

## The importance of importance

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Failure to distinguish between ‘importance’ and ‘intensity’ of competition has hindered our ability to resolve key questions about the role interactions may play in plant communities. Here we examine how appropriate application of metrics of importance and intensity is integral to investigating key theories in plant community ecology and how ignoring this distinction has led to confusion and possibly spurious conclusions. We re-explore the relationship between competition intensity and importance for individuals across gradients, and apply our review of concepts to published data to help clarify the debate. We demonstrate that competition importance and intensity need not be correlated and show how explicit application of the intensity and importance of competition may reconcile apparently incompatible paradigms.

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Competition is a key process that structures plant communities (Grace and Tilman 1990). The struggle for light, water, nutrients or space impacts the growth, reproduction or survival of plants in many natural systems. However, quantifying the impact of competition relative to the physical environment, stochastic events, and consumers is problematic. In particular, heated debate has focused on the impact of competition relative to the severity of the abiotic environment – typically indicated by plant productivity. Resolving this debate is not trivial. Understanding the relative effects of ecological functions along gradients provides insight into generality, conditionality, and mechanism, and provides the baseline information for predicting the impacts of many key environmental drivers.

The debate over the role of competition in plant communities is complex, but opinions are commonly allotted to one of two opposing dominant camps. On one hand it is argued that competition plays a similar role in plant communities irrespective of system productivity, but that the mechanisms by which plants compete change (Newman 1973, Tilman 1982, 1987, 1988, Grubb 1985). As the argument goes, in productive, abiotically moderate environments plants compete strongly for light or space, while in harsh, unproductive environments plants compete just as strongly, but for water or soil nutrients. The opposing view is that competition is a predominant force within plant communities in productive environments, but when productivity decreases and environmental severity increases the role of competition

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in plant communities decreases (Grime 1979, Huston 1979, Keddy 1989). In addition to these two dominant models, Taylor et al. (1990) proposed a third model in which competition is independent of productivity but is driven by the ratio of resource supply to resource demand, which in turn depends upon the frequency of disturbance events. Experimental evidence supported all three of these points of view, and several reviews have attempted, through a survey of the available empirical evidence, to find some degree of reconciliation (Goldberg and Barton 1992, Goldberg et al. 1999). These reviews have made progress, but the opposing views continue to be discussed as though they are irreconcilable at a fundamental level.

Grace (1991) suggested that debate over the models of Grime and Tilman was fuelled by a failure to clearly distinguish between two key components of competition, the intensity of competition and the importance of competition, previously defined by Welden and Slauson (1986). The intensity of competition is a reduction in the growth of species A as a consequence of the presence of species B. The importance of competition is the impact of B on A expressed as a proportion of the impact of the whole environment on A. These concepts are illustrated in Fig. 1. For species 1, the total reduction in success (the “total strain” reducing the growth of a species below its optimum physiological state *sensu* Welden and Slauson) due to competition and other factors is 24 arbitrary units, of which competition accounts for 18 units: the intensity of competition is therefore 18 units whilst the importance of competition (the impact of competition as a proportion of the total impact of the environment) is  $18/24 = 0.75$ . For species 2, although the intensity of competition is the same, i.e. 18 units, because the impact

of other factors is now far greater, the importance of competition is reduced to  $18/36 = 0.50$ .

Grace (1991) stated that Grime’s model “is one that is explicitly based on tradeoffs in the relative importance of selective forces”. It is therefore concerned with the relative importance of competition. Tilman’s model, on the other hand, examines the factors that control plant growth and population dynamics within an environment. It does not try to separate competition from other components of the environment, instead these other components are considered to be integral parts of a plant’s ability to tolerate a lower resource supply than its neighbors. Tilman’s model is therefore concerned with the intensity of competition.

Given that the intensity and importance of competition are clearly different and, as illustrated in Fig. 1, “need not be correlated” (Welden and Slauson 1986), it is essential that we distinguish between the two. This is not simply to help us equitably examine the predictions of Grime and Tilman, but also because the two different measures of the role of competition address fundamentally different questions. However, very few studies of competition have clearly made this distinction, and this may have led to serious misunderstandings. For example Reader et al. (1994) compared the relative growth rate (RGR) of *Poa pratensis* in the presence and absence of neighbors in 12 different communities encompassing a wide range of productivity levels, and expressed the results using an index of competition intensity. They argued that these findings, showing a lack of relationship between competition intensity and system productivity, contradicted the model of Grime. However the predictions of Grime, related to the importance of competition (*sensu* Welden and Slauson 1986), cannot be tested using an index that measures competition intensity. It is impossible therefore to say whether the experiment of Reader et al. actually tests the predictions of Grime.

