

FORUM

Towards a more exact definition of the importance of competition – a reply to Freckleton *et al.* (2009)

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Summary

1. Freckleton, Watkinson & Rees (2009) criticize a recent paper by ourselves in this journal (Brooker & Kikvidze 2008) as well as our earlier work on competition importance (Brooker *et al.* 2005). In response, here we clarify our ideas with the aim of defining more clearly the key points of scientific debate, specifically (i) the definition of the importance of competition and (ii) its measurement.
2. Freckleton, Watkinson & Rees (2009) interpret the classic paper by Welden & Slauson (1986) such that importance as a concept relates to long-term, population-level consequences of competition. However, we consider competition importance to be the proportional impact of competition relative to the overall impact of the environment, and our index C_{imp} expresses changes in competition importance – as defined by ourselves – along productivity gradients. We argue that our definition more accurately reflects the work of Welden & Slauson, as well as a more recent use of the concept (Grace 1991), which precedes the work of Freckleton & Watkinson (2001).
3. We highlight that C_{imp} was never proposed as a general index of competition importance, but is readily applicable in certain circumstances. Notably, our index and the approaches to measuring competition importance as set out by Freckleton, Watkinson & Rees (2009) are not unrelated.
4. We also discuss some recent additional responses to both our (2008) paper and that by Freckleton, Watkinson & Rees (2009), including applications of the concept of competition importance. Although the authors of these papers may not have used our index C_{imp} , they follow the same definitions for the overall concept of competition importance as ourselves.
5. *Synthesis.* We conclude that the complex topic of biotic interactions, including the specific issue of the importance of competition, invites a range of approaches. Importantly, these approaches can be complementary and not conflicting. Here, we propose what we see as a sensible resolution to the current debate concerning the definition of competition importance, a resolution which is backed by the original source article, literature precedent and current usage.

Key-words: biotic interactions, competition, competition importance, facilitation, indices, neighbour effects, plant interactions, population dynamics, productivity gradients, stress

Introduction

The importance of competition to an organism was originally defined as ‘the relative degree to which competition contributes to the overall decrease in growth rate, metabolism, fecundity, survival, or fitness of that organism below its optimal condition’ (Welden & Slauson 1986). This concept was largely overlooked, although Grace (1991, 1993) concluded that distinguishing the importance of competition from its intensity is critical for understanding the role of competition in structuring

plant communities and for handling some of the apparent contradictions in the long-running Grime–Tilman debate. Welden & Slauson (1986) had also discussed Grime’s (1977) work in relation to the concepts of competition importance and intensity, but Grace (1991, 1993) went further in explicitly proposing that Grime’s theories related to the importance of competition, whereas those of Tilman focused instead on its intensity.

Although several subsequent attempts were made to utilize the concept of competition importance, its experimental measurement appeared to be confused: some works claimed to address the Grime–Tilman debate, but employed quantitative

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tools that still measured – albeit in a variety of ways – the intensity of competition (see Brooker *et al.* 2005 and references therein). Brooker *et al.* (2005) suggested one possible option: using maximum performance of a phytometer, experimentally isolated from neighbour competition, as a reference for assessing changes in the relative impacts of competition and the overall environment along a productivity gradient. This resulting index, C_{imp} , was used by Brooker *et al.* to reanalyse a classic data set (Reader *et al.* 1994) to show that although competition importance (as measured using C_{imp}) increased with productivity, competition intensity did not change along this gradient, supporting the proposition that this distinction could reconcile conflicting views on the role of competition in structuring plant communities (Brooker *et al.* 2005; Grime 2007).

However, the utility of the concept of competition importance continued to be overlooked. For example, Wilson (2007) presented two new indices of competition – relative crowding (D_r) and interaction strength (I) – to provide ‘a valid method to track the effects of changing habitat conditions on the components of competition’. However, in discussing these new indices, Wilson (2007) suggested that one of their possible uses might be clarifying the Grime–Tilman debate. Brooker & Kikvidze (2008) assessed this specific proposal, examining these new indices and comparing them with C_{imp} , and concluded that they were measuring different components of competition *intensity* but not the *importance* of competition. They then went on to propose that this was indicative of a more general oversight or confusion in the plant competition literature concerning the concept and measurement of competition importance.

