

## REVIEW

# A new family of standardized and symmetric indices for measuring the intensity and importance of plant neighbour effects

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## Summary

1. Measurements of competition and facilitation between plants often rely upon intensity and importance indices that quantify the net effect of neighbours on the performance of a target plant. A systematic analysis of the mathematical behaviour of the indices is lacking and leads to structural pitfalls, e.g. statistical problems detected in importance indices.

2. We summarize and analyse the mathematical properties that the indices should display. We review the properties of the commonly used indices focusing on standardization and symmetry, which are necessary to avoid compromising data interpretation. We introduce a new family of indices ‘Neighbour-effect Indices’ that meet all the proposed properties.

3. Considering the commonly used indices, none of the importance indices are standardized, and only RII (Relative Interaction Index) displays all the required mathematical properties. The existing indices show two types of symmetries, namely, additive or commutative, which are currently confounded, potentially resulting in misleading interpretations. Our Neighbour-effect Indices encompass two intensity and two importance indices that are standardized and have different and defined symmetries.

4. Our new additive intensity index, NInt<sub>A</sub>, is the first of its kind, and it is generally more suitable for assessing competition and facilitation intensity than the widely used RII, which may underestimate facilitation. Our new standardized importance indices solve the main statistical problems that are known to affect  $C_{imp}$  and  $I_{imp}$ . Intensity and importance with the same symmetry should be used within the same study. The Neighbour-effect Indices, sharing the same formulation, will allow for unbiased comparisons between intensity and importance, and between types of symmetry.

**Key-words:** competition, facilitation, plant–plant interactions indices

## Introduction

Plant–plant interactions exert a major impact on the structure and composition of plant communities (Bertness & Callaway 1994; Callaway 1995; Brooker *et al.* 2008). While earlier studies focused on the changing role of competition between plants across productivity gradients (Grime 1977; Tilman 1982), recently additional emphasis on the role of facilitative interactions has been introduced (Callaway & Walker 1997; Pugnaire & Luque 2001; Bruno, Stachowicz & Bertness 2003; Callaway 2007; McIntire & Fajardo 2014; Michalet & Pugnaire 2016). Another shift in focus has occurred between earlier studies considering the intensity of the net effect of plant interactions,

and more recent discussions assessing also their importance, defined as the effect of the interactions on performance, relative to the environmental effects on performance (Welden & Slauson 1986; Brooker & Kikvidze 2008; but see also, e.g. Freckleton, Watkinson & Rees 2009; Damgaard & Fayolle 2010; Rees, Childs & Freckleton 2012; Brooker *et al.* 2013; Mingo 2014a for a debate on the concept of importance).

Normally, the effects of interactions between plants are evaluated by measuring the performance of a target plant, or community of plants, with and without a neighbouring plant species. Performance indicators can be biomass, species richness, cover or seed production, to name a few. The performances measured with and without neighbours are then used to estimate the net effect of the interactions, which may be negative (i.e. competition), neutral, or positive (i.e. facilitation). Indices based on the difference between the performance of a

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species with and without neighbours are commonly used, including, among others: the relative competition index (RCI; Wilson & Keddy 1986), the relative neighbour effect (RNE; Markham & Chanway 1996), and the relative interaction index (RII; Armas, Ordiales & Pugnaire 2004) for intensity; the competition importance ( $C_{imp}$ , Seifan *et al.* 2010; modified from  $C_{imp}$  Brooker *et al.* 2005) and  $I_{imp}$  (Seifan *et al.* 2010) for importance.

Most of these indices, especially the ones conceived for assessing competition, lack some crucial properties to accurately represent the effects of facilitation. The need of comparing the incidence of negative vs. positive effects has led to the realization that indices need to be symmetric (Armas, Ordiales & Pugnaire 2004), or, in other words, they need to return the same value, but with opposite sign, for equivalent cases of competition and facilitation. This understanding has brought in an important correction to the intensity and importance indices, resulting in the introduction of the widely used RII (Armas, Ordiales & Pugnaire 2004) and  $I_{imp}$  (Seifan *et al.* 2010), respectively.

An index is used to quantify an effect by placing it on a certain scale. This scale is inherent to the index, and it has been required to be bounded (Hedges, Gurevitch & Curtis 1999; Armas, Ordiales & Pugnaire 2004; Gómez-Aparicio *et al.* 2004; Oksanen, Sammuli & Mägi 2006; Seifan *et al.* 2010; Mingo 2014b) between a minimum and maximum value. Usually, these values are required to be even, i.e. equal in absolute values (Armas, Ordiales & Pugnaire 2004; Seifan *et al.* 2010; Mingo 2014b). However, it has been shown recently that uneven boundaries are inevitable for  $I_{imp}$  (Mingo 2014b), and therefore importance index ranges should be reported with results (Seifan & Seifan 2015). The boundary (un)evenness is connected to the index symmetries (Seifan & Seifan 2015), which can be of different types (e.g. Seifan & Seifan 2015 defined recently 'additive' and 'multiplicative' symmetries). These symmetries are used interchangeably in intensity and importance indices so far, and the implications for their ecological meaning have not been clarified. Also, the problematic nature of multiplicative importance indices has been established (Seifan & Seifan 2015), but no alternative for this symmetry has been proposed. In general, we lack a comprehensive analysis of the mathematical properties of intensity and importance indices, while importance indices still suffer from unresolved statistical problems (Rees, Childs & Freckleton 2012; Brooker *et al.* 2013; Mingo 2014a).