Other similar examples of this type of confusion exist (Goldberg 1994, Markham and Chanway 1996) and perpetuate the debate. Sammul et al. (2000) acknowledge the need to differentiate between intensity and importance in their study of population-level impacts of competition along productivity gradients. They use two indices for examining the importance of competition. The index IC is “the percentage of variation, accounted for by the [non target removal] treatment effect, which equals to the sum of the squares of deviations, due to removal of neighboring plants... divided by the total sum of squares of deviations”. This index is developed from the approach suggested by Welden and Slauson (1986). IC does not measure the impact of competition to be expressed relative to the total impact of the environment. Rather, it is a measure of interaction intensity, and sampling error can affect the total sum of squares, and thus the value of IC. Their alternative index R, which is described as the difference between mean population

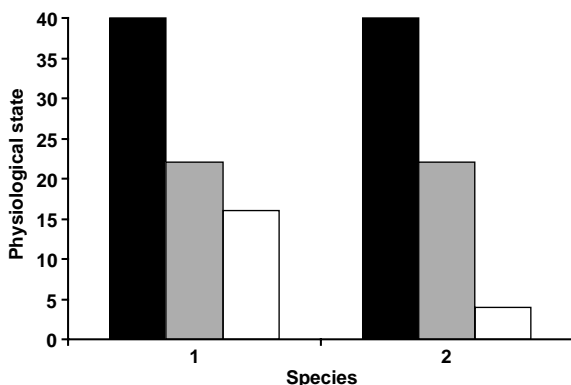


Fig. 1. Graphical illustration of the difference between the intensity and importance of competition based on Fig. 1, Welden and Slauson 1986. The figure shows the hypothetical physiological states of 2 species under three different conditions: optimum growth (dark grey), the state resulting purely from competition (light grey) and the state resulting from the combined effect of competition and other environmental factors. For discussion of the figure see text.

density ( $N_{\text{cmean}}$ ) and maximum potential population density ( $N_{\text{max}}$ ), but which is actually expressed as a ratio rather than an absolute difference (given as  $R = N_{\text{max}} N_{\text{cmean}}^{-1}$ ), is simply another measure of competition intensity as it is not placed within the context of the total environmental impact. In addition it is not a good measure of competition intensity as it is vulnerable to increased sampling as the value used for  $N_{\text{max}}$  is, up to a point, likely to increase as sample size increases.

Further illustrative of the confusion surrounding this issue is the paper by Grace (1993) wherein he again approaches the question of selecting the correct index to express competition with respect to the differing predictions of Grime and Tilman. However he discusses the relative merits of absolute competition intensity (ACI) versus relative competition intensity (RCI). Both of these indices are, as their names imply, indices of competition intensity rather than importance and so should not be used to test the predictions of Grime. Although the relationship between productivity and competition expressed as ACI appears to support Grime, this is simply a consequence of changing plant size along productivity gradients, an artifact that led to the development of the RCI index.

We suggest that one reason why the distinction between competition intensity and importance is still rarely made is a lack of a common analytical approach, particularly with respect to the expression of competition importance. Our aims in this paper are firstly to examine one possible solution for the expression of the importance of competition, secondly to examine its relationship to competition intensity, and thirdly to demonstrate how reanalysis of existing data can lead to clarification of the debate outlined above.

Here on, to be clear when we refer to importance with specific reference to the "importance of competition" as defined by Welden and Slauson, we shall use  $C_{\text{int}}$  and  $C_{\text{imp}}$  to symbolize competition intensity and importance respectively.

