Journal of Ecology

British Ecological Society

Journal of Ecology 2010, **98**, 356–361 doi: 10.1111/j.1365-2745.2009.01621.x

FORUM

Facilitating an importance index

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Summary

1. An unresolved question in plant ecology is how the balance between positive and negative interactions changes with environmental conditions. Recently, the debate has been expanded by Brooker & Kikvidze (2008), reintroducing the importance, rather than the intensity, of interactions as the appropriate concept for empirical studies. Importance is the difference in performance with interactions relative to all affecting factors.

2. Positive interactions among plants (facilitation) are common in nature. However, the advocated importance indices fail to address facilitation and can thus not be applied to studying shifts in the balance between positive and negative interactions. The deficiencies of the current importance indices are both conceptual as well as mathematical. In particular, their maximum performance estimator is based on the assumption that it can only be attained in the absence of neighbours.

3. We suggest two major improvements. First, we use the target's overall maximum performance as a surrogate for the plant optimum, i.e. we allow the possibility of higher performance with neighbours (i.e. facilitation). Second, we propose an alternative approach to treat the factors affecting measured performance. The new index is limited in its range [−1, 1], is symmetrical for competition and facilitation, and it preserves the intuitive nature of the original index by Brooker & Kikvidze (2008).

4. *Synthesis*. The concept of interaction importance is useful for studying interactions along environmental gradients. In contrast to previous indices, our index accommodates facilitative interactions and thus offers a significant conceptual and methodological advancement. We advocate its use in future empirical studies.

Key-words: competition, environmental gradients, facilitation, indices, plant interactions

Introduction

One of the common goals in plant ecology is to understand the role of biotic interactions in structuring plant communities relative to abiotic environmental effects. As the direction and intensity of plant–plant interactions critically depend on abiotic conditions, it is especially important, although empirically difficult, to disentangle these relationships. Although theory provides a conceptual framework (e.g. the stress gradient hypothesis based on Bertness & Callaway 1994), only recently has an attempt been made to quantify these relationships and unify the quantification onto a common scale (Brooker *et al.* 2005; Brooker & Kikvidze 2008). At the centre of this attempt lies a renewed interest in the conceptual distinction between intensity and importance (Welden & Slauson 1986). Namely, intensity describes the absolute impact of interactions on plant performance, irrespective of other factors in the system (Brooker *et al.* 2005). Importance, on the other hand, is a relative measure which describes the difference in an organism's performance in the presence of interactions relative to the impact of other factors, of which the abiotic environment is a central one (Welden & Slauson 1986).

When quantifying the role of biotic interactions relative to other factors, it is important to maintain applicability for experimental studies. Specifically, measuring the importance of an interaction requires knowledge of the organism's performance under optimal conditions, as well as the separate effect of the biotic and abiotic interactions (Welden & Slauson 1986). Because it is extremely difficult to isolate all possible environmental factors, direct measurement of importance is practically impossible. This is especially true when importance of interactions is measured via their impact on population growth (e.g. Freckleton, Watkinson & Rees 2009). Nevertheless, Brooker and his colleagues suggested an index which was especially designed to measure the importance of such interactions relative to other influential factors on plant performance, and

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in particular relative to the effect of environmental stress (Brooker *et al.* 2005; Brooker & Kikvidze 2008). An appealing property of this index is that it can be calculated from field data that are obtained from studies measuring the intensity of interactions via neighbour removal.

