

FORUM

The concept and measurement of importance: a comment on Rees *et al.* 2012

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Summary

1. The importance of competition has been defined as the impact or role of competition relative to the total impact of the environment, and the intensity of competition is its absolute impact. Understanding the distinction has been proposed as key in reconciling long-running ecological debates.
2. An index of competition importance, C_{imp} , has been used in a number of recent studies. Rees, Childs & Freckleton (2012) present a strong attack on the competition index C_{imp} (and the associated interaction index I_{imp}) and question the underlying rationale for the concept of competition importance. We assess their critique and challenge it in a number of areas.
3. Rees *et al.* conflate criticism of the index C_{imp} with criticism of the concept of competition importance. Their approach to assessing the properties of C_{imp} (and I_{imp}), including the use of target plant success in the absence of neighbours (P_{NC}) as a measure of environmental severity, is biased towards demonstrating a simple linear relationship between severity and C_{imp} , and supporting the argument that there is no need for separate measurements of importance.
4. We consider the proposal by Rees *et al.* for the use of variance partitioning to assess importance. Although providing a measure of the relative role of competition, it is unable to assess the shape of the importance–severity relationship, something central to testing important ecological theories such as those of Grime (1979) or Bertness & Callaway (1994). We discuss alternative approaches which might address this question.
5. *Synthesis.* Responding to Rees *et al.* has been beneficial in clarifying points of difference between our approaches, and the need to visualize the shape of the importance–severity relationship. From this response we draw three broad conclusions. We need: (i) metrics of environmental severity that are independent of the success of target species; (ii) analytical approaches that avoid the statistical problems associated with ratios whilst enabling us to assess the shape of the severity–importance relationship; (iii) new data to assess the generality of proposed relationships. Studies incorporating these elements will take forward our understanding of the role of competition in plant communities.

Key-words: competition importance, competition intensity, interaction indices, plant competition, plant facilitation, plant–plant interactions, response, severity gradient, severity gradient

Introduction

Rees, Childs & Freckleton (2012) – hereafter ‘Rees *et al.*’ – discussed previous work on the concept of the importance of competition. They criticized the concept and indices

developed to express competition importance and (more broadly) interaction importance and put forward variance decomposition as an alternative analytical approach.

Unfortunately, their work perpetuates on-going confusion about the concept and its mathematical expression, and in some places is either potentially misleading or inaccurate. Fuller detail of some of these arguments has been set out and

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responded to elsewhere (e.g. Kikvidze & Brooker 2010; Seifan *et al.* 2010; Kikvidze, Suzuki & Brooker 2011a). However, we feel that there is still a need to point out some of the main inaccuracies within the work of Rees *et al.* (2012) and to respond to the major points of criticism. Our aim is to do this in as brief a manner as possible whilst making our reasoning clear. To this end, we have set out our main arguments within this study, and have also provided supporting information with more detailed discussions particularly concerning the critique of the C_{imp} and I_{imp} indices in Appendix S1 in the Supporting Information.

Here, we first outline the development of the concept of competition importance. We then respond to Rees *et al.*'s criticism of the concept of competition importance, their assessments of the indices C_{imp} and I_{imp} , and their proposal for the use of variance decomposition as an alternative analytical approach. Finally, we lay out some potential next steps which we believe should promote progress.

Development of the concept of competition importance

Welden & Slauson (1986) first defined the intensity of competition as its absolute impact, and the importance of competition as its impact relative to that of all the factors in the environment that influence plant success. Note that the measurement of plant success is itself a complex problem that impacts on many aspects of plant population, community and evolutionary ecology (see for example Aarssen & Keogh 2002; Malkinson & Tielbörger 2010). We return to this particular problem below (see *The importance of what*), but for now assume that the measurement of success is possible.

Grace (1991) argued that, in the debate concerning the apparently conflicting theories of Grime (1974, 1979) and Tilman (1982, 1987) on the role of competition along environmental gradients, Grime's theory was focussed on the importance of competition and Tilman's on its intensity. By explicitly recognizing that these theories discussed the different facets of competition described by Welden and Slauson, Grace argued that it was possible to resolve their apparent contradictions.

Sammul *et al.* (2000) noted that intensity had been the focus of considerable study but that importance remained widely overlooked, whilst Brooker *et al.* (2005) argued that a number of studies purporting to address the predictions of Grime used inappropriate indices of competition intensity. They modified the competition intensity index relative competition intensity (RCI; hereafter referred to as C_{int}) to produce the competition importance index C_{imp} , calculated as:

$$C_{\text{imp}} = (P_{T+N} - P_{T-N}) / (\text{Max}P_{T-N} - y) \quad \text{eqn 1}$$

where P_{T+N} and P_{T-N} are the success of target plants (P_T) in the presence (+N) and absence (-N) of neighbours, $\text{Max}P_{T-N}$ is the maximum value of P_{T-N} observed along the severity gradient being examined and y is the smaller of either P_{T+N} and P_{T-N} . C_{imp} allows the impact of competition at a given point along a severity gradient ($P_{T+N} - P_{T-N}$) to be

expressed as a proportion of the total impact of the gradient as calculated relative to the point of maximum success ($\text{Max}P_{T-N} - y$). It does not give an absolute value for competition importance, and any value of C_{imp} – and observed relationships between C_{imp} and the severity gradient – is therefore relevant only to the severity gradient and species in question (Brooker *et al.* 2005).