## Expressing competition intensity and importance

Throughout this paper we follow the convention that net competitive interactions are given a negative value and net facilitative interactions a positive value. Therefore increasingly negative values for  $C_{\text{imp}}$  or  $C_{\text{int}}$  indicate an increasingly competitive effect, whereas increasingly positive values indicate an increasingly facilitative effect (Callaway 1995, Brooker and Callaghan 1998). Additionally many studies now refer to the importance or intensity of neighbor effects in general rather than competition alone, acknowledging the important role of facilitation. Here we discuss competition, and have named our indices  $C_{\text{imp}}$  and  $C_{\text{int}}$ , in order to aid

comparison with previous research. However, the arguments presented with respect to the importance and intensity of interactions cover both competitive and facilitative neighbor effects.

### Competition intensity- $C_{\text{int}}$

$C_{\text{int}}$  is the impact of competition irrespective of the impact of other factors such as abiotic stress. Therefore suitable indices for expressing  $C_{\text{int}}$  are RCI, the relative competition intensity index (Grace 1993), or the more recent RNE, relative neighbor effect (Markham and Chanway 1996, Armas et al. 2004). RNE allows for the symmetric expression of the intensity of both facilitative and competitive interactions. The formula can be rearranged to give a more intuitive version where negative values indicate competition and positive values indicate facilitation (Callaway et al. 2002):

$$C_{\text{int}} = \text{RNE} = (P_{\text{T-N}} - P_{\text{T+N}})/x \quad (1)$$

where  $P_{\text{T+N}}$  and  $P_{\text{T-N}}$  are the performance of target plants ( $P_{\text{T}}$ ) in the presence (+N) and absence (-N) of neighbors, and  $x$  is the greater of the two; either  $P_{\text{T+N}}$  or  $P_{\text{T-N}}$ . This index does not try to scale the impact of competition (or facilitation) relative to the impact of other factors in the environment such as abiotic conditions or herbivory. This is why we refer to RNE as an index of competition intensity ( $C_{\text{int}}$ ).

### Competition importance- $C_{\text{imp}}$

As stated, and in contrast to  $C_{\text{int}}$ , there is no commonly applied index of  $C_{\text{imp}}$ .  $C_{\text{imp}}$  is the impact of competition relative to the impact of all the factors in the environment on plant success (ultimately taken as reproductive success, but commonly measured as some form of growth increment). In order to express  $C_{\text{imp}}$  we must be able to quantify the total impact of the environment upon plant success. This is difficult. However, it is possible to obtain a restricted index for  $C_{\text{imp}}$  by quantifying changes in  $C_{\text{imp}}$  across environmental gradients. By using a common phytometer across a given productivity gradient, for example the use of *Poa pratense* by Reader et al. (1994), we can infer the importance of competition relative to other environmental parameters. For example, if we compare the growth of plants without neighbors at two points along the gradient, A and B, the difference in growth can be assumed to be due to differences in the impact of the environment excluding neighbours at points A and B. If we scale the impact of competition at point B (i.e. the difference in growth between plants with and without neighbors) to this measure of the impact of the neighbour-free environment, we can produce an index of the importance of competition. Importantly, the

length of the gradient explored is limited to the tolerance of particular phytometer species, although we may be able to lengthen the studied gradient by overlapping different phytometer species with different abiotic tolerances (although we should be cautious because the relationship between plant success and severity may differ between species, so that for a given increase in severity species A may show a different response to species B). However, as long as we express the impact of competition at all other points along our gradient relative to the impact of the abiotic environment as calculated in comparison to point A, this index enables us to examine the relationship between our environmental gradient and  $C_{imp}$ , even if we do not have an absolute measure of  $C_{imp}$ . We therefore define  $C_{imp}$  as:

$$C_{imp} = (P_{T+N} - P_{T-N}) / (\text{Max}P_{T-N} - y) \quad (2)$$

$\text{Max}P_{T-N}$  is the maximum value of  $P_{T-N}$  along the gradient (e.g. our neighbor free plant at point A) and  $y$  is the smaller of either  $P_{T+N}$  or  $P_{T-N}$ .  $C_{imp}$  is similar to an index proposed by Corcket et al. (2003); RECI – the relative environmental constraint intensity, which provides a measure of the impact of the environment across a productivity gradient. However,  $C_{imp}$  moves one step beyond RECI because it expresses the impact of competition as a proportion of the impact of the total environment. At this point it is worth discussing some features of  $C_{imp}$  that impact upon its application:

1. The selection of  $\text{Max}P_{T-N}$  as the point against which to scale the impact of competition, provides a usable index for analyzing the relative change in competition importance and intensity within a gradient for a particular species. However, this makes it difficult to directly compare  $C_{imp}$  values between species. Direct comparisons are possible if the absolute maximum level of  $P$  for all the species of interest is known. Nonetheless, comparison of the slopes of regression lines provides a possible means for making multi-species comparisons of the rate of change of the importance of competition across environmental gradients.
2. The response of a single species to multiple gradients can be compared as long as  $\text{Max}P_{T-N}$  is the maximum value of  $P$  for all the gradients considered. In this case we would be able to compare both absolute values of  $C_{imp}$  and the rates of change, as long as we had a common explanatory variable for all gradients. This is essentially the approach that makes the multi-site comparison of Reader et al. (1994) possible.
3. The calculation of  $C_{imp}$  (and RECI) necessitates the use of a phytometer species. The problem then arises as to which phytometer to use. The competitive ability and stress tolerance of the phytometer will

influence the relationship between  $C_{int}$  and  $C_{imp}$  and the productivity gradient. For example a phytometer with a high competitive ability and low stress tolerance will show a sizable change in  $C_{imp}$  because of a large change in  $P_{(T-N)}$ . In addition there is the choice of native and non native, common versus rare or large versus small phytometers. Some studies have used species that are native to the communities investigated (Pugnaire and Luque 2001), but this is not always possible, for example if the study covers a wide range of environments. However, the factors reducing the success of a non native phytometer within a community may be different to those acting upon a native that has already adapted (at least to some extent) to that environment. Perhaps the choice of phytometer should be related to the question under consideration. If we are interested in the pressures currently acting within a community we should consider using a native phytometer, if one with sufficiently broad ecological amplitude is available. Alternatively if we are interested in the forces to which native species have already adapted, i.e. “the ghost of competition [or environment] past” (Connell 1980, our insert), perhaps a non-native would be appropriate. The response will be phytometer specific, and should be interpreted accordingly. However, this is not necessarily a problem. It is likely to be the case that the genuine relationship between the role of competition and environmental gradients will, to some extent, be species-specific. What we need to do is consider enough species and gradients to detect higher-level generic patterns. This is best achieved by using a phytometer as it enables us to make standardized relative comparisons.

### Advantages and limitations of competition indices

Before exploring the use and characteristics of  $C_{int}$  and  $C_{imp}$ , it is necessary to mention two areas of debate surrounding this type of analytical tool. First, there has been recent general criticism of the use of indices in ecological research. Many indices such as  $C_{imp}$  and  $C_{int}$  can be classified as ratios, and all ratios are limited in their suitability for standard statistical analysis (Jasienski and Bazzaz 1999). However, if the sample size is sufficient (i.e.  $n > 5$ ) ratios can be rigorously tested by means of randomisation tests (Manly 1997, Fortin and Jacquez 2000). In addition randomisation tests have proved to be effective in analysing other nonratio indices that are difficult to test by standard statistical methods, for example for spatial distribution (Roxburgh and Matsuki 1999) and community structure analyses (Wilson and Roxburgh 2001, Kikvidze and Ohsawa 2002).

Second, Freckleton and Watkinson (1997a,b, 1999) discuss potential problems specific to competition indices. They state that such indices are inherently flawed because they do not allow the partitioning of the components of any competitive (or facilitative) impact of neighbor plants on the target individual into interspecific and intraspecific competition. Therefore, when competition is found to vary along a gradient, be it either change in  $C_{int}$  or  $C_{imp}$ , it is impossible to tell whether this change is due to an absolute change in the amount of competition experienced, or to a change in the relative equivalence of neighboring species. However it has been counter-argued that, despite these problems, the RCI (and implicitly the RNE) still provide a reasonable measure of net interactive effects and that the alternative response surface analysis is impossible (or at least beyond the practicable) in field experiments (Markham 1997, Peltzer 1999). The aim of this paper is not to attempt to resolve this debate. Although any index represents an integration and simplification of a variety of processes, indices are an easily applied and therefore popular method of expressing plant interactions. As long as they are used, and importantly as long as researchers refer to the large body of literature that has already developed using them, we must be able to clearly differentiate between  $C_{int}$  and  $C_{imp}$ .