However, the suggested importance index (C_{imp}) and the discussion concerning its use are centred on negative interactions, and the index cannot be applied without problems to cases in which facilitation is involved. This is surprising for several reasons. First, the importance index was developed by authors who have worked intensively on positive interactions and have highlighted their ubiquitous nature (e.g. Brooker *et al.* 2008). Second, there has been ample discussion concerning indices of interaction intensity (e.g. Weigelt & Jolliffe 2003), including their usefulness for quantifying positive interactions. As a result, earlier intensity indices were replaced by others because they could not be satisfactorily applied to cases in which positive interactions were observed (Markham & Chanway 1996). More recent and frequently used intensity indices, such as the lnRR (Goldberg *et al.* 1999), RNE (Markham & Chanway 1996) and RII (Armas, Ordiales & Pugnaire 2004), were developed especially to be consistent with the presence of facilitative interactions (e.g. Weigelt & Jolliffe 2003; Armas, Ordiales & Pugnaire 2004). According to these studies, intensity indices should ideally be relative and include a limited numerical range, thus enabling comparison of results generated in different conditions and ecosystems, and they should be symmetrical for reflecting negative and positive interactions on a common scale (Armas, Ordiales & Pugnaire 2004).

Preferably, indices of importance should conform to similar requirements as do interaction intensity indices. However, as we will demonstrate, current indices do not fulfil these requirements. Therefore, we propose adjustments to overcome some of the conceptual and methodological insufficiencies, mainly their failure of adequately addressing positive interactions. Unfortunately, because of conceptual differences, not all criteria suggested for intensity indices can be equally applied to importance indices. Intensity indices study local performance of a target plant and evaluate the change in performance because of neighbours' presence. Importance indices, on the other hand, assume that the observed plant performance is smaller than its performance under optimal conditions because of environmental constraints. Their goal is to assess the contribution of neighbours to the deviation from the optimum relative to that of other factors. When neighbours negatively affect the target plant, performance is further distanced from the optimum. When neighbours positively affect plant performance, their effect partially compensates for environmental factors and brings the plant closer to its optimal performance. Consequently, importance indices use three parameters, rather than two (namely, performance with and without neighbours and optimal performance). Therefore, an importance index can be either intuitive and simple or symmetrical, but not both (see Appendix S1 in Supporting Information for an elaboration on the problem). Based on the aforementioned criteria, we present here a significant improvement to current indices that will enable a better and more flexible use of the concept of importance in the future. In the following, we describe the conceptual and mathematical problems inherent to existing importance indices. We then propose simple but effective improvements that not only maintain the initial features, but also fulfil the requested characteristics.

C_{imp} – characteristics and critiques

The ecological literature has witnessed intense debates concerning the role and effectiveness of indices assessing interaction strength and contribution (e.g. Freckleton & Watkinson 1999; Peltzer 1999; Weigelt & Jolliffe 2003). It was often argued that such indices are not informative, because they confound several effects (e.g. inter- and intraspecific effects), or because they are based on short-term effects and a limited range of performance parameters within the organism's life cycle. Thus, these indices were criticized for not providing clear insights into population dynamics (Freckleton & Watkinson 1999; Freckleton, Watkinson & Rees 2009). In addition, the analysis of their statistical properties is complex as it is based on ratios (Jasienski & Bazzaz 1999). In this note, we do not attempt to answer or refute these statements. Rather, we assume that indices can be applied to any performance parameter, including integrative 'fitness' measures which are entirely subject to the experimenter's decision. Additionally, with the rapid development of modern and flexible statistical tools (e.g. GLM models and randomization tests) and cautious interpretation, the simple and unifying characteristics of interaction indices make them a useful tool for comparative studies in both community and population ecology. Finally, we believe that their frequent usage and popularity, particularly in disentangling the role of interactions along environmental gradients, justifies improvements of existing indices for the benefit of future studies.

