

## FORUM

# Importance: an overlooked concept in plant interaction research

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## Summary

1. Numerous approaches have been taken to analysing the relationship between plant interactions and environmental severity. Considerable debate surrounds this relationship and its implications for the evolution of plant strategies and traits. This debate is commonly associated with the names of two of its main protagonists: Grime and Tilman.

2. However, because researchers often fail to make explicit the distinction between two concepts – the importance and intensity of competition – they perpetuate this debate. To illustrate this point we discuss a new approach to examining plant interactions across gradients proposed by Wilson.

3. We support the main thrust of Wilson's work – improving the information provided by interaction indices. However, we highlight what we believe to be an oversight in Wilson's Discussion: the proposal that his new indices can shed light on the Grime–Tilman debate. We argue that this is not possible as Wilson's indices measure competition *intensity* (competition's absolute impact), whereas Grime's theories relate to competition *importance* (competition's relative impact).

4. We support our argument through re-analysis of the data explored by Wilson, demonstrating that the relationships between competition importance, competition intensity, Wilson's new indices and biomass (a surrogate of productivity) are both complex and variable.

5. Wilson's discussion is part of a body of literature that overlooks the distinction between competition importance and intensity. We examine a number of other well-known studies, demonstrating how this oversight and associated confusion are widespread, may have originated with the concept's original source, and unnecessarily perpetuate debate.

6. *Synthesis.* The concepts of competition intensity and importance are central to resolving key ecological debates, but are still overlooked in contemporary research. Their uptake and careful application would greatly aid advances in plant ecology.

**Key-words:** competition importance and intensity, evolution, Grime–Tilman debate, indices, plant communities, plant competition, plant interactions, productivity, stress, theory

## Introduction

Plant ecologists have invested considerable effort in understanding how the role of competition varies under changing environmental conditions (Goldberg *et al.* 1999). A complicating factor is competition's multi-faceted nature. It can be, for example, either intra- or interspecific, and can operate at the individual- or population-level. Given its complexity it is not surprising that researchers have intensely debated the relevance of different aspects of competition to particular theories, and the optimum approach to measuring competition.

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One debate in particular is being prolonged by the use of inappropriate approaches to measuring competition (Grace 1991; Brooker *et al.* 2005; Grime 2007). This debate is commonly known by the names of two of its main protagonists, Grime and Tilman (for a summary, see e.g. Goldberg *et al.* 1999; Brooker *et al.* 2005). A critical omission from many studies addressing this debate has been a clear distinction between the concepts of the intensity and importance of competition. The intensity of competition is its absolute impact, whereas the importance of competition is its impact relative to that of all the factors in the environment that influence plant success (Welden & Slauson 1986). Although it has been reasonably argued that Grime's theories concern the importance of competition and Tilman's its intensity (see e.g. Grace 1991),

the concept of competition importance is still frequently overlooked. This leads to widespread confusion within the ecological literature including, for example, the misapplication to the theories of Grime of analytical techniques that examine competition intensity.

In order to highlight this issue we look in particular at the recent paper by Wilson (2007). Wilson's work contains many interesting ideas, but it is also illustrative of this ongoing problem. First, we set out Wilson's new ideas and their research context: the need to develop more detailed indices of plant interactions. We then examine some of the proposed implications of this work, in particular the relevance of these new indices to the Grime–Tilman debate. Using a re-analysis of the data explored by Wilson, and examples from related studies, we illustrate our primary point: plant ecologists are not grasping the simple and useful concept of competition importance.

### Refined interaction indices: a holy grail for plant ecologists?

A common experimental design for assessing competition in plant communities is neighbour removal, which is often associated with the use of interaction indices for data analysis. Numerous interaction indices exist (see Weigelt & Jolliffe 2003 for a review) but they have been criticized for examining only the net outcome of interactions and masking underlying processes, especially with respect to examining changes in interactions along environmental gradients (Freckleton & Watkinson 1997, 1999, 2001; Watkinson & Freckleton 1997). As an alternative approach Freckleton & Watkinson (1999, 2001) focus on nonlinear regression models as originally proposed by Law & Watkinson (1987). However, in multi-species systems this method is difficult to apply (Markham 1997; Peltzer 1999), although some researchers have done so (Rees *et al.* 1996; Law *et al.* 1997).

Ideally we would have an approach that combines the refinement of output from nonlinear regression modelling with the ease of application of interaction indices. The recent paper by Wilson (2007) appears to bridge this gap by providing an index-based but 'valid method to track the effects of changing habitat conditions on the components of competition'.