### Applying the new index

We have argued that ignoring the distinction between  $C_{imp}$  and  $C_{int}$  has led to confusion over the role of competition across productivity gradients, and that arguments surrounding  $C_{imp}$  have not been properly addressed because of the use of indices that actually measure  $C_{int}$  (Reader et al. 1994). We re-analyzed the data of Reader et al. (1994; data taken directly from Fig. 1) for the phytometer *Poa pratensis* to calculate  $C_{int}$  and  $C_{imp}$  using the indices proposed above, with growth rate of plants in the most productive environment in the absence of neighbors as our fixed reference point ( $MaxP_{T-N}$ ). We found that although  $C_{int}$  showed no response to system productivity (as shown by Reader et al. in their plot of  $CI_b$ , Fig. 2A),  $C_{imp}$  declined with decreasing system productivity supporting the predictions of Grime (Fig. 2B).

However, the relationship between  $C_{imp}$  and  $C_{int}$  found for *Poa pratensis* will not necessarily be the same for other phytometers or other systems. For example, Pugnaire and Luque (2001) examined the interactions between *Artemisia barrelieri* (the target species) and *Retama sphaerocarpa* shrubs (the neighbor matrix) along an environmental severity gradient in semi-arid southeast Spain. Re-analysing their data (F. Pugnaire, pers comm.) we find that both the intensity and importance of competition were related to system

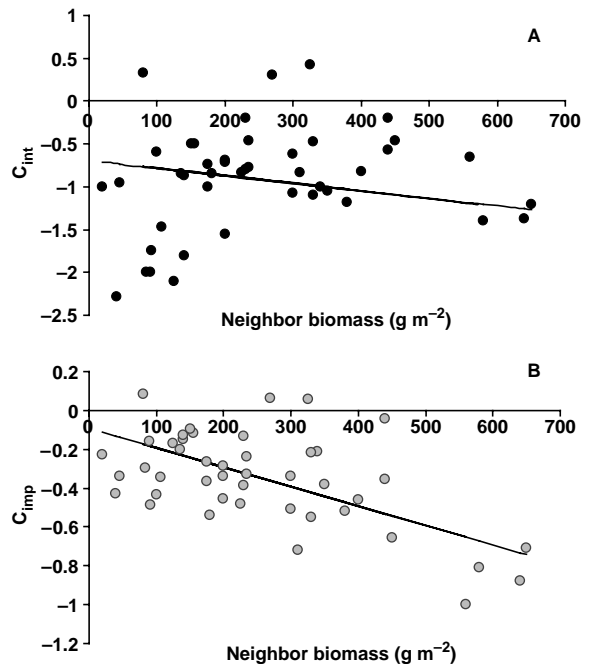


Fig. 2. (A) Competition intensity  $C_{int}$  and (B) competition importance  $C_{imp}$  vs neighbour biomass ( $g\ m^{-2}$ ) recalculated from the data of Reader et al. (1994, Fig. 1). Fitted lines show results of generalised linear mixed model analysis performed using the MIXED procedure SAS version 8.0 (SAS Institute 1999).  $C_{int} = -0.00088\ neighbor\ biomass - 0.6957$ ,  $F_{1,39} = 2.76$ ,  $P = 0.1047$ .  $C_{imp} = -0.00100\ neighbor\ biomass - 0.09264$ ,  $F_{1,42} = 27.32$ ,  $P < 0.0001$ . Site was specified as a random effect, degrees of freedom were calculated using the Satterthwaite option, and data normality was tested using the UNIVARIATE procedure.

productivity (in this case indicated by  $P_{T-N}$ ) with decreasing intensity and importance of competition (and increasing importance and intensity of facilitation) with reduced system productivity (Fig. 3). In this case, in contrast to the Reader et al. data set, both  $C_{int}$  and  $C_{imp}$  were strongly correlated to system productivity. These examples demonstrate that the relationship between  $C_{int}$  and  $C_{imp}$  across productivity gradients may not be constant and, as Welden and Slauson stated, competition intensity and importance need not be correlated.