Brooker & Kikvidze (2008) repeated the message that studies addressing the theories of Grime focussed inappropriately on measurements of interaction intensity, but their study was criticized by Freckleton, Watkinson & Rees (2009), who considered the importance of competition to relate only to long-term, population-scale measurements of the impact of competition. Freckleton *et al.* also criticized C_{imp} . Kikvidze & Brooker (2010) responded by pointing out internal inconsistencies in the original work by Welden & Slauson (1986), arguing that the vast majority of Welden and Slauson's argument focussed on whether it is the relative role of competition (its importance) or its absolute impact (its intensity) that is of interest. Kikvidze & Brooker (2010) also pointed out that C_{imp} was not proposed by Brooker *et al.* (2005) as a general approach to measuring competition importance: Brooker *et al.* (2005) set out limitations of the C_{imp} index (as described above), and Kikvidze & Brooker (2010) argued that despite these limitations, it is useful as an illustrative tool for application under specific circumstances, specifically to examine how the effects of competition vary along environmental gradients.

Having provided this brief summary of some of the research context, we now examine the main criticisms put forward by Rees *et al.* of both the concept of competition importance and approaches to its measurement.

Criticism of the concept of competition importance

THE LACK OF UNDERLYING ECOLOGICAL THEORY

A central argument proposed for the rejection of the concept of competition importance, also imposed on the index C_{imp} (point 3 of Rees *et al.*'s list of ideal properties for ecological indices), is that it has no underlying theoretical basis.

To us, the theoretical basis is clear. Grime's C-S-R theory (Grime 1974, 1979) classifies plant strategies according to their level of adaptation to three main drivers: stress, disturbance and competition. It predicts that in either highly disturbed or stressed environments, the relative role of competition as a community structuring or selective force is reduced: competition becomes less important. Grime (2007) specifically states that it is 'evident that we must recognize that competition declines in importance under the impacts of reduced productivity and/or severe disturbance'. This provides the basic rationale for examining the shape of the relationship between the importance of competition for regulating plant success or community structure and gradients of stress and/or disturbance.

Rees *et al.*'s argument that the concept of competition importance has no theoretical basis might stem from one of

two sources. First, they may not think that the work of Grime and colleagues constitutes an ecological theory. Alternatively, they may be referring to a lack of an underlying mathematical as opposed to conceptual model. Interestingly, Rees (2012) examines the application of short-term manipulation experiments to the questions raised by the Grime–Tilman debate. Rees states that ‘there is currently no theory that predicts when particular patterns will be observed or guides the interpretation of the experimental studies’. Perhaps, it is with respect to within-experiment processes and specific types of severity gradient (as discussed below) that Rees believes there is a lack of theoretical underpinning.

We prefer to leave consideration of what constitutes theory (in a broad sense) to those more philosophically inclined (for example see Colyvan 2011; Gorelick 2011), but the work of Grime and colleagues is widely regarded as one of the major theories within plant ecology, and we take it as the theoretical basis for our work. Furthermore, other theories are relevant to the concept of competition importance. The original work by Welden & Slauson (1986) is theoretical in nature, whilst the exploitation ecosystems hypothesis (EEH) theory of Oksanen *et al.* (1981) also explores changes in the relative roles of community-structuring processes along environmental gradients. In the EEH, it is the relative role of trophic levels in regulating one another’s productivity that is examined, generating largely convergent predictions to the work of Grime and colleagues but through different mechanisms.

THE IMPORTANCE OF WHAT

A second argument put forward for the rejection of the concept of competition importance is ‘the importance of what’ argument, that is, that we must define the factor and response variable (the importance of what to what) when discussing the concept or its measurement. We argue that this is not necessary. The definition of competition importance, as given above, explicitly states that the factor is the impact of competition (relative to the impact of other environmental factors), and the response variable is some measure of community structure or plant success.

As also noted above, the definition and measurement of plant success are a problem that is not specific to the topic of competition importance. Success in an evolutionary sense is the contribution of an individual to the next generation, and competitive ability is then ‘the relative ability of the individual to leave descendants when resources are contested’ (Aarssen & Keogh 2002). However, measuring the lifetime contribution of an individual plant to the next generation of reproductive adults (and consequently, the extent to which competition in an environment suppresses this contribution and therefore acts as an evolutionary force) is extremely difficult: it necessitates following all offspring of an individual to reproductive maturity. To handle this problem, plant ecologists generally measure what are assumed to be proxies for this ultimate measure of success: biomass, levels of flowering, seed production and seed viability have all been used (Goldberg *et al.* 1999; Malkinson & Tielbörger 2010). However,

under different circumstances, these may or may not be good proxies, and it is widely recognized that the use of different measurements can result in different conclusions being drawn with respect to the impact of regulatory factors such as competition (Goldberg *et al.* 1999; Aarssen & Keogh 2002; Trinder, Brooker & Robinson 2013). What is critical to remember here is that the measurement of plant success, or the forces structuring community composition (which can be assessed as the average role of competition in regulating success for the suite of species within a community), and our ability or otherwise to assess this through the use of proxies, is not a problem specific to the issue of competition importance. Defining and developing measurements of genuine success – and understanding how they relate to commonly used proxies – are challenges for plant ecology in general.

