



# Competition depends more on the functional structure of plant community than on standing biomass

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**Abstract:** Hypothesising that competition is a major ecological factor that filters plants on the basis of traits, we tested whether competition intensity and importance were better explained by the functional structure of communities than by standing biomass. We re-analysed data of three experiments in which one to four species of phytometers have been transplanted with or without vegetation in communities displaying a range of standing biomass. Changes in performance of phytometers among communities were used to assess competition intensity and importance. The functional structure of each community was characterized by the mean and functional divergence of plant height, a trait significantly related to resource depletion by competition. Relationships between competition components and standing biomass or functional structure of communities were calculated for each experiment. Competition importance was explained more significantly by the mean of plant height than by the standing biomass of communities. When the range of functional diversity was large enough, the importance of competition was high in communities with low functional diversity because of similarity in functioning among highly competitive plants, and low in more diverse communities. Competition intensity generally showed lower or no relationship with standing biomass or functional structure of communities. These results confirm the dependence of competition on functional structure of communities.

**Abbreviations:** CWM–Community-level Weighted Mean; FDiv–Functional Divergence; RGR–Relative Growth Rate.

## Introduction

The identification of rules governing community assembly, and especially the role of competition relatively to other ecological factors, is of major importance for community ecology. To that aim, the changes in the two components of competition originally proposed by Welden and Slauson (1986) must be identified across sites because they have different impacts on species and communities. The *intensity of competition* is defined as the reduction in plant performance due to neighbours, independently of other environmental factors. By contrast, the *importance of competition*, defined as the proportional impact of competition on plant performance relative to other factors, represents the component of competition that directly modulates plant fitness at a site. Until recently, competition components could not be distinguished because of analytical difficulties. The proposal of new indices based on the responses of transplanted plants (phytometers) to the competitive effect of undisturbed vegetation (Grace 1993, Brooker et al. 2005, Brooker and Kikvidze 2008), allowed to re-explore the relationships between competition intensity and importance across environmental gradients. A major result was to show that competition importance significantly increased with standing biomass, in contrast to competition intensity that did not vary. In these studies, the standing biomass was identified as

a proxy of environmental severity, confirming the stress gradient hypothesis for competition (Bertness and Callaway 1994).

Assessing competition with phytometers remains the reference in competition ecology to which other approaches must be compared. Indeed, this method allows to compare sites without measuring environmental variables, that represents a major advantage when environmental factors modulating competition at a site are hard to assess (e.g. soil nutrient availability). However, this approach has major limitations. Because it concentrates on individual-level effects, it does not unravel the community-level processes that drive changes in interactions along gradients, such as processes related to population dynamics (Freckleton et al. 2009). A second set of limitations is due to the experimental constraints associated with the use of phytometers: i) heavy disturbance of the site (e.g. transplantation of phytometers, continuous removal of plants in control plots, final harvest of phytometers...), explains why studies are generally performed at a low number of sites with few target species and across relatively short periods of time; ii) results depend on the species used as target (Goldberg 1996) because the interaction between the effects of competition and of other environmental factors most probably differ with ontogeny (Violle et al. 2006) and growth strategy (Suding 2001); iii)

the response of a target species to different gradients can be compared only if the reference state, “the optimal condition of an organism” (Welden and Slauson 1986) is the same everywhere, which is hardly true when gradients are complex; iv) the use of a single species as phytometer can be tricky if the gradient includes extreme environmental conditions; v) in perennial communities where phytometers are chosen among established plants, there is no certainty that plants are strictly equivalent in terms of size (especially for below-ground parts) and local environment. The aim of this study is to assess competition components at the community-level, using a non-destructive and mechanistically-sound approach that avoids the limits of the phytometer approach.

Assuming that interactions are a major ecological factor that filter individuals on the basis of traits (Keddy 1992, Navas and Violle 2009), the functional structure of a community, assessed by the distribution of traits directly related to competition, should unravel more the effects of competition at the community level than standing biomass. Indeed, the standing biomass of a community represents the net result of plant functional and demographic responses to all abiotic and biotic factors and is not the sole consequence of plant interactions. The novelty of the trait-based approach for assessing competition is linked to the ability of this non-destructive method to give general and predictable assessments independently of flora, that are mechanistically-sound assessment of processes. Plant height is a relevant candidate trait for assessing competition at the community level. This trait is a proxy of the competitive effect of individual plants (Huston and Smith 1987, Gaudet and Keddy 1988, Westoby 1998), because it varies with more complex architectural traits (e.g. leaf angle, distribution and position of leaves along the stem, Falster and Westoby 2003) that are directly related to light interception. Furthermore, the mean plant height of a community depicts light depletion over the season (Violle et al. 2009, and references therein). Therefore, the distribution of mean plant height at a site should reflect the competition for light prevailing within the community (McGill et al. 2006, Navas and Violle 2009).