Calculation of  $C_{int}$  and  $C_{imp}$  depends on two common factors, the success of plants in the removal and control treatments ( $P_{T-N}$  and  $P_{T+N}$ ). Therefore we might expect in some circumstances for  $C_{imp}$  and  $C_{int}$  to be closely related. We can explore this relationship visually by constructing a hypothetical, illustrative model system where the values of  $P_{T-N}$  and  $P_{T+N}$  range freely between 0 and 10. We can then calculate  $C_{imp}$  and  $C_{int}$  for this range of  $P_{T-N}$  and  $P_{T+N}$  values and examine the relationship between  $C_{imp}$  and  $C_{int}$  by plotting  $C_{imp} - C_{int}$  (an indication of the degree to which the

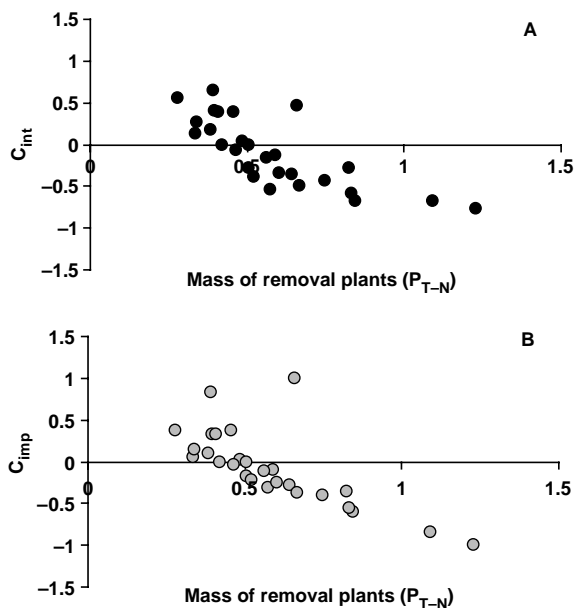


Fig. 3. (A)  $C_{int}$  and (B)  $C_{imp}$  experienced by *Artemisia barrelieri* due to the presence of *Retama sphaerocarpa* vs mass of *A. barrelieri* plants without neighbours ( $P_{T-N}$ ; used here as an index of system productivity in the absence of information on system neighbour biomass) recalculated from Pugnaire and Luque (2001), data from F. Pugnaire (pers. comm.). The Pearson correlation coefficient between  $C_{imp}$  and  $P_{T-N}$  is  $-0.74$ ,  $P < 0.001$ , and between  $C_{int}$  and  $P_{T-N}$  is  $-0.77$ ,  $P < 0.001$ ,  $N = 27$  in both cases, (SAS version 8.0, SAS Institute 1999).

two indices diverge) against our range of  $P_{T-N}$  and  $P_{T+N}$  values (Fig. 4).

With this approach we can see that, across our range of  $P_{T-N}$  and  $P_{T+N}$  values, there are two lines of equality between the two indices. First, and somewhat trivial, the difference between them is 0 when both are themselves equivalent to 0 (i.e. when  $P_{T-N} = P_{T+N}$ ). Second, they converge when the sum of  $P_{T+N} + P_{T-N} = \text{Max}P_{T-N}$ . This means that in some natural environments it is possible to find conditions where  $C_{imp} = C_{int}$ . If removal experiments are conducted where such a balance between  $C_{int}$  and  $C_{imp}$  occurs, we would conclude that  $C_{int}$  and  $C_{imp}$  were equivalent. Elsewhere on the response surface  $C_{int}$  and  $C_{imp}$  diverge markedly, again reinforcing the message of Welden and Slauson that competition intensity and importance need not be correlated.

A mathematical analysis of the equations for  $C_{int}$  and  $C_{imp}$  demonstrates the same points. In situations of competition and facilitation respectively:

$$C_{imp} = C_{int} \times (P_{T-N} / (\text{Max}P_{T-N} - P_{T+N})) \quad (3)$$

$$C_{imp} = C_{int} \times (P_{T+N} / (\text{Max}P_{T-N} - P_{T-N})) \quad (4)$$

therefore  $C_{int} = C_{imp}$  when  $P_{T+N} + P_{T-N} = \text{Max}P_{T-N}$ , and when  $C_{int} = 0$ , corresponding to the two lines of convergence visible on the response surface plot (Fig. 4).