To return to our main subject, the answer to the question ‘the importance of what’ is then ‘the importance of competition’ with ‘importance’ having already been defined; the answer to the associated question of ‘to what’ is ‘plant success or community structure’, noting the general challenge that this represents in terms of measurement. Analytical approaches, particularly with respect to assessing the theories of Grime, must then allow us to assess changes in the relative role of interactions – that is, changes in their importance – along environmental gradients, and in particular, the underlying shape of this relationship (as discussed in more detail below under ‘variance decomposition and other analytical alternatives to competition indices’).

The use of short-hand terminology, avoiding the need to repeat detailed definitions, is not unusual in ecology (for example, use of the term ‘evolution’). The term ‘competition importance’ comes from the work of Welden & Slauson (1986). We would be interested in workable proposals for an alternative and less cumbersome terminology, but also wonder whether it is genuinely needed. As pointed out by Rees *et al.*, the concept of competition importance is being increasingly discussed throughout the ecological literature and with, we suggest, generally a good level of accuracy irrespective of any problems associated with its measurement.

Assessment of properties of the C_{imp} and I_{imp} indices

Throughout the study by Rees *et al.*, the concept of competition importance appears to be equated with proposals for its measurement. In their Discussion in particular, their analyses of C_{imp} (and I_{imp}) are used as justification for rejecting the general principle of competition (or interaction) importance, despite the fact that it is illogical to reject a concept simply because of criticism concerning approaches to its measurement.

Although defence of the concept of importance need not necessarily be a defence of the indices C_{imp} and I_{imp} , given that criticism of the indices is a substantial part of Rees *et al.*’s study, it is clearly necessary to consider whether these criticisms are reasonable. The evidence suggests that they are not. The same arguments (and responses) hold for the criticisms of

both C_{imp} and I_{imp} , except for specific inaccuracies concerning the discussions of the work by Seifan *et al.* (2010) with respect to I_{imp} . In the following discussion, we therefore refer only to the C_{imp} index, and it is implicit that the same points can be made concerning the assessment of I_{imp} . We provide greater detail on some of the following arguments in Appendix S1, but the key points are captured here.

REES ET AL.'S ANALYTICAL APPROACH

Rees *et al.* conclude that the relationship between the indices and severity is very simple and can be estimated as the ratio $P_{\text{NC}}/P_{\text{max}}$ (where P_{NC} is plant success in the absence of competition, and P_{max} is the maximum value of P_{NC} observed along the gradient). This conclusion is supported by analyses of randomly generated data and data from the study by Kadmon (1995). There are at least three areas where these conclusions can be challenged:

1 The use of P_{NC} as a measure of 'productivity'

Because P_{NC} is one of the variables used to calculate C_{imp} , the use of P_{NC} as the metric of severity (i.e. the use of P_{NC} as the explanatory variable, as well a component of the response variable) leads to the conclusion that severity – or 'productivity' – and C_{imp} are closely related. The use of P_{NC} in this way is unusual, although some of us have previously adopted Rees *et al.*'s approach (Brooker *et al.* (2005), where we used P_{NC} to analyse the data of Pugnaire & Luque (2001)) and we must recognize that this might have influenced the reported results.

Rees *et al.* utilize P_{NC} as a measure of productivity on the grounds that this 'simplifies presentation, helps clarify the underlying relationships between variables of interest and is the approach used in several studies'. If we examine the studies listed by Rees *et al.* in support of this approach, none of them use P_{NC} as an indicator of habitat productivity in their analyses (Table S1 in Supporting Information). The nearest equivalent is the use by Gross *et al.* (2010) of $P_{\text{NC}}/P_{\text{optimum}}$ as a measure of 'strain' (*sensu* Welden & Slauson 1986). Gross *et al.* do not claim that this represents habitat productivity or environmental severity.

So what should we use as an explanatory variable? The fundamental question being addressed is how the relative impact of competition (or interactions) on plant success or community structure changes along gradients of environmental severity, that is, stress or disturbance or some combination of the two. The measurement of severity would then be the key stress or disturbance variable(s) that compose the severity gradient and these would be measured independently from the success of the target species. However, environmental severity is often assessed using biomass proxies, commonly standing crop or NPP, and the use of such proxies leads to 'productivity' being equated to 'severity'. A common solution is to use stand-level metrics of productivity, for example, biomass produced per unit area per unit time (NPP) as a more independent measure of severity than P_{NC} ? But depending on the proportion of standing crop or NPP contributed by our target species, they may correlate closely with P_{NC} , and hence, our

explanatory variable will not be independent of our response variable. Alternatively, severity can be assessed using abiotic environmental proxies, such as nutrient or water availability, but as has been pointed out recently with respect to debate concerning the stress gradient hypothesis, severity gradients can involve multiple abiotic environmental drivers, necessitating refinement of theoretical predictions with respect to particular types of abiotic stress (Brooker *et al.* 2008; Maestre *et al.* 2009).