In this paper, we used data from three experimental studies (Reader et al. 1994, Fayolle 2008, Liancourt et al. 2009) to assess the changes in competition intensity and importance across environmental gradients. We selected studies comparing the performance of transplanted phytometers among herbaceous communities. As the experiments differed in environmental conditions, we used the variation in standing biomass among communities as a proxy for the change in environmental severity (Scurlock et al. 2002). In each study, one to four species were used as phytometers, and grown isolated or with vegetation along the gradient. We assessed the functional structure of communities by calculating the mean and variability of plant height for each community, using attributes extracted from flora books. The use of traits not directly measured at the sites is actually favoured in functional ecology when different conditions are met. First, candidate traits must display more variation between species than at the intra-specific level (Garnier et al. 2001). Second, compari-

sons of data must be performed using trait values obtained with similar procedures. These conditions are met here: plant height fulfils the first condition (Kattge et al. 2011) and statistical comparisons were made per experiment to take into account potential differences in evaluation of maximal heights among flora books. We then analysed the changes in competition importance and intensity among communities for each experiment. We expected to find i) a positive link between competition importance and standing biomass and probably no general relationship between competition importance and intensity (Brooker et al. 2005); ii) a stronger positive link between competition importance and mean plant height, as a proxy of competition for light. Moreover, we suspect that competition importance should decrease with increasing variability in plant height because variability in height gets larger with co-occurrence of distinct competitive strategies that limit the impact of interactions among plants (Navas and Violle 2009).

## Material and methods

### Experimental data sets

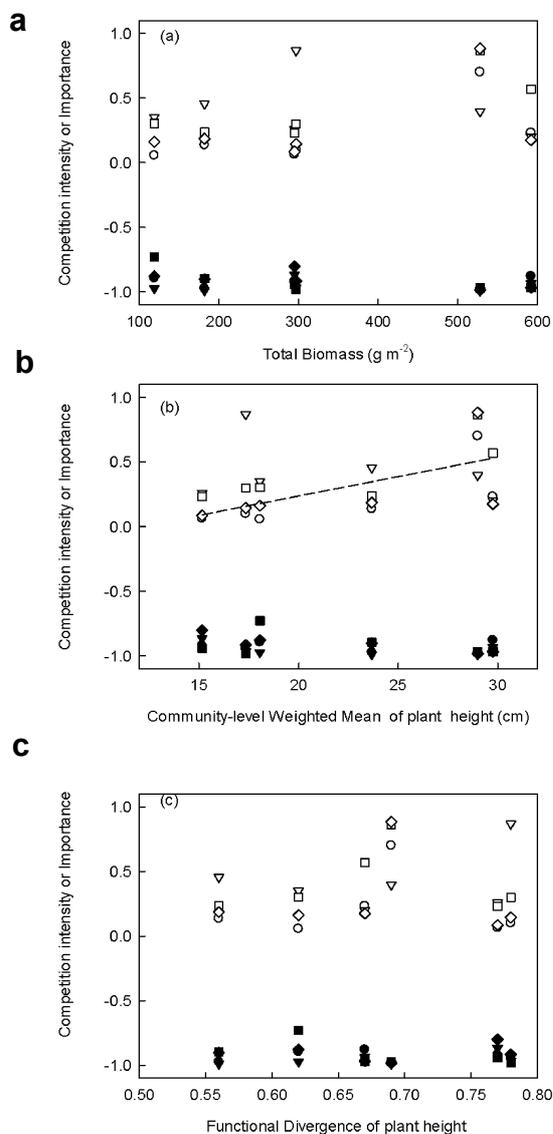
*Experiment 1* was run in rangelands located on the “Causse du Larzac” in southern France (43°55′N, 3°05′E, 790 m above sea level) in a sub-humid Mediterranean climate (Fayolle 2008). Three sites differing in geological substrate (limestone or dolomite) and intensity of management (sheep grazing and fertilization) were selected 150 to 1500 m apart. There were two replicated 15 to 20 ha paddocks per community, each individually fenced. Treatments have been constantly applied for 28 years and represented a gradient of decreasing availability of nutrient and water, that resulted in a decreasing standing biomass from the fertilized and highly-grazed communities on limestone (mean biomass = 560 g m<sup>-2</sup>), grazed communities established on limestone (mean biomass = 239 g m<sup>-2</sup>), to low-productive grazed communities established on dolomite (mean biomass = 208 g m<sup>-2</sup>) (Fig. 1a).