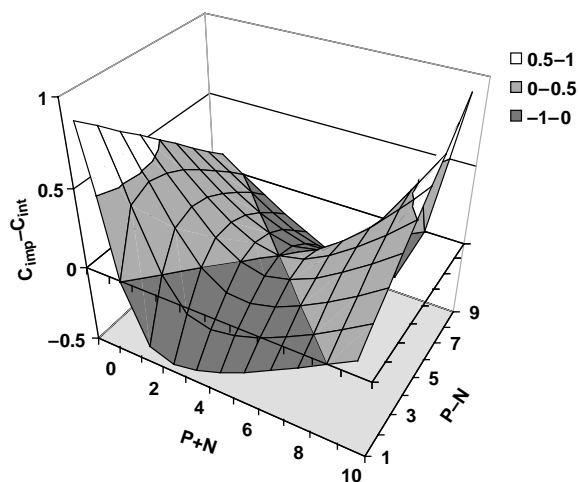


Fig. 4. The impact of changes in the performance of hypothetical target plants both with and without neighbors ( $P_{T+N}$  and  $P_{T-N}$  respectively) on  $C_{imp} - C_{int}$ , the difference between the importance of competition ( $C_{imp}$ ) and the intensity of competition ( $C_{int}$ ). The figure has been drawn using values of  $P_{T+N}$  from 0 to 10 and  $P_{T-N}$  from 1 to 9 thus avoiding the trivial situations where either  $C_{int}$  or  $C_{imp}$  equate to infinity (when  $P_{T+N}$  and  $P_{T-N}$  both equal either 0 or 10 respectively). See text for full details.

We can test this proposed relationship between  $C_{int}$  and  $C_{imp}$  by using the data of Reader et al. (1994). A simple statistical summary of these data shows that the mean  $P_{T+N}$  (0.0022) is almost an order of magnitude less than the mean  $P_{T-N}$  (0.0221), while the coefficient of variance (CV) shows that  $P_{T-N}$  (CV=0.56) is almost 8 times less variable than  $P_{T+N}$  (CV=4.5). From this we can conclude that, in these experiments, neighbors compete intensely with the phytometer along most of the gradient. Therefore  $x \approx P_{T-N}$  (Eq. 1) and  $y \approx P_{T+N}$  (Eq. 2). The following predictions can then be inferred:

1. Because  $C_{int} = (P_{T+N} - P_{T-N}) / P_{T-N} = P_{T+N} / P_{T-N} - 1$ , and because  $P_{T-N}$  is practically constant relative to  $P_{T+N}$ , we can hypothesize that  $C_{int}$  approximates a simple linear function of  $P_{T+N}$ :

$$C_{int} = P_{T+N} / \text{Mean } P_{T-N} - 1 = P_{T+N} / 0.021 - 1;$$

2. Because  $C_{imp} = (P_{T+N} - P_{T-N}) / (\text{Max}P_{T-N} - P_{T+N})$ , and because  $P_{T+N}$  in fact is of a negligibly small value relative to  $P_{T-N}$ , we can hypothesize that  $C_{imp}$  approximates a simple linear function of  $P_{T-N}$ :

$$C_{imp} = P_{T-N} / -P_{T-N\text{max}} = P_{T-N} / -0.057 - 0.$$

Using the same data set, there is a highly significant relationship between  $C_{int}$  and  $P_{T+N}$  ( $C_{int} = 35.34P_{T+N} - 1.021$ ,  $F_{1,42} = 56.18$ ,  $P < 0.001$ , Fig. 2 for details of analysis). The reciprocal value of the slope  $1/45.34 = 0.021 =$  the mean  $P_{T-N}$ , and the intercept =  $-1.021$ . Therefore the observed response of  $C_{int}$

approximates closely the predicted response of  $P_{T+N}/\text{mean}P_{T-N} - 1$ , and the first of our predictions is supported. Second, the strength of the relationship between  $C_{\text{imp}}$  and  $P_{T-N}$  is also very high ( $C_{\text{imp}} = 19.32P_{T-N} - 0.075$ ,  $F_{1,41} = 292.66$ ,  $P < 0.001$ , see Fig. 2 for details of analysis). In this instance the reciprocal value of the slope  $1/19.32 = 0.052 \approx \text{Max}P_{T-N}$ ; at the same time the intercept does not differ significantly from 0 ( $P = 0.073$ ). This means that the response of  $C_{\text{imp}}$  very closely approximates the ratio  $P_{T-N}/\text{Max}P_{T-N}$  thus confirming the second prediction. These simple tests indicate that our predicted relationships between  $C_{\text{int}}$  and  $C_{\text{imp}}$  hold true for one of the most extensive and important data sets in the literature.