Ultimately, and as for the measurement of success, the measurement of severity is a generic problem for plant ecology and is not specific to the issue of competition importance. The fundamental point is that if a measure of system severity that is independent of the biomass of the target species is used, there is no inevitability in the relationship between C_{imp} and severity. We believe that this is a key point of differentiation between ourselves and Rees *et al.*: the way in which ecologists perceive variation in the abiotic environment and its relationship to other factors, such as the impact of competition on plant success, is completely different depending on whether we estimate it using individual plant success (e.g. P_{NC}), community-level measures such as NPP, or abiotic variables, such as temperature. Depending on which of these is used as the explanatory variable, there will be a more or less 'inevitability' in the relationship between our measure of environmental severity and response variables such as C_{imp} that are derived from measurements of plant growth.

This possibility for confusion is why we have used the terminology 'severity gradient' throughout this study, in an attempt to distinguish these larger-scale gradients of environmental severity – which impact upon both stand-level and individual productivity – from finer scale variation in the productivity of the target species itself. In addition, if the aim of a study is to test community-structuring forces – for example, the importance of competition for regulating the composition of a community in order to test some of the predictions of models such as the CSR theory of Grime (as well as the EEH theory of Oksanen *et al.* (1981)) – then a community-level metric of severity is necessary. We return to this fundamental difference in approach in our simulation analyses, below.

2 The use of C as an index of competition

Rees *et al.* use C ($P_{\text{NC}}/P_{\text{C}}$) as an index of competition, where P_{C} is plant success in the presence of competition. We see two particular problems with their use of C . The first concerns the ease with which C can be interpreted. Apparently, simple relationships between P_{NC} and C used by Rees *et al.* (Rees *et al.*'s Fig. 1a) hide underlying complexity in the raw data, particularly P_{C} . We know both P_{NC} and C , and so can calculate P_{C} , and from this realize that its relationships with P_{NC} (Fig. S1 in Supporting Information) are not readily assessed from the relationships between P_{NC} and C . These more complex relationships of P_{NC} and P_{C} then in part drive the relatively complex pattern of relationship between P_{NC} and C_{imp} shown in Rees *et al.*'s Fig. 1b (see also *The complexity of the response of C_{imp} to 'productivity'*, Appendix S1).

Secondly, Rees *et al.* use randomly generated values of C to assess the relationship of C_{imp} to P_{NC} . The problem with this

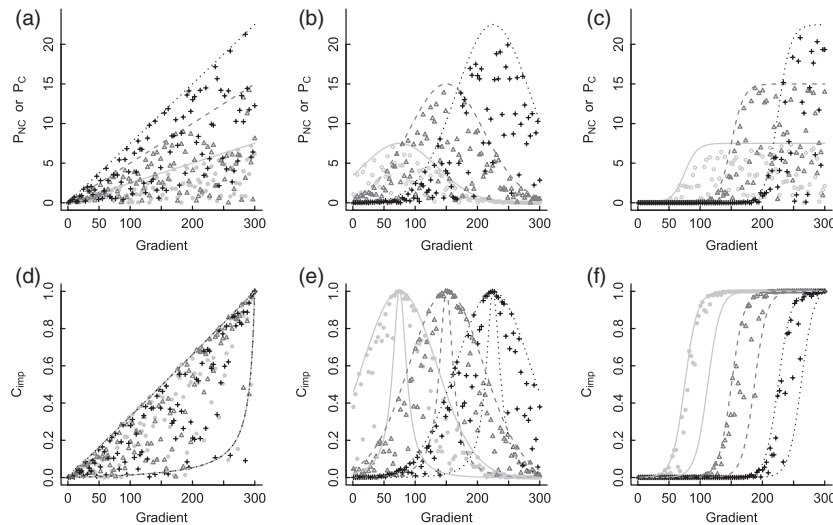


Fig. 1. Simulation of variation in P_{NC} , P_C and C_{imp} along a gradient of environmental severity (with low to high system severity represented by arbitrary values of 0–300), demonstrating the capacity of these variables to vary relative to one another. Note that in all of these simulations $P_{NC} > P_C$, and so the response of I_{imp} has exactly the same form as that of C_{imp} . Each case is illustrated using simulated data for three different hypothetical species with different growth maxima and distributions along the severity gradient: highest stress tolerance and lowest species-level success (species 1 – solid line and circles); intermediate stress tolerance and success (species 2 – dashed line and triangles); lowest stress tolerance and highest species-level success (species 3 – dotted line and crosses). The figures illustrate the outcome of the simulation in relation to three different assumptions about the pattern of variation in P_{NC} along the gradient: (a, d) species success is linearly related to the gradient; (b, e) each species has a different point of optimum growth along the gradient, with variation in growth showing a Gaussian pattern around this optimum, whilst maximum species success is higher for species with an optimum at the less severe end of the gradient; (c, f) species success increases up to an asymptote, and species reaching this asymptote in the lower part of the gradient have a lower maximum success. (a–c) show the maximum potential species success without competition at any point along the gradient (P_{NC} ; solid, dashed, and dotted lines), as well as 100 randomly drawn values for success with competition (P_C ; calculated from values of $1/C$ drawn in a uniform distribution between 0 and 1 separately for three different species). (d–f) show values for C_{imp} computed for the 100 simulated values of P_C (points) as well as the 95% quantiles of C_{imp} (lines). C_{imp} ranges between 0 and 1, in contrast to the more recent convention of stronger competitive interactions being given more negative index scores; we have taken this approach to aid comparison with Rees, Childs & Freckleton (2012).