Four grasses were used as phytometers: *Bromus erectus* Huds., *Brachypodium pinnatum* (L) P. Beauv., *Festuca christiannii-bernardii* Kerguelen and *Koeleria vallsiana* (Honck.) Gaudin. These species differed in local abundance: *B. erectus* was dominant everywhere, *B. pinnatum* was abundant only in unfertilized places, the other two species were subordinate in all treatments (A. Fayolle, unpublished data). Two pairs of with and without vegetation plots (10 m × 4 m) were established per paddock in early fall 2006 and fenced to prevent grazing. At the same time, four individuals per target species were randomly transplanted within each plot (with or without vegetation). At the end of the experiment in late July 2007, the above-ground biomass of each surviving phytometer was collected and oven-dried two days at 60°C before being weighed.

The floristic composition of each paddock was assessed in May 2007 within eight one-square-meter quadrats close to the experimental plots. The vegetation of each quadrat was cut at soil level, separated per species, oven-dried for two

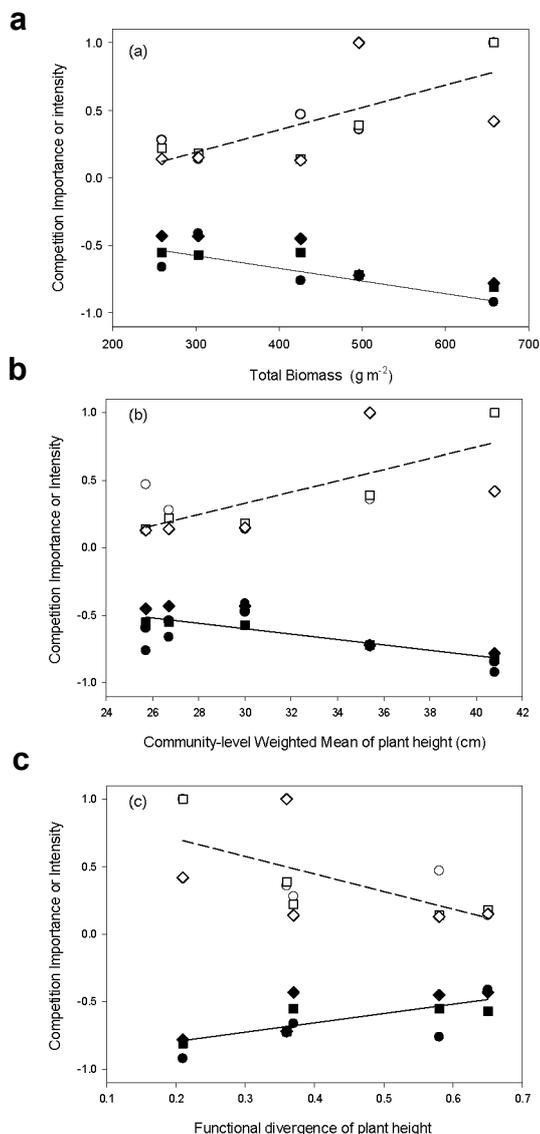
days at 60°C before being weighed. The proportion of biomass of each species was calculated within each community. Plant height attributes of species were extracted from a local flora (Bernard 2008).