To overcome some of the limitations of commonly used indices Wilson proposes two new ones:  $D_r$  (relative crowding) and  $I$  (interaction strength). They are derived independently, but when multiplied produce the commonly-used index relative competition intensity,  $CI_r$  (Grace 1993). Hence they 'break down' net competition into two subcomponents:

$$CI_r = \frac{y_{\text{iso}} - y_{\text{mix}}}{y_{\text{iso}}} = \frac{z_{\text{mix}}}{y_{\text{iso}}} \times \frac{y_{\text{iso}} - y_{\text{mix}}}{z_{\text{mix}}} = D_r I \quad (\text{eqn 1})$$

Here we use the same symbols as Wilson:  $y_{\text{iso}}$  and  $y_{\text{mix}}$  are performance of target plants without and with neighbours, respectively, and  $z_{\text{mix}}$  is neighbour biomass;  $D_r = z_{\text{mix}}/y_{\text{iso}}$  and  $I = (y_{\text{iso}} - y_{\text{mix}})/z_{\text{mix}}$ .

Wilson's paper focuses on explaining how these indices are derived and function. However, it is not the derivation of the

indices that we wish to consider in detail here. Instead, we wish to examine their application as proposed in Wilson's Discussion, in particular their relevance to the Grime–Tilman debate. We feel that by overlooking the concept of competition importance, Wilson's Discussion section perpetuates this debate. We will now explore this point in more detail.

### Indices of intensity and questions of importance

At the start of his Discussion (p. 306), Wilson notes the following:

'Treatments [or studies?] of plant species interactions along habitat gradients have focused on the effect of productivity or biomass changes on patterns of competition intensity ... One school of thought holds that competition increases as productivity increases; another believes that although the type of resource [for which species compete?] shifts along the productivity gradient, competition intensity remains unchanged (Grace 1991). The method of measuring competition intensity – for example absolute competition intensity ( $CI_a$ ) vs. relative competition intensity ( $CI_r$ ) – can influence which view is supported ... The more biologically meaningful indices of relative crowding ( $D_r$ ) and interaction strength ( $I$ ) shed new light on these conflicting views.'

Wilson is referring to the Grime–Tilman debate. However, Wilson overlooks the critical distinction between the importance and intensity of competition. Consequently, Wilson's Discussion suggests that his new indices can shed light on the Grime–Tilman debate, whereas his new indices in fact measure competition *intensity* rather than *importance*, and as such may not be applicable to testing the theories of Grime.

To explain in more detail, competition importance (hereafter  $C_{\text{imp}}$ ) can be quantified based on the classic model of Welden & Slauson (1986; Brooker *et al.* 2005). Here we present the equation for  $C_{\text{imp}}$  in a slightly modified form:

$$C_{\text{imp}} = C_{\text{int}} \times \frac{y_{\text{iso}}}{Y_{\text{max}} - y_{\text{mix}}} \quad (\text{eqn 2})$$

where  $C_{\text{int}} = CI_r$  (relative competition intensity),  $Y_{\text{max}}$  is the maximum performance of the isolated target plant observed at the optimum point for growth on the gradient, and  $y_{\text{iso}}$  and  $y_{\text{mix}}$  are performance of target plants without and with neighbours, respectively. This equation shows that  $C_{\text{imp}}$  is a product of competition intensity  $C_{\text{int}}$  and a function  $y_{\text{iso}}/(Y_{\text{max}} - y_{\text{mix}})$ , the latter scaling the impact of competition relative to the overall impact of the environment. The new indices proposed by Wilson are therefore essentially subcomponents of  $C_{\text{int}}$ , whereas it is the measurement of  $C_{\text{imp}}$  that is relevant to the theories of Grime.

It may be, however, that the effect of this scaling is actually relatively small. If the new indices correlate closely with  $C_{\text{imp}}$ , and thus respond in a similar manner to changes in severity or productivity, they might be used to address Grime's theories. We can examine this empirically by re-analysing the three classic data sets used by Wilson to explore his indices (Reader

**Table 1.** Correlations between measures of biomass (standing crop) and competition indices as calculated from three data sets – Belcher *et al.* (1995), Kadmon (1995) and Reader *et al.* (1994). Transformations are the same as those used in the original work. Data shown are Pearson correlation coefficients and their associated significance values, except for analysis of relationships with biomass in the Belcher *et al.* data, where Spearman Rank correlations are used. Bold figures show a significant relationship, and trends ( $P < 0.10$ ) are shown in italics. Correlations were undertaken using STATISTIX 8 (Analytical Software, Tallahassee, FL)