approach is that C is a ratio, more often expressed as RR (the response ratio). $\ln RR$ is commonly used to account for the inherent statistical issues associated with ratios (see, for example, Kikvidze & Armas 2010). General problems associated with the analysis of ratios have been discussed widely, and we return later to this topic; here, we are concerned with the use specifically of C in this particular set of analyses. In theory C can vary between 0 and ∞ , with values >1 indicating situations of competition. Generating a uniform distribution of C between 1 and 100, as used by Rees *et al.* to provide synthetic data to test the C_{imp} – P_{NC} relationship, results in a non-uniform distribution of P_C such that in general $P_C \ll P_{NC}$ (as shown in Fig. S2b). This strongly biases the simulated data towards very high competition, such that a very tight relationship between C_{imp} and P_{NC} is found. It is also worth noting that real world values for C are often relatively small. For example in the studies by Carlyle, Fraser & Turkington (2010) and le Roux & McGeoch (2010), values of C range from 1.15 to 2.8 and from 0.02 to 1.34 (based on Figs 1 and 2c of these studies, respectively). Assessing the relationship between P_{NC} and C_{imp} using values of C evenly spread between 1 and 100 may under-sample that area where many experimental studies sit, but the use of C to illustrate data obscures this bias in P_C . Generation of random values of P_C allows better coverage of parameter space (Fig. S3) and provides a better assessment of the potential variability

in the C_{imp} – P_{NC} relationship (see also *Selection of random data*, Appendix S1).

3 The use of only the data from Kadmon (1995) to explore the C_{imp} – P_{NC} relationship in field studies

As for the synthetic data of Rees *et al.*, the empirical data from the work by Kadmon (1995) show also a strong relationship between C_{imp} and P_{NC} . Again, Rees *et al.* use P_{NC} as the measurement of severity (productivity), and as discussed above, this has predictable consequences for detected relationships. But in addition to this, Kadmon's study is of a very specific situation, focussing on annual plants in an extreme desert habitat with small scale variation in soil surface conditions leading to highly localized changes in severity over small spatial scales (metres). Because of the extreme environmental conditions, it is not surprising that a strong positive correlation between interaction importance and severity is found in *this study*. In such harsh conditions, the availability of water is the main factor governing plant abundance and thus also the nature of biotic interactions within the area. In addition, because this study was conducted on a very limited geographical scale, it is perhaps unrepresentative of the responses found in gradient studies in general. Consequently, it is unwise to assume that data from this study, interesting though it is, are broadly representative of patterns found in all field data. It is notable that data from other field studies

do not necessarily show the same tight relationship between P_{NC} and C_{imp} (Fig. S4; see also 'An exploration of relationships using field data', Appendix S1).

A BETTER APPROACH TO ASSESSING THE SEVERITY- C_{imp} RELATIONSHIP

We take a different approach to assessing the properties of C_{imp} and I_{imp} . Our simulation (Fig. 1) explores the response of three hypothetical plant species to variation in environmental severity. We assume that – as in the ideal case described above – the gradient of severity is assessed using a metric such as water or nutrient availability which represents the key severity drivers, but which is also independent of the success variables used to calculate C_{imp} . C_{imp} is therefore free to hold any value at a given point along the severity gradient, and we can assess independently the responses of P_C , P_{NC} and C_{imp} to variation in severity.

We use three alternative assumptions about the way in which plant success without competition (P_{NC}) varies in relation to environmental severity, relating to three different models of variation in success along severity gradients.

- 1 As in Rees *et al.*, success is directly and linearly related to the severity gradient, declining with increasing severity.
- 2 The success optimum of each species is in a different location along the severity gradient, and success varies in a Gaussian distribution around this optimum. In addition, absolute maximum success is higher for species with an optimum towards the less severe end of the severity gradient. This distribution pattern is based on the concept of differences in species' fundamental niches.
- 3 Species' success increases up to an asymptote, and species reaching this asymptote under more severe environmental conditions have a lower maximum success. This pattern of distribution is based on the concept of shifting competitive hierarchies (Keddy 1989).

In all simulations, species with optima in the more severe environments might be considered typical stress tolerants (*sensu* Grime) and are capable of achieving a lower level of maximum success relative to more competitive species from the less severe end of the gradient. Further details of the assumptions behind our simulation are given in Fig. 1, and the R script used for these analyses is available in Appendix S2.

Overall, the analyses (Fig. 1) show that for any type of variation in success along the gradient, variation in C_{imp} is related to variation in P_{NC} . This is no surprise: as we have pointed out (above and in Appendix S1), P_{NC} is one of the components of C_{imp} , and so their distributions will inevitably be coupled. However, there is substantial potential for C_{imp} to deviate away from P_{NC} . But perhaps, more importantly, it is not inevitable that C_{imp} declines with increasing environmental severity. Although this can occur (Fig. 1d), it depends on the related response of plant success to the severity gradient (Fig. 1a). If success has a different response to the severity gradient, this can result in a different response pattern for

C_{imp} , including bell-shaped distributions (Fig. 1e) and asymptotic relationships (Fig. 1f). What is critical is that C_{imp} can in theory have any kind of relationships with severity depending on variation in plant success.