*Experiment 2* was performed in the French Alps (45°10'N, 5°50'E) in three sites dominated respectively by *Bromus erectus* Huds., *Brachypodium rupestre* (Host) Schubler and Martens and *Arrhenatherum elatius* (L.) P. Beauv. Ex J. Presl



**Figure 1.** Competition intensity (solid symbols) and importance (open symbols) assessed with four perennial grasses as phytometers in rangelands differing in intensity of management (Experiment 1; Fayolle 2008). Variations in competition intensity and importance are related to (a) standing biomass of communities, (b) Community-level Weighted Means of plant height, (c) Functional divergence of plant height assessed by Rao's index. Symbols for different phytometers; circle: *Bromus erectus*; triangle: *Brachypodium pinnatum*; square: *Festuca christianii-bernardii*; diamond: *Koeleria vallesiana*. The regression line is shown for marginally significant relationship ( $P < 0.10$ ) (see Table 1).

and C. Presl (Liancourt et al. 2009). Half parts of the first two communities were fertilised during two years (NPK 12:12:17). Five different communities were recognized after treatment: although fertilization induced a 50% increase in accumulated biomass of the low-productive communities dominated by *Bromus erectus* and *Brachypodium rupestre* (from 259 and 303 to 496 and 426  $\text{g m}^{-2}$ , respectively), the community dominated by *Arrhenatherum elatius* remained the most productive (658  $\text{g m}^{-2}$ ; Fig. 2a). Changes in standing



**Figure 2.** Competition intensity (solid symbols) and importance (open symbols) assessed with three perennial grasses as phytometers in alpine grasslands differing in productivity (Experiment 2; Liancourt et al. 2009). Variations in competition intensity and importance are related to (a) standing biomass of communities, (b) Community-level Weighted Means of plant height, (c) Functional divergence of plant height assessed by Rao's index. Symbols are for different phytometers; circle: *Bromus erectus*; square: *Brachypodium rupestre*; diamond: *Arrhenatherum elatius*. The regression lines are shown for significant ( $P < 0.05$ ) or marginally significant ( $P < 0.10$ ) relationships (see Table 1).

**Table 1.** A comparison of the three experiments. The ranges in standing biomass, CWM and functional divergence of plant height are given for each experiment. The coefficient of correlation  $r$  of the linear regressions between competition importance (Importance) or intensity (Intensity) and standing biomass (BIO), CWM of plant height (CWM\_H), or functional divergence of plant height (FDiv\_H) are shown together with their corresponding P-values. Pearson coefficient of correlations between competition intensity and importance are given in the last row, with corresponding P-values.

	Experiment 1 (Fayolle, 2008)	Experiment 2 (Liancourt et al., 2009)	Experiment 3 (Reader et al., 1994)
<i>Range in values</i>			
Biomass g m <sup>-2</sup>	185-592	259-658	78-390
CWM_H cm	15-30	26-41	8-153
FDiv_H	0.56-0.78	0.21-0.65	0.56-0.75
<i>Relationships</i>			
Importance / BIO	$r = 0.57; P = 0.23$	$r = 0.94; P = 0.02$	$r = 0.47; P = 0.29$
Importance / CWM_H	$r = 0.71; P = 0.10$	$r = 0.96; P = 0.02$	$r = 0.71; P = 0.07$
Importance / FD_H	$r = 0.24; P = 0.88$	$r = -0.82; P = 0.08$	$r = 0.03; P = 0.96$
Intensity / BIO	$r = -0.61; P = 0.19$	$r = -0.95; P = 0.01$	$r = 0.10; P = 0.83$
Intensity / CWM_H	$r = -0.64; P = 0.12$	$r = 0.85; P = 0.06$	$r = -0.66; P = 0.11$
Intensity / FD_H	$r = -0.04; P = 0.96$	$r = 0.83; P = 0.08$	$r = -0.16; P = 0.73$
Importance / Intensity	$r = -0.71; P = 0.12$	$r = -0.98; P < 0.01$	$r = -0.28; P = 0.53$

biomass went with tremendous change in floristic composition: the community initially dominated by *Bromus erectus* turned to be more diverse in relation to the 25% decrease in proportion of this species and 500% increase in the subordinate *Arrhenatherum elatius*, *Dactylis glomerata* and *Holcus lanatus*; similarly the community initially dominated by *Arrhenatherum elatius* showed a 50% decrease in proportion of this species whereas *Bromus erectus* proportion showed a 25% increase. Therefore, the five communities were considered as independent in statistical analyses.

The three dominant species were used as phytometers: 24 plants of each species were transplanted per community, half of them in places where above-ground biomass had been removed. Changes in performance of phytometers among treatments were assessed after two years of growth by the differences in leaf number between plants grown with and without neighbours. At the same time, the above-ground biomass of the five communities was clipped at ground level within two areas of 0.25 m × 0.5 m. Species were sorted and individually dried at 70°C for 72 h before being weighed. Proportions of biomass were calculated per community for the five dominant species. Plant height attributes for dominant species were extracted from the electronic flora of French Alps ([www.floreAlpes.com](http://www.floreAlpes.com)).