Belcher <i>et al.</i> (1995)				
	Biomass (g 0.0625 m <sup>-2</sup> )	$C_{imp}$	$C_{int}$	$D_r$
$C_{imp}$	0.1947 <i>P</i> = 0.3693			
$C_{int}$	0.2374 <i>P</i> = 0.2726	0.4795 <b><i>P</i> = 0.0206</b>		
$D_r$	0.5672 <b><i>P</i> = 0.0054</b>	-0.3387 <i>P</i> = 0.1139	-0.1213 <i>P</i> = 0.5813	
$I$	0.1285 <i>P</i> = 0.5546	0.9609 <b><i>P</i> &lt; 0.0001</b>	0.4765 <b><i>P</i> = 0.0215</b>	-0.2617 <i>P</i> = 0.2276
Kadmon (1995)				
	Biomass (g m <sup>-2</sup> ) log-transformed	$C_{imp}$	$C_{int}$	$D_r$
$C_{imp}$	0.6552 <b><i>P</i> = 0.0207</b>			
$C_{int}$	0.7821 <b><i>P</i> = 0.0026</b>	0.5360 <i>P</i> = 0.0725		
$D_r$	0.7027 <b><i>P</i> = 0.0108</b>	0.2333 <i>P</i> = 0.4656	0.4158 <i>P</i> = 0.1788	
$I$	-0.6222 <b><i>P</i> = 0.0307</b>	-0.2445 <i>P</i> = 0.4437	-0.0800 <i>P</i> = 0.8048	-0.4989 <i>P</i> = 0.0987
Reader <i>et al.</i> (1994)				
	Biomass (g m <sup>-2</sup> )	$C_{imp}$	$C_{int}$	$D_r$
$C_{imp}$	0.3590 <b><i>P</i> = 0.0167</b>			
$C_{int}$	-0.0489 <i>P</i> = 0.7528	0.2456 <i>P</i> = 0.1081		
$D_r$	0.4440 <b><i>P</i> = 0.0025</b>	-0.4153 <b><i>P</i> = 0.0051</b>	-0.0114 <i>P</i> = 0.9413	
$I$	-0.4731 <b><i>P</i> = 0.0012</b>	0.2189 <i>P</i> = 0.1535	0.3824 <b><i>P</i> = 0.0104</b>	-0.4099 <b><i>P</i> = 0.0057</b>

*et al.* 1994; Belcher *et al.* 1995; Kadmon 1995). These studies looked at the effects of competition across productivity gradients (with biomass/standing crop acting as a surrogate for productivity), using as response variables above-ground biomass of target plants (Belcher *et al.* 1995), seed production (Kadmon 1995) and relative growth rate (Reader *et al.* 1994). To examine the relationship between the new indices and  $C_{imp}$ , and hence whether the new indices can test Grime's theories, we calculated all four indices ( $C_{imp}$ ,  $C_{int}$ ,  $D_r$  and  $I$ ) and these indices' correlations both with one-another and with biomass of neighbouring plants (standing crop) using the data sets analysed by Wilson.<sup>1</sup>

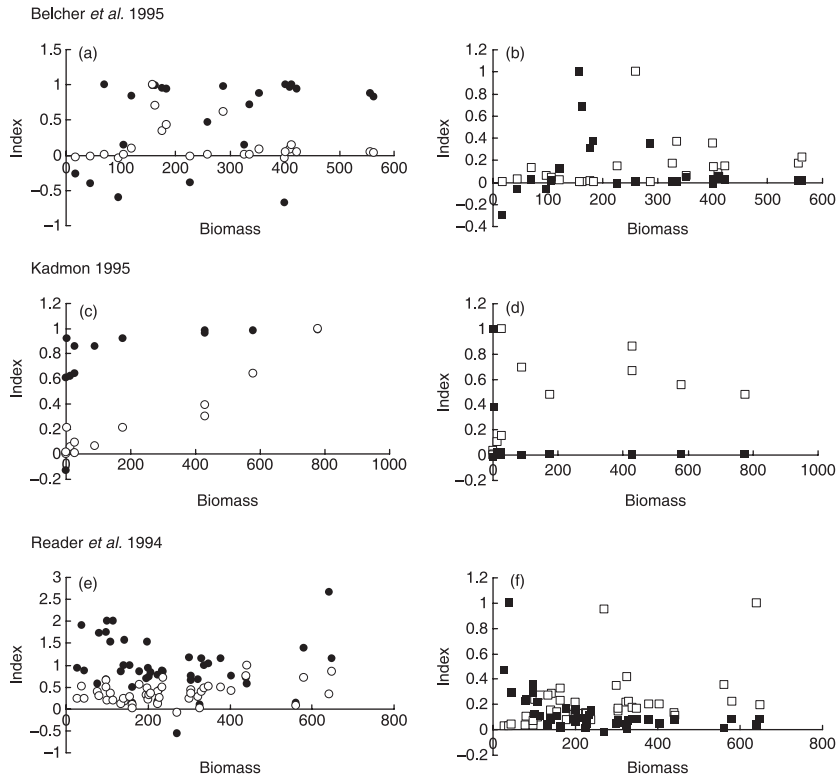
The relationships that we find between neighbour biomass and  $D_r$ ,  $I$  and  $C_{int}$  (=  $CI_r$ ) are similar to those found by Wilson (Table 1, Fig. 1f; Table 2 of Wilson 2007). However, our