A careful understanding of the index properties, including boundaries and symmetry, is required for all ecological applications, and is especially relevant now, as the complexity of the analysis based on intensity or importance indices has progressively increased. The first studies merely asserted the existence of facilitation and/or looked for the general trend of neighbour effects over stress gradients (e.g. indices as increasing, decreasing or hump-shaped functions of stress, e.g. Callaway *et al.* 2002; Brooker *et al.* 2006). Recently, the numerical values of the indices are used in more involved calculations, such as relating them with other types of ecosystem properties (Wang *et al.* 2014), using them to estimate the relevance of indirect

interactions (Michalet *et al.* 2015), to compare beneficiary effects with the feedback effect of the target species on its benefactor (Schöb *et al.* 2014), to estimate the impact of climate change on plant communities (Metz & Tielbörger 2016) and as parameters to simulate plant interactions (Xiao *et al.* 2012; Bulleri *et al.* 2014) or in large-scale metastudies (He, Bertness & Altieri 2013). In several cases, studies use more than one index to analyse a single data set because they recognized that each index provided different insights on the properties of the system (e.g. Goldberg *et al.* 1999; le Roux & McGeoch 2010; He *et al.* 2012).

Here, we provide guidelines to choose the appropriate index (or indices) for a given study. To achieve our aim, we first list a set of mathematical properties that any intensity or importance index should display. We show that index symmetry, which is fundamental for determining the index ecological meaning, is still not completely defined for importance. Surprisingly, we find that all of the current indices for intensity and importance fail to show all of the necessary properties (except for the intensity index RII). To overcome these problems, we introduce a new general set of indices, encompassing intensity and importance, which display all of the properties, and we compare them in terms of their symmetry and their ecological meaning. We finally illustrate the use of these indices, and present some general guidelines to their use, with the help of examples where the indices are applied to previously published data.

## Mathematical properties of intensity and importance indices

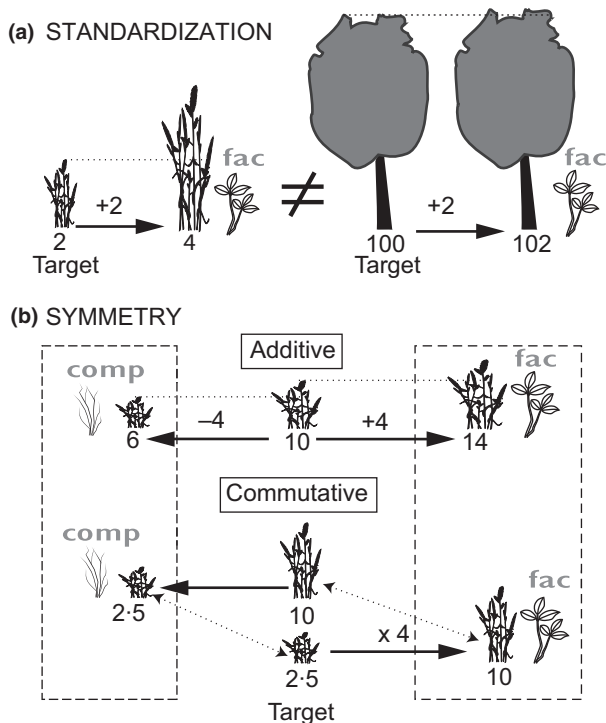
Here, we define a minimal set of properties that any neighbour-effect index should display. We introduce these properties having in mind that indices need to be mathematically consistent and intuitive, and partly based on considerations reported in previous works (Hedges, Gurevitch & Curtis 1999; Armas, Ordiales & Pugnaire 2004; Seifan *et al.* 2010; Mingo 2014a,b; Seifan & Seifan 2015). Tables 2 and 3 summarize how the indices mentioned in this study perform for each criterion.

### STANDARDIZATION

Any index should reflect the effect of neighbours in relation to a certain species-specific quantity that allows for comparisons across a large set of conditions. For instance, the relevance of a certain increase in biomass (due to facilitation) will depend on the type of plant studied. For example, an increase of 2 biomass units should weigh more for a small plant (e.g. biomass change from 2 to 4 biomass units, Fig. 1a left) than for a large plant (biomass change from 100 to 102 biomass units, Fig. 1a right).

### SYMMETRY

An index is symmetrical if 'equivalent' cases of competition and facilitation have the same value but opposite sign. Symmetry is essential because it guarantees unbiased comparisons



**Fig. 1.** Graphical comparison of neighbour treatments to illustrate standardization and symmetry properties: (a) The performance of two target species (small grass, left; and large tree, right) experienced the same increase in biomass ( $\Delta P = 2$ ) when introducing a facilitative ('fac') neighbour. The relative effect of neighbours on the biomass in each target species is different (symbol 'not equal') because of the different initial sizes (2 for grass and 100 for tree). A proper standardization is meant to correct for this type of effects. (b) Competitive (left, 'comp') and facilitative (right, 'fac') treatments are applied to a target species of 10 units of biomass. Additive symmetry (top panel) sets two situations displaying increasing (facilitation) or decreasing (competition) plant biomass by 4 units. Commutative symmetry (bottom panel) sets two reciprocal cases, facilitation from 2.5 units to 10 units and competition from 10 units to 2.5 units, as opposite and equivalent neighbour effects.

between competition and facilitation (Hedges, Gurevitch & Curtis 1999; Armas, Ordiales & Pugnaire 2004; Seifan *et al.* 2010). Even though this concept of equivalence may seem ecologically difficult to define, it is, however, implicitly present in all the indices.