*Experiment 3* was an intercontinental study performed by Reader et al. (1994) to evaluate the relationship between competition intensity and standing biomass. We selected seven sites scattered over three continents for which data on target performance and on community structure were avail-

able (Table 1, p. 1755 in Reader et al. 1994): four sites in Canada were dominated by perennial dicots and graminoids, one site in Australia and one in Netherlands were dominated by perennial grasses and the last one in Sweden was dominated by perennial dicots. The standing biomass of selected sites varied from 80 to 400 g m<sup>-2</sup> (Fig. 3a).

In this removal experiment, the relative growth rate (RGR) of transplanted *Poa pratensis* L. was compared in the presence and absence of neighbours. We extracted data from the original paper to get RGR of phytometers grown in mixture and without vegetation, the proportions of the most abundant species in communities and the biomass of the neighbouring vegetation. We collected data on plant height of the dominant species from electronic floras ([www.efloras.org](http://www.efloras.org); [www.tela-botanica.org](http://www.tela-botanica.org); [//plants.usda.gov](http://plants.usda.gov) [//plantnet.rbgsyd.nsw.gov.au/](http://plantnet.rbgsyd.nsw.gov.au/)).

#### *Assessing competition intensity and importance*

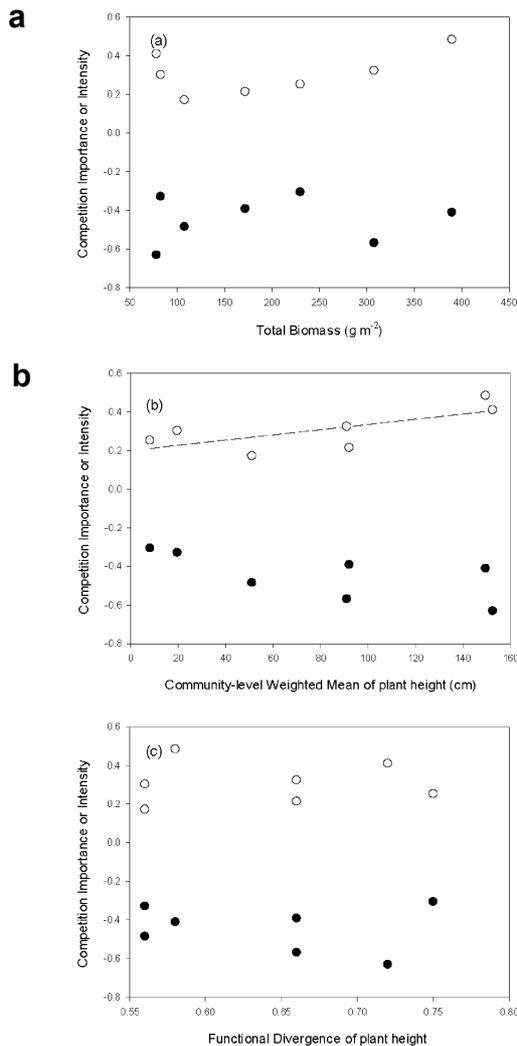
Brooker et al. (2005) proposed new indices for assessing the intensity and importance of competition based on the original definitions by Welden and Slauson (1986). Competition intensity was estimated by the change in local performance of a phytometer grown with or without neighbours, whereas the assessment of competition importance included the impact of other factors than competition on the performance of the phytometer. These indices calculated for each target species  $i$  within each community  $k$  are as follows:

$$C_{\text{Intensity } i,k} = \frac{B_{\text{mix } i,k} - B_{\text{is } i,k}}{\text{Max}(B_{\text{mix } i,k}, B_{\text{is } i,k})} \quad (1)$$

$$C_{Importance\ i,k} = \frac{Bis_{i,k} - Bmix_{i,k}}{Max_k(Bis_{i,k}) - Min(Bis_{i,k}, Bmix_{i,k})} \quad (2)$$

with  $Bmix_{i,k}$  and  $Bis_{i,k}$  as the biomass of phytometer  $i$  grown with and without vegetation, respectively, in community  $k$ . In experiment 2, the values of indices were directly extracted from Liancourt et al. (2009). In experiment 3, the indices were calculated with RGR. Because some RGR values within mixtures were negative (Fig. 1, p. 1758 in Reader et al. 1994), we transformed all data before calculation.