<sup>1</sup> In these analyses, we use the data provided at <<http://esapubs.org/archive/ecol/E080/006/>> for both the Kadmon (1995) and Reader *et al.* (1994) studies, as used by Wilson (2007). It should however be noted that there appear to be substantial discrepancies between the data provided in this archive, and fig. 1 of Reader *et al.* (1994), which is supposedly plotted from the same data (and which was used as the basis for re-analysis by Brooker *et al.* 2005). Data for Belcher *et al.* (1995) were obtained from this paper's appendix.

additional analyses demonstrate the complexity of the relationships between these indices, biomass and  $C_{imp}$ . The only relationship which is consistent in all three studies is the positive correlation of  $D_r$  and biomass, suggesting that neighbour biomass per unit area consistently increases at a faster rate than the mass in isolation ( $y_{iso}$ ) of the target plant. In contrast, the relationships between the other indices and biomass, and between the indices themselves, show considerable variation between studies.

In the study of Belcher *et al.*  $C_{imp}$  is positively correlated with  $C_{int}$  and  $I$ , but not with  $D_r$ ;  $D_r$  is the only index correlated with biomass. Both  $C_{imp}$  and  $I$  peak at low-to-intermediate biomass (Fig. 1a,b). At higher biomass other factors, for example, an increasing impact of facilitation in these water-limited systems (Brooker *et al.* 2008), may be limiting the role of competition. Consequently, although  $D_r$  continues to increase with biomass, both  $I$  and  $C_{imp}$  decline. Alternatively it may be that biomass is a poor surrogate for productivity. If  $C_{imp}$  is related to productivity, whilst  $D_r$  is related to biomass, a peak of productivity at intermediate levels of biomass will mean that  $C_{imp}$  will not change in a similar manner to  $D_r$  with increasing biomass.

In the study by Kadmon, none of the indices are inter-correlated but all respond to biomass (Fig. 1c,d), although there are trends



**Fig. 1.** Relationships between biomass (standing crop) and four indices of plant interactions  $C_{imp}$  and  $C_{int}$  (a, c and e, open and closed circles, respectively) and  $D_r$  and  $I$  (b, d and f, open and closed squares, respectively) as calculated from three data sets: Belcher *et al.* (1995; a and b), Kadmon (1995; c and d) and Reader *et al.* (1994; e and f). In all cases neighbour biomass is in  $g\ m^{-2}$  (calculated from  $g\ 0.0625\ m^{-2}$  for the Belcher *et al.* data). For presentation purposes values of  $D_r$  and  $I$  are normalized between  $-1$  and  $1$ , whilst raw data were used for analysis of correlations (Table 1).

( $P < 0.10$ ) towards a negative relationship between  $D_r$  and  $I$ , as noted by Wilson, and towards a positive relationship between  $C_{int}$  and  $C_{imp}$ . However, in contrast to the gradual increase of  $C_{imp}$ ,  $C_{int}$  appears to be comparatively high at all biomass levels. This demonstrates that under certain circumstances although competition can be very intense its importance may be relatively low, as supported by recent theoretical and empirical work (Brooker *et al.* 2005; Lamb & Cahill in press).

In the study of Reader *et al.*  $C_{imp}$ ,  $D_r$  and  $I$  are again related to biomass. As highlighted by Wilson, increases in  $D_r$  are counterbalanced by decreases in  $I$  such that  $C_{int}$  shows no response to biomass (Fig. 1e,f). Neither  $I$  nor  $C_{int}$  are related to  $C_{imp}$ , and although both  $D_r$  and  $C_{imp}$  are both positively related to biomass, they are themselves negatively correlated. In this instance none of the other indices would give a clear indication of the response of  $C_{imp}$  to neighbour biomass.