Critically, relaxing the assumption that P_{NC} varies linearly along the severity gradient demonstrates that C_{imp} is not *designed* to show a decline with increasing severity to support a particular conceptual framework (such as that of Grime). Instead, C_{imp} depends on the response of plant success. The question of how plant success (P_{NC}) varies along the severity gradient therefore is crucial in the analysis of the importance of competition, linking it to the very considerable body of literature focusing on the processes that regulate species distributions in relation to environmental drivers including, for example, the works by Whittaker (1975), Keddy (1989), and Bigelow & Canham (2002).

Variance decomposition and other analytical alternatives to competition indices

Irrespective of the approach adopted to analyse the properties of C_{imp} , clearly, there are statistical problems associated with the application of C_{imp} as there are with any other ratio-based indices. Some ratios such as C , RCI and C_{imp} suffer from asymmetry, whilst even symmetric indices such as RNE suffer from nonlinear responses towards their extremes. For further discussion of these points see, for example, Jasienski & Bazzaz (1999), Armas, Ordiales & Pugnaire (2004), Oksanen, Sammul & Mägi (2006) and Seifan *et al.* (2010).

Given the statistical problems associated with the use of ratios, what are the alternatives? Some are proposed by Kikvidze, Suzuki & Brooker (2011b), including the use of the determination coefficient (R^2), originally proposed by Welden & Slauson (1986). From regression of a demographic parameter against organismal density, interaction intensity can be measured as the slope of the regression relationship and importance as the proportion of variation explained (R^2). But there are also problems associated with this approach (Petraitis 1998). And although R^2 might tell us about the role of competition at any given point on a gradient, it does not tell us how the importance of competition might vary along an environmental gradient, although Dhondt (2010) overcame this problem by calculating R^2 at many sites along a severity gradient.

VARIANCE DECOMPOSITION AND ITS APPLICATION TO GRADIENT ANALYSES

One of the alternative approaches suggested by Kikvidze, Suzuki & Brooker (2011b) is the use of variance partitioning. Rees *et al.* also suggest the use of variance partitioning – or as they describe it variance decomposition – illustrating its application by re-analysing the data of Kadmon (1995).

As discussed, key ecological theories, such as those of Grime *et al.*, the EEH (Oksanen *et al.* 1981), or the Stress Gradient Hypothesis (Bertness & Callaway 1994), predict a particular pattern of change in the relative role of interactions across environmental gradients. Any analytical approach rele-