Symmetry of neighbour-effect indices has been addressed before (Armas, Ordiales & Pugnaire 2004; Seifan *et al.* 2010; Seifan & Seifan 2015), but different concepts have been used interchangeably (Seifan *et al.* 2010; Mingo 2014b), and there is no theoretical frame for symmetry that suits both intensity and importance indices (Seifan & Seifan 2015). Here, we use the additive symmetry (formally defined in Seifan & Seifan 2015) and introduce formally the 'commutative' symmetry (implicitly used in Armas, Ordiales & Pugnaire 2004), which is closely related to multiplicative symmetry (as defined by Seifan & Seifan 2015), but it is also suitable for importance indices.

Let us consider a 'classical' experimental set-up, where the performance  $P$  of the target species is measured in: (i) isolation, i.e. the control case ( $P_{-N}$ ; see Table 1 for symbols used in this study), and (ii) in the presence of neighbours

**Table 1.** Main symbols used in this study

Symbol	Meaning
$P_{-N}$	Performance of the target species without neighbours
$P_{+N}$	Performance of the target species with neighbours
$\Delta P = P_{+N} - P_{-N}$	The total impact of neighbours
$P_{\text{sum}} = P_{+N} + P_{-N}$	Sum of the performances of the target species with and without neighbours
$P_w$	Generic weighting term in Neighbour-effect Indices
$MP_{-N}$	The maximum value of target species without neighbours along the gradient
$MP_{\text{sum}}$	The maximum value of the sum of the performances of the target species with and without neighbours along the gradient.
$N\text{Ind}_S$	Neighbour-effect Indices
$N\text{Int}_A$	Neighbour-effect Intensity index with additive symmetry
$N\text{Int}_C$	Neighbour-effect Intensity index with commutative symmetry
$N\text{Imp}_A$	Neighbour-effect Importance index with additive symmetry
$N\text{Imp}_C$	Neighbour-effect Importance index with commutative symmetry

( $P_{+N}$ ). Indices displaying different symmetries will differ in the following way:

- 1 An additively symmetric index (called additive index hereafter for brevity) provides equal but opposite values when equivalent 'amounts' of competition and facilitation modify the performance in the absence of neighbours ( $P_{-N}$ ), by the same amount  $\Delta P$ , which is defined as the difference between the performance with and without neighbours ( $\Delta P = P_{+N} - P_{-N}$ ; e.g., 4 biomass units in Fig. 1b, top panel). An additive index assigns the same absolute value to these two cases, but with opposite sign. Additive symmetry is the most intuitive symmetry in most experimental set-ups because an equal amount of biomass increase or decrease corresponds to the same but opposite index values.
- 2 A commutatively symmetric index (commutative index in the following) provides equal but opposite values when the target performances alone ( $P_{-N}$ ) and under a competitive (or facilitative) neighbour, ( $P_{+N}$ ), are exchanged (Fig. 1b). For example (Fig. 1b, bottom panel), an intensity commutative index will indicate that two treatments are opposite and equivalent when one reduces biomass from 10 to 2.5 units while the other increases biomass from 2.5 to 10 units.

Commutative symmetry coincides with multiplicative (*sensu* Seifan & Seifan 2015) for intensity indices (see Appendix S1, Supporting Information for a formal proof). However, commutative symmetry has the advantage of being applicable also for importance indices, while multiplicative symmetry has flows for these (Seifan & Seifan 2015). Noticeably, we show that it is not possible to define multiplicative standardized importance indices, as they would display counterintuitive values (see Appendix S2 for a proof, and an illustration in Fig. S4).

## BOUNDEDNESS

The limits of the indices should be finite (Hedges, Gurevitch & Curtis 1999; Armas, Ordiales & Pugnaire 2004; Gómez-Aparicio *et al.* 2004; Oksanen, Sammul & Mägi 2006), providing a fixed frame so that values of different experiments can be compared. Finite boundaries are usually standardized to  $-1$  and  $1$ , implicitly assuming that limits need to be even as well (e.g. Mingo 2014b).

We argue here that for both intensity and importance defining indices with even boundaries is fundamentally not always possible because of the intrinsic differences between competitive and facilitative effects. In the classical experimental set-up described above ('Symmetry' section), neighbours can reduce the performance of the target species to the point of competitive exclusion. Thus, the difference between the performance with and without neighbours ( $\Delta P$ ) can vary between zero and a finite negative value ( $-P_{-N} \leq \Delta P \leq 0$ ). Facilitative neighbours, however, can *a priori* increase the performance of a target species to a non-finite larger value (i.e.  $P_{+N} < \infty$  and  $0 \leq \Delta P < \infty$ ), which is not as clearly bounded as  $0$ , as is the case with competitive neighbours. For this fairly common experimental set-up, competitive and facilitative effects are not additively symmetric (as defined by Seifan & Seifan 2015 and above). Therefore, for additive indices we do not consider equal limits for facilitation and competition as a necessary requirement for a neighbour-effect index.