$C_{intensity\ i,k}$  varies from -1, when the species  $i$  is excluded by competition at site  $k$ , to +1 when species  $i$  occurs only if facilitated. Indices calculated for one species but different



**Figure 3.** Competition intensity (solid symbols) and importance (open symbols) assessed with *Poa pratensis* in a three-continent study (Experiment 3; Reader et al. 1994). Variations in competition intensity and importance are related to (a) Community-level Weighted Means of plant height, (b) Functional divergence of plant height assessed by Rao's index (c). The regression line is shown for marginally significant relationship ( $P < 0.10$ ) (see Table 1).

sites are independent.  $C_{importance\ i,k}$  varies from  $-\infty$ , when species  $i$  is facilitated at site  $k$ , to +1 when species  $i$  performs the best as an isolated plant at site  $k$ . Indices calculated for one species but different sites are not independent because they are normalised by the best performance of an isolated plant. Because of these mathematical properties, the indices of competition importance obtained for different experiments with different phytometers cannot be included in a unique analysis.

### Functional structure of communities

We characterized the functional structure of each community by calculating two variables. The Community-level Weighted Mean (CWM) of plant height is the mean trait value weighed by species abundance, i.e. the trait value of a randomly chosen individual, and is calculated as:

$$CWM_k = \sum_{i=1}^n p_{ik} H_{ik} \quad (3)$$

with  $p_{ik}$  as the relative abundance and  $H_{ik}$  the mean height of species  $i$  in community  $k$ . This statistic is built on the mass-ratio hypothesis (Grime 1998) which proposes that the controls on function by species are proportional to abundance. CWM has been successfully used to assess the resource-use of communities (Garnier and Navas 2011), especially in comparative studies, because of low sensitivity to methods estimating the relative abundance of species (Lavorel et al. 2008).

The functional divergence (FDiv) of plant height represents the heterogeneity of trait values within the community. It was assessed by the Rao index that represents the expected dissimilarity in trait values for two randomly selected individuals (Leps et al. 2006) :

$$FDiv_k = \sum_{i=1}^S \sum_{j=1}^S d_{ijk} p_{ik} p_{jk} \quad (4)$$

with  $p_{ik}$  as the relative abundance of species  $i$  in the community  $k$  and  $d_{ijk}$  as dissimilarity between species  $i$  and  $j$  in community  $k$ . Dissimilarity between species was calculated as  $d_{ijk} = 1 - O_{ijk}$  where  $O_{ijk}$  is the overlap between the probability density functions for the height of species  $i$  and  $j$  in community  $k$ .  $O_{ijk}$  was estimated using the normal approximation for each of the functions. Calculations were performed with the Excel Macro (<http://botanika.bf.jcu.cz/suspa/FunctDiv.php>).

### Statistical analyses

We are aware of the low number of communities compared within each experiment that constrains the significance of statistical analyses. However, competitive experiments generally compare a few sites because of large experimental constraints; therefore the three selected studies are among experiments including the larger range in environmental conditions.

For all experiments, the relationships between the means of  $C_{Intensity\ i,k}$  or  $C_{Importance\ i,k}$  calculated among phytometers

per community and the standing biomass, CWM or FDiv of plant height were tested with linear models. For experiments 1 and 2, differences among communities on competition intensity and importance was tested with ANOVAs, using the different targets as replicates. In order to test whether different species of phytometer rank communities similarly according to the intensity and importance of competition, we compared among pairs of species the  $C_{Intensity\ i,k}$  and  $C_{Importance\ i,k}$  values obtained for a given community with Spearman correlation coefficients ( $rS$ ). Pearson coefficient of correlation was calculated between  $C_{Intensity\ i,k}$  and  $C_{Importance\ i,k}$  for each experiment.