C_{imp}, as advocated by Brooker and his colleagues (Brooker *et al.* 2005; Brooker & Kikvidze 2008), appears to suffer from both conceptual and mathematical deficiencies. Conceptually, the importance index quantifies the plant's deviance from its optimum (Welden & Slauson 1986). Theoretically, an optimal performance must be higher than or at least equal to the performance with biotic interactions. However, from a realistic point of view, an absolute optimum cannot be attained. Growing the species in controlled artificial conditions may provide an optimum estimation, but it will always be biased. Therefore, both Welden & Slauson (1986) and Brooker *et al.* (2005) suggested using the restricted knowledge from the current experiment to approximate a local optimum. Specifically, the maximum value of plant performance without neighbours along the studied environmental gradient may be used as a proxy for the plant's optimal performance. However, this definition fails when positive interactions occur, which are common in many ecological systems (Callaway 1995; Brooker *et al.* 2008). In such cases, the presence of neighbours may ameliorate environmental conditions (e.g. resource availability), so that

conditions become more similar to the ones provided in the theoretical, unknown optimum point.

This conceptual problem has also mathematical consequences that are highly undesirable for an index (see Table 1 for abbreviations of parameters in the following text). As summarized in Table 2, the problems of calculating C_{imp} (*sensu* Brooker *et al.* 2005) in the presence of facilitation can be best observed when the index is calculated for the point along the gradient for which the estimated optimum conditions (maximum performance) were obtained (i.e. $P_{-N} = MP_{-N}$). Once $P_{-N} = MP_{-N}$, then for all neighbour densities greater than zero, $C_{imp} = -1$ when the net biotic interactions are negative (competition); $C_{imp} = \frac{P_{+\mathrm{N}} - P_{-\mathrm{N}}}{0}$, if plants experience facilitation; and $C_{imp} = \frac{0}{0}$, which is undefined mathematically, in cases where biotic interactions do not affect the plants (neutral interactions or balance between positive and negative interactions).

A simple solution to the above conceptual and methodological deficiencies is to change the parameter describing the optimum estimator (MP_{-N}) to allow also cases in which maximum performance is found in the presence of neighbours ($MP_{\pm N}$). This first step is similar to the derivation of RNE from previous intensity indices (Markham & Chanway 1996), but is based on a somewhat different justification. In the practical definition of the importance index, maximum performance is used as a surrogate for the plant's performance in optimum conditions. Thus, when neighbours improve conditions (e.g. Callaway 2007), the target's theoretical optimum may be closer to a condition with rather than without neighbours.

The index's new form is then:

$$C'_{\mathrm{imp}} = \begin{cases} \frac{P_{+\mathrm{N}} - P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}} - \min\{P_{-\mathrm{N}}, P_{+\mathrm{N}}\}} & P_{-\mathrm{N}} \neq P_{+\mathrm{N}} \\ 0 & P_{-\mathrm{N}} = P_{+\mathrm{N}} \end{cases} \qquad \text{eqn 1}$$

The characteristics of the suggested index are summarized in Table 2. As can be seen, the modified index has now a limited range [−1, 1] and thus is closer to the desired properties. When only negative interactions are observed,

Table 1. Parameters in the text. Plant performance can be either physiological measurements, taken at a single point in time, or demographic performance, either measured at one point in time or as integrated fitness measure

Symbol	Meaning
$P_{-\mathrm{N}}$	Performance of the target plant in the absence of neighbours
$P_{+\mathrm{N}}$	Performance of the target plant in the presence of neighbours
$MP_{-\mathrm{N}}$	The maximum $P_{-\mathrm{N}}$ value in the studied system
$MP_{\pm\mathrm{N}}$	The maximum value of plant performance in the studied system, regardless of neighbours
N_{imp}	Neighbour contribution to plant performance (see eqn 3)
E_{imp}	Environmental contribution to plant performance (see eqn 4)

Table 2. Properties of the four importance indices. C_{imp} is the index used by Brooker *et al.* (2005); RNI was suggested by Kikvidze & Armas (2010); C'_{imp} and I_{imp} are variations suggested here. Parameters are defined in Table 1. In this table, we ignore conditions, in which indices are not defined ($P_{-\mathrm{N}} = MP_{-\mathrm{N}}$, for C_{imp} and $P_{+\mathrm{N}} + P_{-\mathrm{N}} = 2MP_{-\mathrm{N}}$ for RNI). Note that facilitation does not necessitate $MP_{-\mathrm{N}} < MP_{\pm\mathrm{N}}$ and competition does not necessitate $MP_{+\mathrm{N}} < MP_{\pm\mathrm{N}}$