## ERROR ESTIMATIONS AND STATISTICAL SIGNIFICANCE

To be used in statistical analyses, indices should allow the calculation of their confidence interval, which requires continuity and differentiability. For this reason, indices that include terms that vary in case of facilitation or competition (e.g. max or min functions as in RNE or  $C'_{\text{imp}}$ ) are not preferred (Armas, Ordiales & Pugnaire 2004).

In addition to the formal properties just mentioned, which can be mathematically defined and checked (see Appendix S1), we maintain that indices should pass a more subjective test: they should have an intuitive interpretation. An index transforms data by simplifying the information included. The formulas used to calculate these indices besides satisfying the abovementioned properties should have a fully understandable ecological meaning. In particular, index sensitivity, i.e. how it responds to small changes in the performances, should be checked to verify that it corresponds to its expected behaviour (see Appendix S1).

## Current indices and their properties

By inventorying the properties of the intensity and importance indices most commonly used in the literature, we found that only one of the intensity indices (RII) showed all of the above-listed properties, and that none of the importance indices did (see Table 2). All of the intensity indices were standardized, but, strikingly, none of the importance indices ( $C'_{\text{imp}}$  and  $I_{\text{imp}}$ ) were. This problem in the importance indices resulted from the

definition of importance as the ratio between the neighbour-driven change in performance, and the change in performance driven by 'all the factors in the environment that influence plant success' (Brooker & Kikvidze 2008). Using this approach, the total impact was not expressed relatively to the performance of the target species. Lack of standardization in importance indices means that one cannot use them to compare across situations where species, or other conditions, differ. Referring to the previous example (Fig. 1a, and also Figs 2a,b), an equal change in biomass has a very different relevance for a small or a large plant. This is completely not captured by the current indices, which instead give the same importance value to both situations (see, e.g.  $I_{\text{imp}}$  in Fig. 2a,b). This is a key limitation of the current importance indices that has not been recognized so far, and for which a solution is urgently needed.

Relative competition index and  $I_{\text{imp}}$  showed additive symmetry, whereas RNE, lnRR and RII showed commutative and multiplicative symmetries (Armas, Ordiales & Pugnaire 2004).  $C'_{\text{imp}}$  showed commutative symmetry.

The indices originally designed to assess competition (such as RCI and lnRR for intensity, and  $C'_{\text{imp}}$  for importance) were not bounded as they did not have a finite limit for extreme cases of facilitation (Armas, Ordiales & Pugnaire 2004; Seifan *et al.* 2010). The unboundedness of RCI and lnRR is problematic (Callaway 2007) and, for example, made RCI inapplicable in a large number of cases (Gómez-Aparicio *et al.* 2004; Oksanen, Sammul & Mägi 2006). Some corrections have been proposed *a posteriori* for some of these indices which, however, introduced new issues. The use of terms such as the maximum or minimum performance added, for example, to correct RNE and  $C'_{\text{imp}}$  prevented the calculation of error propagation (as pointed out by Armas, Ordiales & Pugnaire 2004 for RNE; see also Seifan *et al.* 2010). In fact, RNE can be rewritten to avoid such problem, as we show below. All the bounded indices have even boundaries,  $-1$  and  $1$ , with the exception of  $I_{\text{imp}}$  whose practical boundaries are  $-1$  and  $1/2$  (Mingo 2014a,b).

In summary, this examination of current index properties indicated that we were currently lacking a standardized importance index, and that only one intensity index (RII) showed the four required mathematical properties. It is noteworthy that RII is bounded and has a commutative (and thus multiplicative) symmetry, but that none of the additive symmetric intensity indices is bounded, even though, as we noted above, additive symmetry provides the most intuitive interpretation for most standard experimental set-ups (Fig. 1b). To fulfil the need for indices that display all the above-listed properties, in the following section we propose a new family of indices for intensity and importance, including intensity indices with additive or commutative symmetry, and standardized importance indices.

## Neighbour-effect Indices

We introduce a family of symmetrical and standardized neighbour-effect indices that we name Neighbour-effect Indices, in short NInd<sub>S</sub> (where the subscript S highlights their symmetric nature). We choose the word 'effect' to underline that the