The Forum paper of Freckleton, Watkinson & Rees (2009) criticized the paper of Brooker & Kikvidze (2008), as well as our earlier work on the importance of competition (Brooker *et al.* 2005). Having outlined above the recent history of this debate, our aim here is to now respond to these criticisms. Importantly, we genuinely welcome discussion on this issue, as we believe the concept of competition importance is a useful one. Our view, as set out in our previous papers (Brooker *et al.* 2005; Brooker & Kikvidze 2008) is that there has been confusion about the concept and its link to the Grime–Tilman debate. If we have added to this confusion, then it is important that this problem is dealt with. In this article, we focus on what we believe to be the key points of scientific debate, specifically (i) the interpretation of Welden & Slauson’s (1986) work and (ii) the measurement of competition importance.

From here onwards, Freckleton *et al.* will be used to refer to Freckleton, Watkinson & Rees (2009).

Points for debate

INTERPRETATION OF WELDEN & SLAUSON (1986)

Interpretation of the work by Welden & Slauson is a critical component of this current discussion. Whether the C_{imp} index that we have developed can accurately measure competition importance or not is dependent on how competition

importance is defined. Freckleton *et al.*, when assessing our approach to the confusion surrounding competition importance, write:

“Brooker & Kikvidze [2008] do not provide a resolution [to this confusion] because they do not make the distinction between studies that focus on the outcome of competition on, say population growth rate, and those that focus on components of competition, and by accepting the arguments presented in Welden & Slauson (1986) too uncritically. ... the inconsistencies in Welden & Slauson (1986) preclude a meaningful interpretation of either the importance or intensity of competition”.

To Freckleton *et al.*, the examples given by Welden & Slauson ‘are unclear and even contradictory and we would caution against reading this paper uncritically’. Importantly, our (2008) paper specifically details this uncertainty, and we believe that it is the first paper to have done so, despite previous papers (including our own) utilizing the concept of competition importance and citing Welden & Slauson (1986).

Freckleton *et al.* go on to state that

“This contradiction [within the work of Welden & Slauson 1986] is pointed out by Brooker & Kikvidze (2008), but they do not attempt a resolution. To us the only logical way to resolve this contradiction is to regard within-generation competitive effects as being incapable of providing information about the importance of competition in broader terms. For instance, the information in Fig. 1 in Welden & Slauson (1986) (or Fig. 1 in Brooker *et al.* 2005) can only be used to measure the intensity of competition as it does not integrate processes operating across the whole life cycle via estimating population growth rate or fitness”.

It is true that we did not explicitly provide a resolution to the contradiction within the work of Welden & Slauson (1986). With hindsight we consider this a mistake, but at the time we did not believe it necessary. Within our work we have throughout taken a particular interpretation of Welden & Slauson; our definitions and derivation of C_{imp} are very clear and follow on from the work by Grace (1991, 1993), which predates the work by Freckleton & Watkinson (2001) and also a work by Corcket *et al.* (2003). Furthermore, although we acknowledge (again with hindsight) that, given the inconsistencies in the work by Welden & Slauson (1986), it was inaccurate for us (2008) to state that ‘Freckleton & Watkinson (2001) themselves do not distinguish between competition importance and intensity in a manner consistent with Welden & Slauson (1986)’, it is important to recognize that they do so in a manner which is not consistent with the majority of Welden & Slauson’s arguments.

On revisiting Welden & Slauson’s work, we suggest that the vast majority of their arguments utilizes the concept of competition importance as set out at the beginning of this paper – competition importance is the proportional impact of competition, on a given variable, relative to the impact of other factors. We also suggest that some of the potential for

confusion derives because Welden & Slauson's paper is so wide-ranging. They consider numerous 'scales' at which the competition can be measured, cellular-level physiological measurements, individual-scale biomass, fecundity and survival measurements, or measurements of impacts at the scale of multiple individuals, that is, at the population and community scale. They appear to favour the latter because of the problems of extrapolating from cell- or individual-based measurements to populations and communities, but this does not preclude competition importance being calculated at these lower scales. The same is true for their discussion of short-term transient physiological state changes vs. long-term community-level responses. Calculation of competition importance for a particular short-term metric is not precluded – we simply need to acknowledge the potential hazards in extrapolating directly from the short- to the long-term. To the best of our understanding the only place within the work by Welden & Slauson where this general message is contradicted is where they state

“Some experiments measure the importance of competition, if the responses monitored are population-level effects ... In contrast, some field experiments... measure transient physiological states of the organisms, and thus address intensity of competition, not its importance” (*Quarterly Review of Biology*, **61**, 35).