Conditions	C_{imp}	C'_{imp}	RNI	I_{imp}
General equation	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{-\mathrm{N}}-\min\{P_{-\mathrm{N}},P_{+\mathrm{N}}\}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}}-\min\{P_{-\mathrm{N}},P_{+\mathrm{N}}\}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{2MP_{-\mathrm{N}}-P_{+\mathrm{N}}-P_{-\mathrm{N}}}$	$\frac{N_{imp}}{\lvert N_{imp}\rvert+\lvert E_{imp}\rvert}$
Competition ($0 \leq P_{+\mathrm{N}} < P_{-\mathrm{N}}$)	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{-\mathrm{N}}-P_{+\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}}-P_{+\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{2MP_{-\mathrm{N}}-P_{+\mathrm{N}}-P_{-\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}}-P_{+\mathrm{N}}}$
Facilitation ($P_{-\mathrm{N}} < P_{+\mathrm{N}} < \infty$)	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{-\mathrm{N}}-P_{-\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}}-P_{-\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{2MP_{-\mathrm{N}}-P_{+\mathrm{N}}-P_{-\mathrm{N}}}$	$\frac{P_{+\mathrm{N}}-P_{-\mathrm{N}}}{MP_{\pm\mathrm{N}}-2P_{-\mathrm{N}}+P_{+\mathrm{N}}}$
Range according to interaction type				
Competition	$[-1, 0)$	$[-1, 0)$	$[-1, 0)$	$[-1, 0)$
Neutral	0	0	0	0
Facilitation	$(0, \infty)$	$(0, 1]$	$\begin{cases} (0, \infty) & P_{-\mathrm{N}} < P_{+\mathrm{N}} < 2MP_{-\mathrm{N}} - P_{-\mathrm{N}} \\ (-\infty, -1) & 2MP_{-\mathrm{N}} - P_{-\mathrm{N}} < P_{+\mathrm{N}} \end{cases}$	$(0, 1]$
Symmetry	No	No	No	Yes (for $0 \leq P_{+\mathrm{N}} \leq 2P_{-\mathrm{N}}$)

the index is identical to the original C_{imp}. However, it can now accommodate facilitation between the plants.

The suggested C'_{imp} is a simple but efficient first improvement of the existing index, whose main advantage is that it maintains all features advocated by Brooker *et al.* (2005). However, both C_{imp} and C'_{imp} are not symmetrical, complicating the comparison of the index values when both positive and negative interactions occur (see Fig. 1, Appendix S1). Specifically, the indices decrease nonlinearly with negative interactions, but increase linearly with positive interactions.

I_{imp} – an improved index of importance

We propose a different approach for the construction of importance indices, following the original philosophy behind Welden & Slauson (1986). Accordingly, the importance of biotic interactions is their effect relative to that of all processes shifting performance from the optimum. Practically, local plant performance is affected by two components: deviation of the local environmental conditions from the optimum and neighbour effects on performance.

Recently, Kikvidze & Armas (2010) suggested a new index (relative neighbour importance; RNI), which is based on a similar biological logic. The denominator of RNI is calculated as the sum of two differences: the deviation of plant performance from the optimum under a full set of factors, including neighbours ($MP_{-N} - P_{+N}$), and the deviation as a result of local environmental conditions ($MP_{-N} - P_{-N}$):

$$\mathrm{RNI} = \frac{P_{+N} - P_{-N}}{2MP_{-N} - P_{+N} - P_{-N}} \qquad \text{eqn 2}$$