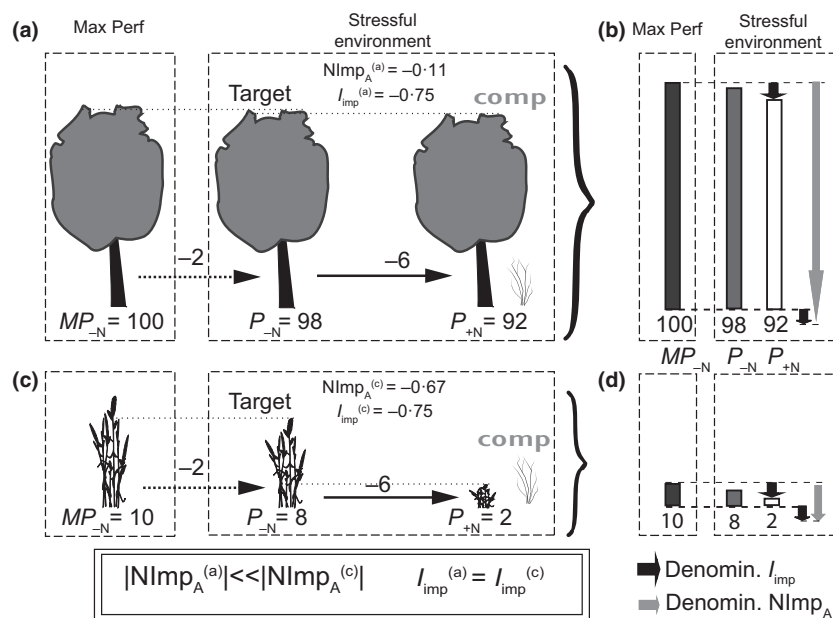


**Table 2.** Summary of the properties of the intensity and importance indices from current literature

Index	Intensity				Importance	
	RCI	RNE	lnRR	RII	$C_{imp}^*$	$I_{imp}$
Formula	$(-)\frac{\Delta P}{P_{-N}}$	$(-)\frac{\Delta P}{\max(P_{-N}, P_{+N})}$	$(-)\ln\left(\frac{P_{-N}}{P_{+N}}\right)$	$\frac{\Delta P}{P_{-N}+P_{+N}}$	$\frac{\Delta P}{MP_{\pm N} - \min(P_{+N}, P_{-N})}^*$	$\frac{\Delta P}{MP_{\pm N} - P_{-N} +  \Delta P }^*$
Standardized	Yes	Yes	Yes	Yes	<b>No</b>	<b>No</b>
Bounded	<b>Unbounded at obligate facilitation</b>	Bounded	<b>Unbounded at extreme competition and obligate facilitation</b>	Bounded	Bounded	Bounded
Min	-1	-1	$-\infty$	-1	-1	-1
Max	$\infty$	1	$\infty$	1	1	+1/2
Symmetry	Additive	Commutative & Multiplicative	Commutative & Multiplicative	Commutative & Multiplicative	Commutative	Additive
Error Estim	Yes	<b>No</b>	Yes	Yes	<b>No</b>	Yes
Reference	Wilson & Keddy (1986)	Markham & Chanway (1996)	Hedges, Gurevitch & Curtis (1999)	Armas, Ordiales & Pugnaire (2004)	Seifan <i>et al.</i> (2010)	Seifan <i>et al.</i> (2010)

\* $MP_{\pm N}$  is the maximum value of target species with and without neighbours along the gradient (Seifan *et al.* 2010).

In bold we underline important shortcomings of the indices. For symbols see Table 1. For the expression of indices errors of RII see Table S1 and Note S1. For the sake of a common notation, the signs of RCI, RNE and lnRR have been changed (negative for competition, positive for facilitation).



**Fig. 2.** Effect of standardization (or lack of) in  $NImp_A$  and in previous importance indices, respectively. Graphical (a, c) and bar chart (b, d). The maximum values ('Max Perf') and the values in a certain stressed environment ('Stressful environment') of the biomasses of a large tree (a–b) and of a small grass (c–d) are measured. The biomasses are  $MP_{-N}$  when maximal (100 and 10 for the tree and grass, respectively),  $P_{-N}$  in a certain stressful environment (98 and 8, respectively) and  $P_{+N}$  with neighbours in the same stressful environment (92 and 2, respectively). The same total impacts of stress (decline of 2) and of neighbours (decline of 6) are observed for both species. The standardized  $NImp_A$  yields to a lower effect of neighbours on the larger plant (a–b) than on the small plant (c–d), whereas the non-standardized  $I_{imp}$  yields to equal values for both plants. The weighing factors, the denominators of the indices, are displayed in panels (b) and (d), black arrows for  $I_{imp}$  (equal length in (b–d)) and grey arrows for  $NImp_A$  (longer arrows in (b) than in (d)). All the biomass values are here expressed in a generic biomass unit. See also Table 1 for symbols.

indices measure the net effects of all the ongoing plant interactions. We define them to have an S-shape (i.e. a sigmoidal function) as:

$$NInd_S = 2 \frac{\Delta P}{P_w + |\Delta P|} \quad \text{eqn 1}$$

where  $\Delta P$  is the total impact of neighbours ( $P_{+N} - P_{-N}$ ) that is positive for facilitation and negative for competition, and  $|\Delta P|$  is its absolute value (i.e. without the sign).  $P_w$  is a weighting, positive term, which will vary case by case as we discuss below (see Table 1 for notation).

Thanks to their sigmoidal formula (eqn 1), the neighbour-effect indices have one general formulation, and show all of the properties listed in the previous section, namely, standardization, boundedness, symmetry and allow for error estimation (see Appendix S1). Other indices proposed before also use the sigmoidal function either explicitly (as in  $I_{\text{imp}}$ , see Table 2 for a rewriting of the index according to our notation) or implicitly (RNE, as we show below). Our indices are bounded and differentiable functions of  $\Delta P$  (as we define  $P_w$  as positive). Thus, our indices overcome all of the common limitations of previous intensity and importance indices. We must note here that the  $\text{NInd}_S$  indices are defined only when plant performance is evaluated with traits that have non-negative values ( $P \geq 0$ ), as is the case for most of the other common indices (Kikvidze & Armas 2010).