As already stated, because of mathematical properties of indices and different sources of data for trait attributes among experiments, the results of the three studies could not be included in a unique analysis. Furthermore, the number of studies was too low to run a meta-analysis. Therefore a qualitative comparison based on significant relationships was performed. Analyses were performed with Statistica v 9 (StatSoft 2009)

## Results

### Experiment 1

Despite a significant effect of community on competition importance ( $F = 4.36$ ,  $P < 0.05$ ), we did not identify a significant relationship with accumulated biomass ( $r = 0.57$ ,  $P > 0.05$ ; Fig. 1a). Competition intensity was independent of treatment ( $F = 2.37$ ,  $P > 0.05$ ) or biomass production ( $r = -0.61$ ,  $P > 0.05$ ). Three target species among the four displayed similar assessment of competition importance among treatments ( $rS > 0.60$ ; for *B. erectus*, *K. vallesiana*, *B. pinnatum*), but differed in assessment of competition intensity.

The importance of competition slightly increased with increasing CWM of plant height ( $r = 0.71$ ,  $P > 0.05$ ; Fig 1b) but did not vary with the functional divergence of plant height ( $r = 0.24$ ,  $P > 0.05$ ; Fig 1c). No relationship was found between competition intensity and CWM or functional divergence of plant height ( $r = -0.64$  and  $-0.04$ , respectively,  $P > 0.10$ ). Competition intensity and importance were not correlated ( $r = -0.71$ ;  $P > 0.05$ ).

### Experiment 2

Both competition importance and intensity, that were highly correlated ( $r = -0.98$ ,  $P < 0.01$ ), significantly varied among communities ( $F = 4.16$  and  $6.27$ , respectively,  $P < 0.01$ ; Fig. 2a). The two components of competition responded to accumulated biomass (importance  $r = 0.94$  and intensity  $r = -0.95$ ,  $P < 0.05$ ), although both seemed to level off at the most productive community. *B. erectus* and *B. rupestre*, the two species dominating low-productive sites, showed similar assessment of competition importance ( $rS = 0.80$ ) whereas *B. rupestre* and *A. elatius* gave similar assessment of competition intensity ( $rS = 0.87$ ).

The importance of competition significantly increased with CWM of plant height ( $r = 0.96$ ,  $P < 0.05$ ), whereas competition intensity showed only marginally significant response to CWM of height ( $r = 0.85$ ,  $P = 0.06$ ; Fig. 2b). Interestingly, in that experiment that displayed the largest range in functional structure among communities, the competition importance decreased ( $r = -0.82$ ,  $P > 0.05$ ) and the competition intensity increased ( $r = -0.83$ ,  $P > 0.05$ ), although non-significantly, with the functional divergence of plant height, then levelled off in the two most functionally diverse communities (Fig. 2c).

### Experiment 3

Reanalysing the data published by Reader et al. (1994), Brooker et al. (2005) showed that competition importance significantly increased with standing biomass whereas competition intensity did not. However, for the subset of sites we selected here, there was no relationship between competition components and standing biomass (importance  $r = 0.47$ ,  $P > 0.05$ ; intensity  $r = 0.10$ ,  $P > 0.05$ ; Fig. 3a). We found that competition importance marginally significantly increased with CWM of plant height ( $r = 0.71$ ,  $P = 0.07$ ) whereas a slighter response was recorded for competition intensity ( $r = -0.66$ ,  $P > 0.10$ ; Fig. 3b). Competition importance and intensity were not correlated ( $r = -0.28$ ;  $P > 0.05$ ) and did not significantly vary with the functional divergence of plant height ( $r = 0.03$  and  $-0.16$ , respectively,  $P > 0.05$ ; Fig. 3c).

### All experiments

The three experiments were characterized by rather similar range in standing biomass but highly differed in functional structure (Table 1). Experiment 3 displayed the largest range in mean plant height but the lowest in functional divergence whereas the opposite trends were recorded for experiment 2. These results confirm that the two statistics we used for describing functional structure may be independent and related to different processes explaining community assembly (Garnier and Navas 2011, and references therein).

Competition importance significantly increased with CWM of plant height in all experiments and with community standing biomass in only one experiment. This index responded to the functional divergence of plant height only in experiment 2, where the functional divergence in plant height was the largest. On the other hand, competition intensity generally showed lower or absence of relationship with community biomass, CWM or functional divergence of plant height. Competition intensity and importance were not related except by a negative relationship in experiment 2.