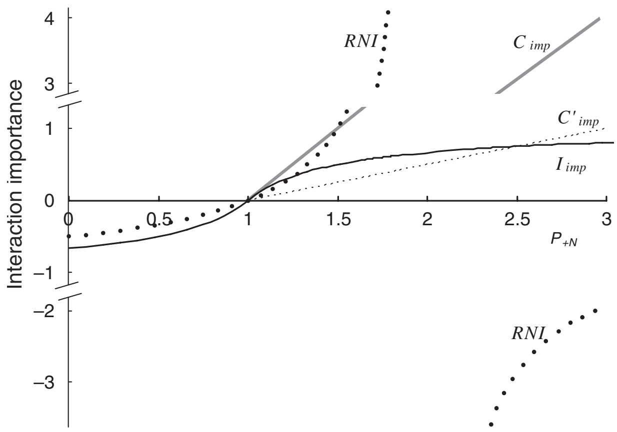

Fig. 1. Indices behaviour as a function of the effect of neighbours (P_{+N}). The example was calculated for the following values: $P_{-N} = 1$; $MP_{-N} = 1.5$; $MP_{\pm N} = 3$. Note that while I_{imp} shows symmetry for P_{+N} values between 0 and 2, and is increasing asymptotically for larger P_{+N} values, both C_{imp} and C'_{imp} show linear increase when facilitation occurs. While C'_{imp} reaches the value 1 once $P_{+N} = MP_{\pm N}$, C_{imp} reaches the value 4 and can reach, under different conditions, much higher values. In cases of competitive interactions C_{imp}, C'_{imp} and I_{imp} indices show similar behaviour. RNI is not limited and discontinuous around $P_{+N} = 2$.

However, mathematically, the performance of RNI under positive interactions is the least desirable among all previous indices (Table 2, Fig. 1).

We therefore present an alternative which maintains a similar biological logic, but performs better mathematically. We calculate separately the absolute magnitude of neighbour and environment effects on the target plants, and then use these two values for calculating the relative contribution of neighbour presence. The contribution of biotic interactions to plant performance, N_{imp}, is defined as the difference between performance with and without neighbours:

$$N_{\mathrm{imp}} = P_{+N} - P_{-N} \qquad \text{eqn 3}$$

where $-P_{-N} \le N_{\mathrm{imp}} < \infty$.

Environmental effects on plant performance can be derived from the difference between the maximum plant performance and its performance in the specific location in the absence of neighbours:

$$E_{\mathrm{imp}} = P_{-N} - MP_{\pm N} \qquad \text{eqn 4}$$

where $-MP_{\pm N} \le E_{imp} \le 0$.

We propose that the new importance index (I_{imp}) be defined as follows:

$$I_{imp} = \begin{cases} \frac{N_{imp}}{|N_{imp}| + |E_{imp}|} & |N_{imp}| + |E_{imp}| > 0 \\ 0 & |N_{imp}| + |E_{imp}| = 0 \end{cases} \qquad \text{eqn 5}$$

This index represents, in an intuitive manner, the magnitude of biotic interactions (either positive or negative) relative to the total magnitude of all factors (environmental and biotic ones) on the plant at the studied location, maintaining the original definition of interaction importance (Welden & Slauson 1986). The characteristics of the index are summarized in Table 2. Because the denominator is not smaller than the absolute value of the numerator, the index has a finite range for both negative and positive interactions. In addition, albeit the inherent problems of attaining symmetry in importance indices (see Appendix S1), our index exhibits symmetry in the range of 0–200% change in plant performance because of neighbour influence (Fig. 1). This range is relatively large and therefore we expect this index to be symmetrical in most ecological studies.

Comparing the indices

To further explore the different dynamics of the four indices, we constructed a hypothetical model system, in which neighbour effect on plant performance varied along an environmental (or stress) gradient. Using the model, we visually compared the indices' behaviour under three neighbour effect scenarios (Fig. 2a): (i) neighbour presence decreased plant performance along the gradient; (ii) neighbour presence increased plant performance along the gradient; (iii) neighbours switched their

effect from negative to positive along the gradient. To facilitate the comparison among indices, scenarios (i) and (ii) were designed to be symmetric relative to the performance without neighbours (P_{-N}). The slope of scenario (iii) is the same as that of scenario (i) (Fig. 2a).