This is – to our minds – in clear contrast with the vast majority of the rest of the paper, although it does tally with Freckleton & Watkinson's (2001) use of the terminology.

Clearly, some form of explicit resolution is necessary, but we disagree with Freckleton *et al.*'s aforementioned statement concerning the 'logical way to resolve this contradiction'. Based on the body of evidence in Welden & Slauson's (1986) paper we suggest that the primary distinguishing feature of a measurement of the importance of competition is its proportionality – its measurement of the impact of competition on some metric (the variable for which competition *is important*) relative to the impact of other specified effects. This is the approach already adopted by Grace (1991) at the community level and by ourselves (Brooker *et al.* 2005, 2008) at the individual level. Whether individual-level competitive effects scale up to long-term population- or community-level impacts or not is a separate – although interesting – debate. Consequently, the statement that

“the information in Fig. 1 in Welden & Slauson (1986) (or Fig. 1 in Brooker *et al.* 2005) [and implicitly the C_{imp} index derived therefrom] can only be used to measure the intensity of competition as it does not integrate processes operating across the whole life cycle via estimating population growth rate or fitness”

is inaccurate. The information in Fig. 1, and C_{imp} , can readily be used to measure competition importance *in specific circumstances* (as discussed next). Again, it is important to explicitly acknowledge that there are a number of ways in which competition importance might be measured, and to separate the concept from its measurement. Freckleton *et al.* fail to do this

when they state ‘We would question whether the concept of “importance” as a single concept or measure is of any value in plant population or community ecology’. One can have a single concept with multiple measures including those at the level of the individual on some short-term basis (‘proximate effects’ *sensu* Freckleton *et al.*), or over the long-term across the whole life cycle. Even ‘proximate effects’ will have importance if placed within the context of overall environmental impact. Such a definition enables a plurality of approaches to assessing competition importance but takes the important step of separating the general concept from competition intensity.

To sum up, we welcome the desire of Freckleton *et al.* to incorporate assessment of the consequences of competition at the population level and across generations within the range of approaches available to measuring the importance of competition. However, we disagree that this is the sole appropriate approach to advancing this field.

CRITICISM OF THE C_{IMP} INDEX

C_{imp} can be expressed as a product of two ratios (see eqns 1 and 2 in Brooker & Kikvidze 2008):

$$C_{imp} = \{[w_m - w(N)]/w_m\} * \{w_m/[w_{Max} - w(N)]\},$$

where w_m is plant performance (e.g. size at the point of measurement) without competition owing to the removal of neighbours, $w(N)$ is plant performance with competition from intact neighbours at the same point on an environmental gradient and w_{Max} is maximum performance of an isolated plant along the productivity gradient. In this form, C_{imp} corresponds to eqn 5 in Freckleton *et al.*, and uses the same symbols.

Freckleton *et al.* criticize our development and use of the C_{imp} index. Importantly, though, this criticism can only be levelled because of Freckleton *et al.*'s interpretation of Welden & Slauson (1986). Principally, C_{imp} was designed for exploring changes in competition importance in particular types of experimental studies. Freckleton *et al.* acknowledge that experimental approaches can be useful:

“There are many types of experiment and manipulation that are impossible to carry out in the field or under uncontrolled conditions and that can only be performed in the short-term under controlled conditions. However, at the same time it needs to be realized that there are limitations in using data from highly controlled conditions to infer the strength of competition under field conditions.”

We have no argument with this statement. The experiments that we discuss (Reader *et al.* 1994; Belcher, Keddy & Twolan-Strutt 1995; Kadmon 1995; Pugnaire & Luque 2001) are indeed short-term controlled studies, as opposed to long-term monitoring data from ‘natural’ communities, as pointed out by Freckleton *et al.* At the same time as supporting the use of such studies and (again as pointed out by Freckleton *et al.*) recognizing their ‘considerable value in testing hypotheses and

elucidating mechanisms', we do not disagree that there are 'limitations in using data from highly controlled conditions to infer the strength of competition under field conditions'.