## Discussion

### Changes in competition across communities

The importance of competition was not consistently modulated by standing biomass, (Table 1) in contrast with previous studies (Sammul et al. 2000, Corcket et al. 2003,

Brooker et al. 2005, Zhang et al. 2008). The absence of relationship for competition intensity was, however, in line with previous studies that showed an increase (TwolanStrutt and Keddy 1996, Gross et al. 2010), a decrease (Goldberg et al. 1999) or no variation with standing biomass (Wilson and Tilman, 1993, Cahill 1999, Goldberg et al. 1999). As a consequence, the two components of competition were generally not correlated, confirming the suggestion by Welden and Slauson (1986) and Brooker et al. (2005). The positive relationship between competition importance and standing biomass is related to the fact that standing biomass is a proxy of productivity (Scurlock et al. 2002) that negatively relates to environmental severity (Brooker et al. 2005). By contrast, competition intensity depends more on the performance of plants grown with neighbours, independently of the severity of the environment, explaining why there is no general relationship between competition intensity and standing biomass. These results suggest that the processes controlling the intensity and importance of competition perceived by an individual are different. On the one hand, the importance of competition reflects by how far the interacting plants deviate from fundamental niche optima (*sensu* Hutchinson 1957), assessed by the maximal performance of an individual grown without neighbours. On the other hand, the intensity of competition depends on the performance of plants grown with neighbours, and varies with species realized niche. Therefore, competition importance is mainly modulated by species fundamental niche that varies with the interaction between phytometer and abiotic factors whereas competition intensity depends more on realized niche that varies with the interaction between phytometer, neighbour species and abiotic factors.

We also found that three among the four species used as targets in experiment 1, that differed in growth rate and/or phenology, displayed similar changes in competition importance among communities, whereas they differed in assessment of competition intensity (Fig. 1). By contrast, targets used in the second experiment differed in assessment of competition among communities (Fig. 2), probably because some of these species were transplanted in communities where they are not usually found. This result emphasizes a strong limitation of the phytometer approach.

#### *Competition and functional structure of communities*

There is actually a debate on the scale at which the importance of competition should be assessed (Kikvidze and Brooker 2010), knowing that it can be defined from cellular to community-level (Welden and Slauson 1986). Assessments performed at the individual-level have been criticized because they cannot be used to predict population dynamics or community assembly (Freckleton et al. 2009). The approach we propose takes a community perspective, in line with other studies (Grace 1991, Damgaard and Fayolle 2009), by linking competition importance and intensity to the functional structure of the community. We show that plant height is relevant to assess competition at the community

level, as previously suggested (McGill et al. 2006, Navas and Violle 2009). The positive link between competition importance and CWM of plant height suggests that the mass ratio hypothesis (Grime 1998) applies in the case of competition: the highly competitive dominant species have a major impact on the fitness of individuals comparatively to other environmental factors. This reflects the disproportionate effect on resource availability of dominant plants over smaller ones (Gaudet and Keddy 1988, Keddy and Shipley 1989) as the consequence of the asymmetry competition for light (Weiner 1990, Schwinning and Weiner 1998). Why this is less true for competition intensity remains to be understood.

The relationships found between competition components and functional divergence differed largely among experiments, probably in relation to differences in range of functional divergence (Table 1). Both competition intensity and importance changed in experiment 2, although non significantly, along a large gradient of functional divergence, whereas no clear change in competition was recorded in the other two experiments of more restricted functional diversity range. One probable explanation is that the range in functional divergence found in experiment 2 was large enough for different processes linked to competition to operate. Communities characterized by intense and important competition have low functional diversity, probably after exclusion of the least competitive species, because successful competitive species display similar values of traits related to resource use (Grime 2006). By contrast, communities characterized by low intensity or importance of competition have high functional divergence in relation to the limiting functional similarity that occurs among interacting plants (Weiher and Keddy 1995, Stubbs and Wilson 2004, Scheffer and Nes 2006). As suggested by Navas and Violle (2009), the functional divergence probably reflects the set of competitive strategies of species: highly specialized individuals occur where competition is very important and intense whereas several strategies of more generalist individuals may co-occur at intermediate values of competition. These preliminary results, obtained from a few number of experiments are thus very promising, because they confirm the occurrence of a relationship between competition and the functional structure of communities.

In conclusion, we advocate that developing a trait-based approach in competition ecology could be a way to tackle the processes underlying the changes in competition components among sites. Coupled with more process-based modelling, this approach could be used to untangle the role of environmental filtering, limiting similarity and competitive exclusion on community assembly, leading to a prediction of community dynamics, as strongly requested by Freckleton et al. (2009).

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