The results confirmed our conclusions that the characteristics of C_{imp} and RNI hinder simple usage and interpretation of the results. In the case of C_{imp}, its asymmetry when comparing facilitative and competitive situations can clearly be detected (Fig. 2b) as can the loss of data when $P_{+N} > MP_{-N}$. In the case of RNI, the asymmetry problem is aggravated by a non-continuous behaviour as stress levels change gradually (Fig. 2c). C'_{imp} and I_{imp} are a clear improvement because both present limited value ranges that enable easier comparison of results (Fig. 2d,e). Nevertheless, the superiority of I_{imp} in capturing the nature of interactions is readily seen. In particular, for scenarios (i) (competition) and (ii) (facilitation), I_{imp} provides symmetrical results. This better represents the similar proportion of neighbour contributions in the two scenarios (Fig. 2e). An inspection of scenario (iii) reveals that the index turns from convex to concave when interactions shift from competition to facilitation. This feature is important mathematically as it is required to attain symmetry and hence to enable similar interpretation of the index values under all possible conditions.

An additional example for performance of the four indices using field data can be found in Appendix S2.

Conclusions

The properties of a useful importance index can be defined in accordance with previous discussions about intensity indices. This index should have a limited range and a relative scale to enable comparisons between ecosystems and experiments. Another convenient property is symmetry under a wide range of conditions, which enables simple and consistent conclusions, irrespective of whether the predominant interaction type is competition or facilitation. Finally, a useful index should be highly intuitive, i.e. specific values should be interpreted with ease.

Three of the importance indices presented here behave identically when only competition is observed (C_{imp}, C'_{imp}, I_{imp}). However, the limitations of the original index (C_{imp}; Brooker *et al.* 2005) are obvious when facilitation occurs in the system. As the main goal of transforming absolute performance observations into unified index units is to enable comparison of results among treatments or between studies, it is particularly important that the index will act similarly under different conditions. This is especially crucial when studying the role of biotic interactions relative to abiotic conditions, where both