The  $\text{NInd}_S$  have a general formulation that, depending on the definition of  $P_w$ , can lead to intensity or importance indices, showing either additive or commutative symmetry. For intensity indices the weighting term  $P_w$  only includes the standardization for size, whereas for importance indices  $P_w$  consists of two weighting terms: the total impact of the environment (stress) and the standardization for size. These weighting terms are specified in the next sections. The general formulation of all the indices within the same family allows for comparing intensity and importance, or indices with different symmetries without introducing spurious differences due to different mathematical formulations of the individual indices.

#### DEFINITION OF NEIGHBOUR-EFFECT INTENSITY INDICES

The effect of neighbours on the performance of a target species is captured within intensity indices by weighting the total impact of neighbours across a wide variety of experimental conditions with respect to a reference performance of the target species. Different choices for this reference performance lead us to define here below an additive index and a commutative (and multiplicative) index.

##### Additive intensity index

We follow here the common practice of using the performance without neighbours as a reference performance (as, e.g. RCI). In our notation, this leads to setting  $P_w = P_{-N}$ , thus obtaining  $\text{NInt}_A$  (Neighbour-effect Intensity index with Additive symmetry):

$$\text{NInt}_A = 2 \frac{\Delta P}{P_{-N} + |\Delta P|} \quad \text{eqn 2}$$

This index will likely be the most common choice for experiments (for reasons that we will illustrate below). This index is  $-1$  for competitive exclusion, and  $+2$  for obligate facilitation and for an infinite increase in the performance of the target species with neighbours.

##### Commutative intensity index

Here, we will use the average of plant performances measured with and without neighbours as a reference term for the impacts of neighbours across studies (similarly to former commutative and multiplicative intensity indices, e.g. RII). In our notation we can choose  $P_w = P_{\text{sum}} = P_{-N} + P_{+N}$  (i.e. twice the average of the plant performances with and without neighbours), thus obtaining  $\text{NInt}_C$  (Neighbour-effect Intensity index with commutative symmetry):

$$\text{NInt}_C = 2 \frac{\Delta P}{P_{\text{sum}} + |\Delta P|} \quad \text{eqn 3}$$

$\text{NInt}_C$  can be reduced to the known RNE (see Appendix S1) with the advantage that our new formulation (eqn 3) solves its main drawback (Armas, Ordiales & Pugnaire 2004). The values of  $\text{NInt}_C$  are  $-1$  for competitive exclusion, and  $+1$  for obligate facilitation and for an infinite increase in performance of the target species with neighbours.

#### DEFINITION OF NEIGHBOUR-EFFECT IMPORTANCE INDICES

Although defined in a more general way (Welden & Slauson 1986), importance has been mainly used for experimental setups including two treatments, where the performance is measured along an environmental gradient and in the absence or presence of neighbours. Importance indices weigh the total impact of neighbours against the total impact of treatments, which include the impact of neighbours and stress (Brooker *et al.* 2005).

We here define two symmetric importance indices, following this definition but taking into account that they also need to be standardized for size (Figs 2 and 3b). The  $\text{NInd}_S$  already include the impact of neighbours in the denominator ( $|\Delta P|$  in eqn 1), thus the weighting term,  $P_w$ , needs to include: (i) an estimation of the impact of the environment on performances and (ii) a term for standardization.

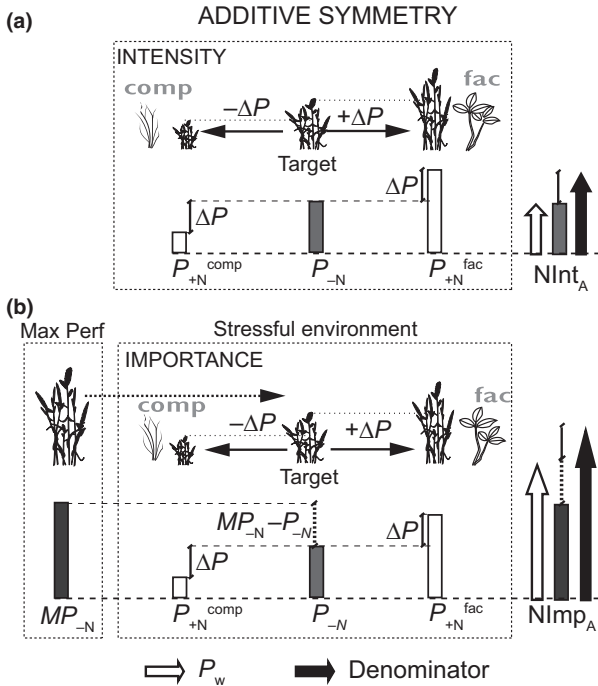
##### Additive importance index

We define the two components of  $P_w$  mentioned above as: (i) the difference in reference performances ( $P_{-N}$ , as for the additive intensity index) between the maximum ( $MP_{-N}$ ) and a given level of stress ( $P_{-N}$ ); and (ii) the maximum of the reference performance along the gradient ( $MP_{-N}$ ). We obtain  $\text{NImp}_A$  (Neighbour-effect Importance with Additive symmetry):

$$\text{NImp}_A = 2 \frac{\Delta P}{2 \cdot MP_{-N} - P_{-N} + |\Delta P|} \quad \text{eqn 4}$$

(see Appendix S2 for a derivation of the formula).