It is not clear why there is such variation between these three studies in the response of the indices to biomass or the relationships between indices. It may be a consequence of differences in the drivers of biomass, the target species or the response variables. Application of the new indices in multiple systems may enable us to elucidate the causes of this variation, and thus generalities and pattern in the response of interactions to environmental drivers. Furthermore, we acknowledge that  $C_{imp}$  used in isolation can also mask underlying detail. With respect to our main argument, however, its application here enables us to see that in these data there is no consistent relationship between  $C_{imp}$  and  $C_{int}$ ,  $I$  or  $D_r$ , or their response to biomass. Given that it is the assessment of  $C_{imp}$ —competition importance—which is relevant

to Grime's theories (by placing the impact of competition within a wider environmental context), the inconsistencies in these relationships clearly illustrates our point that the new indices cannot be used to address Grime's theories. The new indices measure subcomponents of competition intensity, and when applied to 'real-world' data do not give an accurate representation of the response of competition importance to environmental drivers.

### Widespread confusion produces continued debate

Oversight of the concept of competition importance and subsequent misapplication of particular analytical techniques to the concepts of Grime are not uncommon in the ecological literature. For example, Wilson aims to address similar issues to those raised by Freckleton and Watkinson, yet Freckleton and Watkinson themselves do not distinguish between competition importance and intensity in a manner consistent with Welden & Slauson (1986). For example, Freckleton & Watkinson (2001) provide definitions of competition importance and intensity citing Welden & Slauson (1986), yet they attach competition importance to the effects of competition at the population-level, whilst competition intensity is considered to be the effect of competition at the individual-level. Although Welden and Slauson distinguish responses at the population- and individual-levels, they explicitly show the need to incorporate the overall impact of the environment for assessing competition importance, and give a specific model for its quantification (Fig. 1 in Welden & Slauson 1986; see also Brooker *et al.* 2005).

A close examination of Welden & Slauson's (1986) paper may highlight the original source of this confusion. They state (p. 35) 'Some experiments measure the importance of competition if the responses monitored are population-level effects ... or higher-level effects' and 'In contrast, some field experiments measure transient physiological states of the organisms, and thus address intensity of competition, not its importance'. This matches the definitions of Freckleton & Watkinson (2001), but contradicts the majority of what Welden and Slauson write in their paper. For example elsewhere Welden and Slauson calculate competition importance using data on transient physiological states at the individual-level taken from a study by Fonteyn & Mahall (1981). Furthermore, and as repeatedly highlighted by Welden and Slauson, even if you can demonstrate a population-level effect of competition, it remains a measure of competition intensity if you fail to place that effect within the context of population-level effects from other sources.

Perhaps as a result of the inconsistencies in Welden and Slauson's paper, or perhaps because of the general oversight of its central concepts, a clear distinction between competition importance and intensity is commonly missing in studies of plant competition, leading to continued confusion and a lack of clarity in debate. For example, Rees *et al.* (1996) criticize Grime's theory on the grounds that they find evidence for the impact of competition within an apparently stressful environment. However, as Grime (2001) points out, such an interpretation misses the point – simply finding evidence of competition is not the same as assessing the role of competition relative to other factors within the environment. More recently Craine (2005) also criticizes Grime by arguing that competition plays a role in determining success within resource-poor environments. Grime (2007) replies that Craine's criticism 'abandons the classic distinction of Welden & Slauson (1986) between the ultimate and proximal determinants' of success, suggesting that Craine's approach is 'contentious in the extent to which, following Tilman (1982, 1988), it continues to place competition exclusively centre-stage in its search for primary plant strategies'. Craine (2007) replies 'It is clear the concept of relative importance needs to be developed further'. Does it? Possibly so, but we argue that significant progress could be rapidly made and considerable debate avoided if researchers took on board the concept in its already well-developed state.

## Conclusions

We believe that the recent effort by Wilson in attempting to develop new plant interaction indices that account for recent criticisms of index-based approaches is a logical step forward: it would provide practicable approaches whose interpretation would not be open to debate. However, it seems that in his discussion of the relationship of these new indices to classic theories of plant competition he is continuing an unfortunate long-running tendency by overlooking the distinction between the importance and intensity of competition, and the opportunity that this distinction *already provides* for reconciling

apparently contradictory plant interaction theories. In the same way that failing to acknowledge the subcomponents of net interactions can lead to misinterpretation of results based on simple indices, a failure to acknowledge the distinction between the importance and intensity of competition will mean that we continue to misapply even more refined indices to particular issues. We would urge all plant ecologists to look closely at the work of Welden & Slauson (1986) and to bear in mind their concepts – and occasional inconsistencies – when considering key theories of plant interactions.

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