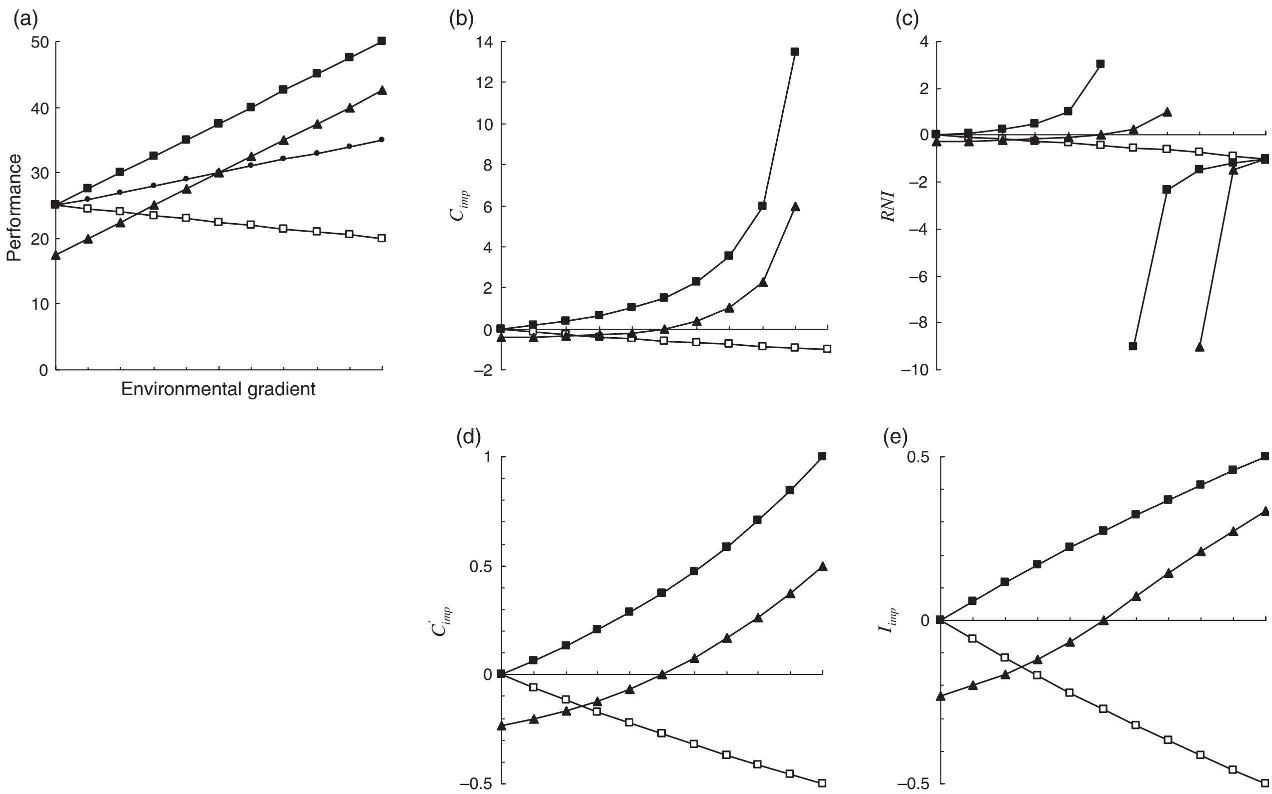

Fig. 2. Comparative behaviour of the indices along a hypothetical environmental gradient. The four indices were calculated for three different scenarios, in which neighbour effects vary continuously along an environmental gradient: (i) facilitation increases along the gradient (■); (ii) competition increases along the gradient (□); (iii) neighbour effect shifts from competition to facilitation (▲). (a) Plant performance (•, performance without neighbours); (b) C_{imp} values under the three scenarios; (c) RNI values; (d) C'_{imp} values; (e) I_{imp} values. The *x*-axis (environmental gradient) has the same scale in all five subfigures.

positive and negative biotic effects are frequently observed in parallel treatments (e.g. Callaway & Walker 1997; Pugnaire & Luque 2001; Maestre, Bautista & Cortina 2003).

Among the two new indices suggested here, I_{imp} is superior, because it has, besides the limited range (which it shares with C'_{imp}), also similar (although not identical) behaviour under both positive and negative interactions. Namely, the index has an additive symmetry around the plant's performance values in the absence of neighbours, so that if $P^1_{+\text{N}} = P_{-\text{N}} - X$ and $P^2_{+\text{N}} = P_{-\text{N}} + X$, we obtain $I_{\text{imp}(P^1_{+\text{N}})} = -I_{\text{imp}(P^2_{+\text{N}})}$. Thus, taking into account the above requirements, I_{imp} best fulfils the requirements for an importance index. However, we also suggest that index values should always be accompanied by relevant performance values in the measured units, to enable a clear interpretation of biotic interactions in the particular context.

Acknowledgements

We thank Z. Kikvidze, the Handling Editor and an anonymous referee for valuable comments and discussion on early version of this manuscript and C. Armas for supporting discussions and help concerning RNI. We acknowledge funding by the DFG (FK Ti 338/4–3) to T.S. and K.T. and the GLOWA Jordan River project, funded by the German Federal Ministry of Education and Research (BMBF), to C.A. and K.T.

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Received 3 July 2009; accepted 17 November 2009
Handling Editor: Jason Fridley

Supporting Informaiton

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Appendix S1. The search for symmetry in importance indices.

Appendix S2. Application of the four importance indices to a case study.

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