We note that  $\text{NImp}_A$  is closely related to the  $C_{\text{imp}}$  importance index (Brooker *et al.* 2005) and even more to the  $I_{\text{imp}}$  importance index (Seifan *et al.* 2010) which is also a sigmoidal additive importance index. Our index is a relevant improvement of the former two as it includes an extra term in the denominator which includes standardization for size for the first time.



**Fig. 3.** Graphical illustration of how the values of the additive Neighbour-effect Indices are calculated: weighing performance,  $P_w$  (white arrow) and the denominator (black arrow) in  $NInt_A$  and  $NImp_A$ . In both panels, the total impact ( $\Delta P$ , continuous line) is the difference between the performance with (void bars) and without (light grey bars) neighbours. The competitive ('comp') and facilitative ('fac') treatments shown are additively symmetric and, consequently, the quantities  $P_w$  and the index denominators are equal for both of them and shown only once for each index. (a) Intensity: in  $NInt_A$  (eqn 2) the weighing value is the performance without neighbours,  $P_{-N}$  (light grey bar), and the denominator is the former value plus the total impact of neighbours,  $\Delta P$  (continuous line). (b) Importance: in  $NImp_A$  (eqn 4) the weighing performance is the environmental impact ( $MP_{-N} - P_{-N}$ , dashed line) plus the total impact of neighbours,  $\Delta P$  (continuous line); the denominator is the sum of the former weighing value and the performance in the optimal environment ( $MP_{-N}$ , dark grey bar).

As importance includes the effect of the environment, we will give the values for competitive exclusion and obligate facilitation when the environment is optimal. In this case, the index is  $-1$  for competitive exclusion (when the performance of the plant alone is equal to the maximum performance,  $P_{-N} = MP_{-N}$ ), and  $2/3$  for obligate facilitation (when the performance of the plant with neighbours is equal to the maximum performance,  $P_{+N} = MP_{-N}$ ). Independently of the environment,  $NImp_A$  is equal to  $+2$  for an infinite increase in the performance of the target plant with neighbours.

*Commutative importance index*

As for the definition of  $NInt_C$ , we define the new commutative importance index using as a reference value the sum of the performances with and without neighbours,  $P_{sum}$ . The two parts of the weighting term  $P_w$  are thus (i) the difference in reference performance between the maximum ( $MP_{sum}$ ) and a given level of stress ( $P_{sum}$ ); and (ii) the maximum of the reference

performance along the gradient ( $MP_{sum}$ ). In other words,  $MP_{sum}$  is defined as the maximum value of the sum of the performances of the target species with and without neighbours along the gradient. We obtain the Neighbour-effect Importance index with commutative symmetry,  $NImp_C$ , as:

$$NImp_C = 2 \frac{\Delta P}{2 \cdot MP_{sum} - P_{sum} + |\Delta P|} \quad \text{eqn 5}$$

As for  $NImp_A$ , we illustrate here the index values in some simple cases where the effect of the environment can be discarded. In these conditions,  $NImp_C$  is equal to  $-1$  for competitive exclusion (when the performance of the plant alone is equal to the maximum of the sum of the performances with and without neighbours,  $P_{-N} = MP_{sum}$ ) and to  $+1$  for obligate facilitation (when the plant performance with neighbours equals the maximum performance without neighbours  $P_{+N} = MP_{sum}$ ).  $NImp_C$  is also equal to  $+1$  for an infinite increase in the performance of the target plant with neighbours ( $P_{+N}$ ,  $P_{sum}$  and  $MP_{sum}$  tend to infinite).

PROPERTIES OF NEIGHBOUR-EFFECT INDICES

*Intensity indices*

The formulae for the defined intensity indices and their key symmetry boundaries are summarized in Table 3 (first row). The formulae for their variance (calculated by error propagation, Ku 1966) are given in Appendix S1. Here, we only highlight the most important aspects.