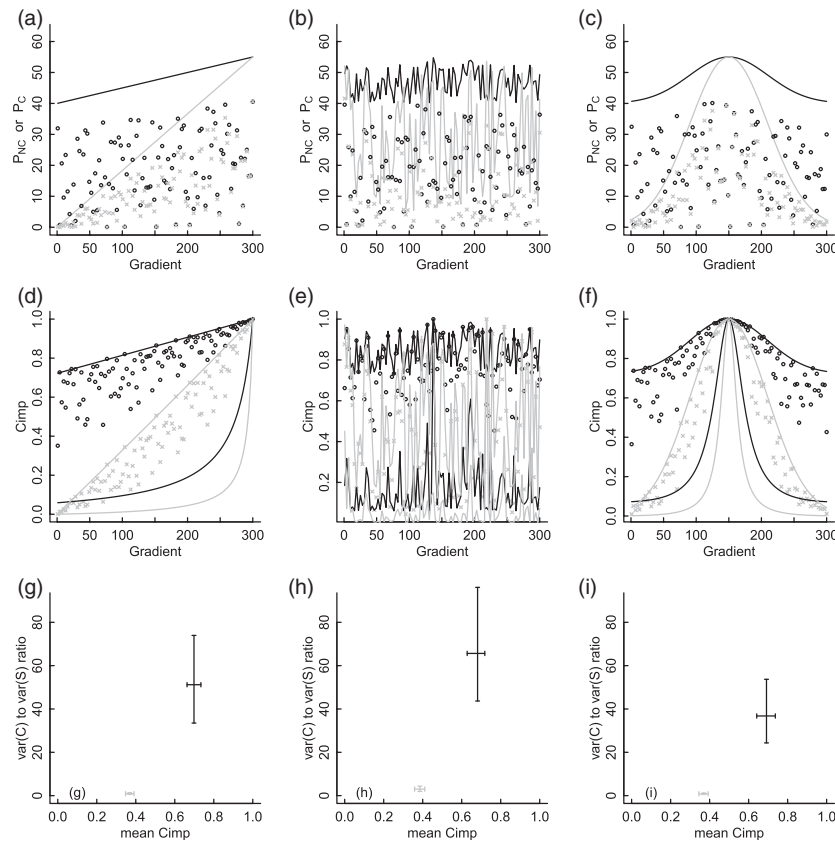


Fig. 2. Simulations of P_{NC} (species' success without competition, indicated by lines) and P_C (species' success with competition, indicated by dots and crosses) in response to a gradient of environmental severity, demonstrating how very different underlying relationships can result in the same $\text{var}(C)$ to $\text{var}(S)$ ratio. Low to high system severity is represented by arbitrary values of 0 to 300 along the environmental gradient, but with three different assumptions about the variation in P_{NC} : (a) as in Rees *et al.* (and the data from Kadmon 1995), P_{NC} is linearly related to the gradient; (b) P_{NC} varies randomly across the gradient; (c) species have an optimum on the gradient (and their success, P , varies in a Gaussian distribution around this optimum). For each scenario two species are represented: (i) black lines and circles show a species whose success without competition is weakly affected by the gradient (a decrease of *c.* 25%) and (ii) grey lines and grey crosses show a species whose success without competition is strongly affected by the gradient (a decrease of *c.* 75%). Dots and crosses represent 100 randomly drawn values for P_C (taken from a uniform distribution between 0 and 1). C_{imp} is then computed from these, as shown in (d–f), where the lines now represent the 95% quantile of C_{imp} based on the null model of competition. (g–i) show plots, for each of the above simulations, respectively, of the estimated values for the $\text{var}(C)$ to $\text{var}(S)$ ratio proposed by Rees *et al.* against the mean C_{imp} values estimated over the full gradient. We followed the Bayesian approach of Rees *et al.*, using a modified version of their code with a bivariate normal distribution for the joint distribution of S and C (see Appendix S3 for an implementation in the JAGS program for analysis of Bayesian hierarchical models, Plummer 2003). Estimation of $\text{var}(C)$ to $\text{var}(S)$ ratio and mean C_{imp} are calculated for replicated simulated data with a random observation error. C_{imp} ranges between 0 and 1, in contrast to the more recent convention of stronger competitive interactions being given more negative index scores; we have taken this approach to aid comparison with Rees, Childs & Freckleton (2012).

vant to these theories must therefore allow us to visualize how the relative role of plant–plant interactions in regulating plant success or community structure changes along the environmental gradient in question. Rees *et al.*'s approach does not allow us to answer this question, it assesses instead how much of the variation in plant success across the entire environmental gradient is due to severity and how much is due to competition, giving a *single value* (the ratio of $\text{var}(C)$ to $\text{var}(S)$) for the relative roles of competition and stress. Consequently, this approach cannot be considered an alternative to the types of analyses we have performed using interaction indices. Its inability to explore the shape of the relationship between plant interactions and the severity gradient can be illustrated readily. We simulate a number of different relationships between P_{NC} (success in the absence of competi-

tion) and a hypothetical gradient of environmental severity. As we can see from these simulations (Fig. 2), there are quite distinct differences in the underlying relationships between P_{NC} and the gradient of environmental severity. However, the final analysis of these relationships, using the approach applied by Rees *et al.*, is insensitive to the substantial differences in their form and appears no more responsive than the calculation of an average value of C_{imp} (Fig. 2). Interestingly, Rees *et al.*'s proposal for the use of variance decomposition appears implicitly to acknowledge this. They state:

If we are examining the effects of competition and the quality of the environment along an environmental gradient, we are likely to be interested in three aspects of the data: (i) how do changes in the quality of environ-

ment in the absence of competition affect plant performance? (ii) How do changes in competition affect performance? And (iii) how do the effects of competition and the environment interact with each other? Of these, the interaction is likely to be of greatest interest, that is, how does the environment affect the reduction in performance due to competition?

Only the third question here is related to the relative role of competition in regulating plant success, and it does not consider the shape of this relationship.

Sears & Chesson (2007) use variance decomposition to test for the spatial storage effect, a proposed mechanism by which dominant and subdominant plants can coexist in a spatially heterogeneous environment. Both Sears & Chesson (2007) and Rees *et al.* define the severity gradient on a species-by-species basis. Sears & Chesson (2007) state 'the storage effect theory defines habitat quality separately for each species based on its response to spatially covarying conditions, rather than by discrete characteristics of the physical environment (such as nitrogen levels). In practice... gradients are defined by individual plant responses to the sum of environmental conditions at each growing location'. This again highlights the fundamental difference between approaches that define environmental gradients through individual species' success (or some proxy of it such as biomass of plants in the absence of neighbours, i.e. P_{NC}), and those that use a metric of stand-level severity such as nutrient or water availability. Both are valid in different circumstances, but there are potentially confusing overlaps in terminology. Consequently, we need to be careful that we do not simply assume that a common parameter name such as 'productivity' or 'severity' is referring to the same type of variable and thus promote the use of a particular analytical technique for addressing a question to which it is not relevant.

OTHER POSSIBLE ALTERNATIVES

Our aim is not to provide a comprehensive assessment of alternative analytical approaches to these problems, but it seems sensible to discuss a few of the possible alternatives, remembering that our focal question is now more clearly defined as: what is the shape of the relationship between the relative role of competition and environmental severity?

First, it may be possible to adapt the variance partitioning approach. The key change would be to describe the severity gradient with a variable independent of P_{NC} , for example nutrient or water availability, or temperature. This would also require modelling of the response of plant success in the absence of neighbours (P_{NC}) to this gradient. The underlying assumption of Rees *et al.* that a linear relationship occurs between the gradient and P_{NC} is the simplest, but many different assumptions for the shape of this response curve can be proposed. The approach proposed by Rees *et al.* is therefore very promising, but needs to be developed such that it tests whether variation in P_{NC} is driven by the severity gradient or not.