It would, therefore, clearly be unwise to unthinkingly take a measure of competition importance that was designed specifically for such studies and then apply it to studies of multispecies communities under field conditions. Such a criticism – which is a central tenet of Freckleton *et al.*'s discussion of the C_{imp} index – might reasonably be levelled at our previous work if we had proposed such a course of action. However, we proposed our C_{imp} index to measure competition importance within a very clearly defined set of circumstances: (i) to measure competition importance as we defined it based on our interpretation of Welden & Slauson 1986 (as set out above) and (ii) using a phytometer in isolation to examine changes in competition importance along environmental gradients. The C_{imp} index, originally outlined in our 2005 paper, was aimed specifically at examining changes in the role of interactions along environmental gradients: we stated that 'it is possible to obtain a restricted index for C_{imp} by quantifying changes in C_{imp} across environmental gradients'. To test the utility of our index for this specific purpose we reanalysed the classic data set by Reader *et al.* (1994), a large spatial-scale experiment, which also examined the changing role of interactions along environmental gradients.

In this sense we are, and always have clearly been 'asking about importance in only one respect, that is, how the effects of competition vary along environmental gradients'. Consequently, we agree that 'This is only one context in which the effects of competition might be explored'. Given this, Freckleton *et al.*'s criticism that our index 'does not integrate processes operating across the whole life cycle via estimating population growth rate or fitness', although accurate, is not relevant. We agree that exploration of competition importance within this context 'can by no means be used to ascribe a general index of "importance" to competition'. But given that Freckleton *et al.* explicitly acknowledge the index's utility in examining changes in interactions along gradients, and given that we have clearly stated that this is our aim in both of our papers on this topic, their criticism of the index on this basis seems unfounded.

Freckleton *et al.* provide an interesting discussion of the similarities of their population-level approach and the C_{imp} index. However, we again believe that some of their arguments – in this case focusing on this specific comparison – are illogical. As pointed out by Freckleton *et al.*, our original equation for C_{imp} (eqn 5 in Freckleton *et al.*) can be simplified when growth with competing neighbours is negligibly less than without them. This produces eqn 6, which shows that the importance of competition will increase with increasing productivity. Likewise, under conditions where the proportions of biomass that converts into seeds and the proportion of seeds that survive to become plants are constant, the importance eqn 7 derived from the population growth model reduces to eqn 8. Equations 6 and 8 mathematically are identical. The fact that the two different approaches arrive at the similar special case confirms – to us – the validity of both logic paths. Yet, Freckl-

eton *et al.* downplay the validity of eqn 6 claiming that it 'simply follows the way the index is constructed'. This last statement conceals the fact that C_{imp} is based on the same assumption as eqn 8: that fitness of plants depends more or less linearly on their biomass. The only real difference is that our assumption is made *a priori* in case of C_{imp} (an assumption derived from our interpretation of Welden & Slauson 1986) and then inherited by eqn 6, whereas eqn 8 is derived *a posteriori* from eqn 7 based on a very similar assumption (that the proportion of biomass that converts into seeds and the proportion of seeds that survive to become plants are constant).

Freckleton *et al.* criticize C_{imp} for the lack of predictive power owing to excessive simplicity and thus an inability to describe complex population dynamics. They argue that plant population growth may depend on many factors, which their model-based eqn 7 can encompass, whereas an index like C_{imp} (eqn 5) cannot. Whether an interaction index can apply to a range of behaviours depends, in the first place, on the experimental design: it is perfectly possible to measure separately germination, seed predation, seedling survival, fecundity and so on as density-dependent processes (see also Aarssen & Keogh 2002). Subsequently, the measured effects can be quantified with indices and used for modelling, hypothesizing and so on. As a most recent example, Lamb, Kembel & Cahill (2009) analysed separately above- and below-ground interactions in experimental plant communities using LnRR (log response ratio) and C_{imp} to quantify intensity and importance of these interactions. These authors were able to perform a subsequent path analysis and construct a structural equation model, which predicts a different importance of root vs. shoot competition for community composition and diversity. Finally, there may be predictions inferred from the reanalyses performed with C_{imp} (Brooker *et al.* 2005; Brooker & Kikvidze 2008). The increased importance of competition at the productive end of the gradient (as shown for at least two data sets – those of Reader *et al.* 1994 and Kadmon 1995; see Brooker & Kikvidze 2008) predicts several measurable consequences of competition at a range of levels: (i) reduced performance of individual plants; (ii) competitive exclusion at the neighbour scale generating an overdispersed pattern of species spatial distribution in a community, as well as guild proportionality, *sensu* Wilson & Watkins 1994 (see also Kikvidze *et al.* 2005); (iii) competitive exclusion at the community scale to explain an absence of species potentially adapted to the given abiotic conditions and not isolated geographically (as hypothesized by Grime).

