same way as the release of competition between prey by predators (Paine 1966; Chase *et al.* 2002).

More generally, by showing how CSR theory can be modelled using the resource-ratio modelling framework, we pave the way for future research aimed at comparing the ability of these two theories to quantitatively predict plant community dynamics. In this agenda, we still need to add to this framework the third strategy axis of the CSR theory, the one of ruderals. This will require leaving the present mean-field approach to embrace the complexity brought about by spatial dynamics (Bolker & Pacala 1999; Leibold *et al.* 2004). Tilman (2004) showed how to deal with stochastic recruitment of invading species from the surrounding landscape in a resource-ratio framework, whilst Mouquet *et al.* (2006) implemented dispersal mechanisms in this same framework to explore the role of landscape spatial heterogeneity. Hence, it should not be a major obstacle for future developments of CSR models, especially for modelling the dynamics of patchily grazed and spatially heterogeneous grasslands and hence, integrating Grime's predictions related to the ruderal strategy.

Acknowledgements

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Supporting Information

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

Appendix S1. Derivation of the analytical results.

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