Modifying the application of indices such as C_{imp} or I_{imp} might provide another alternative approach. Specifically,

given that there is constraint of these indices in relation to P_{NC} (with upper boundaries for values of C_{imp} determined by P_{NC}/P_{max}), it may be possible to disentangle the relative contribution to C_{imp} of two underlying elements: (i) variation in plant success in the absence of neighbours (P_{NC}) along the gradient and (ii) variation in the intensity of competition along the gradient. For instance, it would be possible to simulate C_{imp} under a null model of random competition (as used in our critique of Rees *et al.*'s analysis, above) to show the implications of P_{NC} variation alone. The second step would be to analyse how variation in competition intensity contributes to the remaining variation in C_{imp} .

Finally, Jasienski & Bazzaz (1999) suggest the use of approaches that allow partitioning of variation in an explicit causal model, for example structural equation modelling (SEM) or path analysis. This approach is increasingly common in plant ecology and can be applied to understanding the relative role of different drivers in systems with potentially complex networks of interactions (see for example, the studies by Matias *et al.* (2011) and Lamb & Cahill (2008)). An exciting opportunity is that the Bayesian approach proposed by Rees *et al.* could be combined with the SEM approach in a hierarchical model (see Lee (2007) for a discussion of Bayesian SEM).

We conclude that there are some possible alternatives to the simple use of indices, but that the use of these approaches has to be appropriate to the question. The work of Rees *et al.* has been helpful in forcing us to define more clearly the question which is the focus for many studies, and the pitfalls associated with different measurements and proxies of success and severity. These more explicit definitions can now be used to ensure the relevance of the approach.

Discussion

A response to the recent study by Rees *et al.* has been necessary because of some of the problems with their work, including their oversight of the theoretical underpinning of the concept of competition importance, the inherent biases in their analyses of indices, and their inaccurate associated conclusion that the concept of competition importance is redundant.

It has also resolved some apparent points of difference between our approaches – and their associated underlying questions – which is helpful in moving this debate forward. We have clarified that many of us are interested in the shape of the relationship between gradients of environmental severity and the relative role of plant–plant interactions. From this, come three broad conclusions:

First, the success of individuals in the absence of competition (P_{NC}) is certainly useful for revealing population-level processes such as the storage effect. However, addressing questions concerning processes operating at the community level requires measurements of variables, for example nutrient or water availability or temperature, that accurately represent environmental severity but are independent of measures of target plant success. Importantly, using a stand-level variable to describe environmental gradients is not contradictory to the

view that each species has its own 'perception' of the gradient (Körner 2003), as species-level variables can be related to stand- or higher-level environmental descriptors.

Secondly, we need to develop analytical approaches that, whilst avoiding the issues of ratios, allow us to assess the shapes of the relationships between environmental severity and the relative role of plant–plant interactions. We have discussed some of the possible alternatives. Variance decomposition, although able to assess net interaction importance and how interactions covary with environmental severity, cannot tell us about the shape of the relationship between importance and severity. Similar problems exist with the application of path analysis approaches such as SEM. But extending these approaches to enable us to consider the shape of these relationships seems to us an interesting and worthwhile challenge.

Thirdly, we need new data. We have illustrated our arguments using data from a number of studies (as shown in Fig. S4), but assessment of the generality of proposed relationships needs data from multiple studies. When selecting and analysing data, it is important to remember the issues of suitability of the explanatory and response variables, and also the analytical approach. These same issues must be considered when designing new experimental studies for assessing these relationships in the field.

Despite the complexity of unpicking and responding to the work of Rees *et al.*, we feel that this has been a very informative exercise. Ultimately, it has provided a more thorough assessment of the properties of indices such as C_{imp} and I_{imp} . It has also clarified what appear to be some fundamental differences in philosophy and associated analytical approach, and hopefully, has set out some research challenges for the future.

Acknowledgements

GK was supported by a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme (DEMO-TRAITS project, no. 299340). ZK acknowledges support from Ilia State University. We would like to acknowledge the extremely helpful comments on this MS provided by two anonymous referees and Lauri Oksanen, as well as Hans de Kroon in his capacity as Handling Editor.

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Received 19 December 2012; accepted 6 September 2013

Handling Editor: Hans de Kroon

Supporting Information

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

Figure S1. Our approximation of the change in P_C associated with the values of C and P_{NC} shown in Fig. 1a of Rees *et al.*

Figure S2. Exploration of relationships between C , P_C and P_{NC} .

Figure S3. Exploration of relationships between P_{NC} , C , and C_{imp} that result from selecting randomly-generated values of P_C .

Figure S4. Plots of P_{NC} vs. C_{imp} based on published data.

Table S1. Summary information from studies used by Rees *et al.* to support their use of P_{NC} as an indicator of habitat productivity.

Appendix S1. Exploring the properties of the C_{imp} and I_{imp} indices.

Appendix S2. R Code used for production of Fig. 1.

Appendix S3. R Code used for production of Fig. 2.

Editors' note This Forum article, together with earlier articles by Freckleton *et al.* 2009: *Journal of Ecology*, 97, 379–384; Kikvidze & Brooker 2010: *Journal of Ecology*, 98, 719–724; Kikvidze *et al.* 2011: *Journal of Ecology*, 98, 719–724, and Rees *et al.* 2012: *Journal of Ecology*, 100, 577–585 arose in response to 'Importance: an overlooked concept in plant interaction research' (Brooker & Kikvidze 2008: *Journal of Ecology*, 96, 703–708). The original paper by Brooker & Kikvidze has fulfilled its intended purpose of promoting thought and discussion about the topic. The correspondence on this topic is now closed.