Overall, C_{imp} has not been used specifically for analysing growth and predicting the fate of a single target population, yet C_{imp} was never intended for this purpose. At the same time, it does show a predictive power and versatility despite its simplicity.

OTHER INTERPRETATIONS AND MEASUREMENTS OF IMPORTANCE

Freckleton *et al.* are not the sole proponents for basing measurement of competition importance on population dynamics. Damgaard & Fayolle (2010) present an interesting and

constructive synthesis, which generalizes the existing approaches to quantifying the importance of competition. Notably, they take their definition of competition importance from the work of Grace (1991). Again, this considers competition importance as being a proportional measure of the impact of competition although, as we point out before, Graces' definition concentrates on community-level effects, ours (2005, 2008) on individual-level effects, whereas Welden & Slauson (1986) discuss both, although with an apparent preference for the former. Based on density dependence of interactions, Damgaard & Fayolle (2010) derive their model from the original definition of Welden & Slauson (1986). This general model can be applied to population dynamics measurements (e.g. such as those advocated by Freckleton, Watkinson & Rees 2009), as well as to simple experiments commonly analysed using indices. It is undoubtedly a step forward in unifying our views on competition intensity and importance and, we believe, will stimulate further studies on the mechanisms and consequences of plant interactions.

Dhondt (2010) presents another example of using population density to study the intensity and importance of competition, but this time among birds. It is interesting to see, in this case, the application of the concept of competition importance to another species group. Analysing the dependence of demographic variables such as reproductive rate on population density, Dhondt was able to compare the intensity and importance of intraspecific and interspecific competition across habitats of different quality. Although Dhondt's definition of the concept of competition importance concurs with our own, he uses a method proposed by Welden & Slauson (1986) for its measurement, that is, 'the percentage variation in a demographic parameter that is explained by variation in density alone. When regressing a demographic variable against density the coefficient of determination expresses importance' (Dhondt 2010).

Finally, Seifan *et al.* (2010) present an index that can be used for quantifying the importance of both competition and facilitation. Critically, they are recognizing the links between studies of facilitation and competition, and the need to integrate facilitation into the discussion of measurement of plant–plant interactions in general. This is vital to prevent debates that have occurred concerning measurement of competition resurfacing with respect to facilitation, as recently pointed out by Brooker & Callaway (2009). Seifan *et al.* argue that C_{imp} is poorly suited for measuring importance within a range of negative and positive effects. Seifan *et al.* use our definition of importance, and C_{imp} , to derive the new index. However, we feel that Seifan *et al.* may have overlooked two important points. First, that C_{imp} was not intended as a generic index. To reiterate, C_{imp} was designed specifically for measuring the importance of competition along a productivity gradient. Similarly, the improved index by Seifan *et al.* can be useful on gradients, but provides a valuable improvement as interactions can shift from competition to facilitation (and vice versa) along spatial and temporal gradients (e.g. see Pugnaire & Luque 2001; Kikvidze 1996; Kikvidze *et al.*

2005, 2006 in addition to the examples provided by Seifan *et al.* 2010), and hence the new index has potential for use in studies on gradients. Secondly, they do not deal with the generic problems associated with indices in terms of the limited provision of information as to *why* net interactions change along gradients. We return to our previous point where we discuss the focus of the article by Wilson (2007), that is, trying to find an index-based approach to unravelling the processes that are occurring to drive changes in interactions along gradients. If facilitation research is to move beyond simply examining changes in net interactions (although this research has been very fruitful), then it, too, must address these issues, and it is perhaps unfortunate that Seifan *et al.* (2010) appear to overlook the work of Wilson (2007).

In conclusion, the complex problem of measuring and interpreting biotic interactions invites a range of approaches. Importantly, these various approaches to measurement can be complementary and not conflicting, so long as underlying issues concerning the definition of concepts have been resolved. There are indeed a number of ways to measure the impact of competition relative to other factors. Here, we propose what we see as a sensible resolution to the current underlying debate concerning the definition of competition importance, a resolution which is backed – we suggest – by the original source article, literature precedent and current usage.

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Received 2 December 2009; accepted 3 March 2010

Handling Editor: David Gibson