The linear models obtained from our calculations contain a great deal of information about the  $C_{\text{imp}}$  and  $C_{\text{int}}$  indices. The first model indicates that under strong competition, as in the Reader et al. data set,  $C_{\text{int}}$  depends linearly on the performance of the control plants ( $P_{T+N}$ ). This is not an unexpected result, but the high goodness-of-fit tells us that the model works well. For the second model it is interesting to note that the ratio  $P_{T-N}/\text{Max}P_{T-N}$  is an indicator of the severity of the abiotic environment (more precisely the relative severity of the environment without neighbors). Consequently, the second model demonstrates that  $C_{\text{imp}}$  depends linearly on severity level, an important conclusion for the abiotic stress productivity models for competition (Grime 1979) and for competition and facilitation (Bertness and Callaway 1994). This conclusion is particularly important for variants of these conceptual models that assume linearity in relations between stress and the importance of plant–plant interactions (Brooker and Callaghan 1998, Corcket et al. 2003).

Abiotic severity is closely related to ecosystem productivity, so we can predict that the ratio  $P_{T-N}/\text{Max}P_{T-N}$  is linearly related to standing biomass. Indeed, neighbor biomass in the data of Reader et al. (1994) is significantly related to the ratio  $P_{T-N}/\text{Max}P_{T-N}$  ( $P_{T-N}/\text{Max}P_{T-N} = 0.000864 \times \text{neighbor biomass} + 0.1640$ ,  $F_{1,42} = 27.19$ ,  $P < 0.001$ , see Fig. 2 for details of analysis). This also explains the linear relationship between  $C_{\text{imp}}$  and biomass (Fig. 2B) but the lack of correlation between  $C_{\text{int}}$  and biomass (Fig. 2A). Of crucial importance is that these statistical relationships demonstrate that the choice of index will strongly affect theoretical conclusions drawn from a given set of experimental data.

In summary our reanalysis of the data of Reader et al. has highlighted several key points. Most importantly we have shown that competition intensity shows no relationship to the productivity gradient (supporting Newman 1973, Tilman, 1982, 1987, 1988, Grubb 1985), but competition importance linearly increases (in absolute values) with productivity (thus supporting Grime 1979, Huston 1979, Keddy 1989) and apparently

with a decrease in abiotic severity (supporting Bertness and Callaway 1994, Brooker and Callaghan 1998, Corcket et al. 2003). This is in contrast to the conclusions that were originally drawn from analysis of this data. This reanalysis suggests that the models of Grime and Tilman may not always be in opposition; at a basic level they are asking questions about two quite different aspects of the role of competition in plant communities and both models can be supported by the same set of data, as long as the appropriate and relevant analysis is applied.

In addition this reanalysis has shown that the relationship between competition intensity and importance may differ in different systems, as shown by the contrasting results from Reader et al. (1994) and Pugnaire and Luque (2001). Future research in this field may therefore benefit from firstly application of the phytometer approach which will enable the calculation of  $C_{\text{imp}}$  as well as the more commonly calculated  $C_{\text{int}}$  (whilst bearing in mind the caveats associated with this approach as discussed earlier), secondly studies that enable a comparison of severity or productivity relationships with plant interactions in multiple environments and with multiple phytometers (thus enabling us to examine the generality of relationships and the impact of environmental drivers upon them), and thirdly greater caution and clarity when discussing the role of competition in plant communities.

## Conclusions

One of plant ecology's most intense and protracted debates is fuelled by a misinterpretation of models and misapplication of analytical approaches. In order to resolve this debate we reanalyzed a key published data set and illustrated how a different analytical approach sheds new light on the role of competition in plant communities. Our reanalysis suggests that, in this study, Grime's hypothesis was incorrectly rejected. However, other species and other systems will require their own analysis and model fitting. Once ecologists have examined many different phytometer species on different environmental gradients general statements on the relationship of both the intensity and importance of plant interactions to productivity and environmental stress will be possible. We have demonstrated here that by using simple but relevant indices to summarize the outcome of interactions, we can move the debate away from semantics to the original aims of the exploration of competition as a driving force in nature.

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