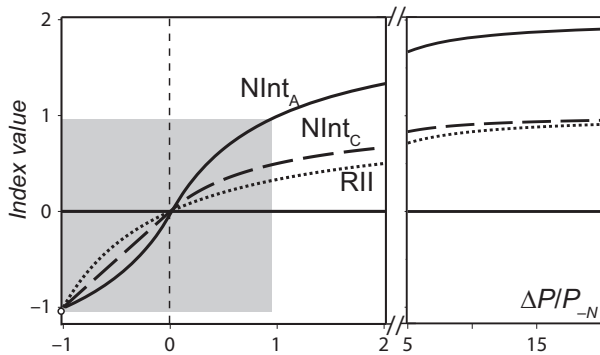
$NInt_A$  is additively symmetric (Fig. 3a) with respect to fixed  $P_{-N}$ . The different terms in the formula of  $NInt_A$  depend on the changes in performance related to either standardization or to the effect of facilitation or competition, as we illustrate with a quantitative bar graph in Fig. 3a. This index, being additive, displays uneven boundaries. As we explained above, this is a consequence of the intrinsic asymmetry of competition and facilitation. For  $NInt_A$ , the additive symmetry leads to considering as equivalent a case with extreme competition ( $P_{+N} = 0$  and thus  $\Delta P = -P_{-N}$ ), and a case where facilitation has the effect of doubling the performance ( $P_{+N} = 2 P_{-N}$  and  $\Delta P = P_{-N}$ ). Within this limited region ( $\Delta P < P_{-N}$ , grey area in Fig. 4), competition and facilitation are equivalent. As a consequence, very large facilitation cases ( $\Delta P > P_{-N}$ , on the right of the grey region in Fig. 4a) have no equivalently large competition situations as  $P_{-N}$  cannot be smaller than zero ( $\Delta P < -P_{-N}$ , left of the grey region in Fig. 4). An additive index necessarily translates such asymmetric nature of the neighbours impact into uneven boundaries. The absolute value of the index for a facilitative effect that tends to infinite ( $NInt_A^{(max)} = +2$  when  $P_{+N} \rightarrow \infty$ ) is twice the absolute value of the index for maximum competition ( $NInt_A^{(min)} = -1$  when  $P_{+N} \rightarrow 0$ ). While this boundary unevenness is a direct consequence of additive symmetry, we must note that the specific maximum value of the index is due to the choice of a sigmoidal formula for the  $NInd_S$ , which was chosen as it allows for a general formulation of the four indices.

**Table 3.** The new family of Neighbour-effect Indices (NInd<sub>S</sub>), with the formulas and limit values of the two intensity and the two importance indices, with additive or commutative symmetry

NInd <sub>S</sub>	Additive symmetry	Commutative symmetry
Intensity	$\text{NInt}_A = 2 \frac{\Delta P}{P_{-N} +  \Delta P }$ Min -1; Max 2	$\text{NInt}_C = 2 \frac{\Delta P}{P_{-N} + P_{+N} +  \Delta P }$ Min -1; Max 1
Importance	$\text{NImp}_A = 2 \frac{\Delta P}{2MP_{-N} - P_{-N} +  \Delta P }$ Min -1; Max 2 (PractMax* 2/3)	$\text{NImp}_C = 2 \frac{\Delta P}{2MP_{\text{sum}} - P_{-N} - P_{+N} +  \Delta P }$ Min -1; Max 1

\*Note that for most experimental set-ups  $MP_{-N}$  can be estimated with the maximum performance available.

All the indices are standardized, bounded and allow for error estimation (for the expression of indices errors see Table S1 and Note S1). For symbols see Table 1. See also Note S2 for boundaries of Neighbour-effect Importance indices.



**Fig. 4.** Values of different intensity indices ( $\text{NInt}_A$ ,  $\text{NInt}_C$  and  $\text{RII}$ ) as a function of the total impact of neighbours. The performance of the target species is fixed at 1 unit ( $P_{-N} = 1$ , or equivalently the horizontal axis represents  $\Delta P/P_{-N}$ ), and the impact of neighbours ranges from maximum competition ( $P_{+N} = 0$ , and thus  $\Delta P = -1$ ) to large values of facilitation ( $\Delta P = 20$ ). The index  $\text{NInt}_A$  is additively symmetric (as evident by the symmetric shape) with respect to  $\Delta P = 0$  in the grey square ( $-1 < \Delta P < 1$ ) and has uneven limit values (minimum equal to  $-1$  and maximum equal to  $+2$ ). The multiplicative character of commutative symmetry of  $\text{NInt}_C$  and  $\text{RII}$  is not apparent in this figure because of the axes chosen (see Fig. S1 with a logarithmic scale for comparison).  $\text{RII}$  and, to a lesser extent,  $\text{NInt}_C$  are further from  $\text{NInt}_A$  at facilitation than at competition, and thus commutative indices, especially  $\text{RII}$ , underestimate facilitation with respect to competition. All the performance values are here expressed in a generic unit.

$\text{NInt}_C$  displays commutative (and multiplicative) symmetry and has even boundaries,  $\text{NInt}_C^{(\text{max})} = +1$  and  $\text{NInt}_C^{(\text{min})} = -1$ .  $\text{NInt}_C$  uses the performance with and without neighbours as a reference ( $P_{\text{sum}}$  in eqn 3), thereby levelling off the asymmetry of competition and facilitation. We note here that  $\text{RII}$  has similar characteristics (Armas, Ordiales & Pugnaire 2004) for analogous reasons (see Fig. S1), but see below ('Recommendation and guidelines') for a more detailed comparison between  $\text{NInt}_C$  and  $\text{RII}$ .

### Importance indices

$\text{NImp}_A$  and  $\text{NImp}_C$  are the first standardized importance indices (Figs 2 and 3b). We report in Table 3 (last row) a summary of the definition and key properties of the Neighbour-effect importance indices (the formulae for variance are given in Table S1).

The standardization for size, which we introduce for the first time in importance indices, not only makes them comparable between different experiments but also it corrects one major flaw of previous importance indices. As pointed out by Rees, Childs & Freckleton (2012) and Mingo (2014a), in a system where environmental conditions are almost optimal, but the effect of neighbours is negligible with respect to the performance of the target plant, all former importance indices (e.g.  $I_{\text{imp}}$ ,  $C_{\text{imp}}$ ) reach maximum absolute values. Our new importance indices solve this issue, and  $\text{NImp}_A$  and  $\text{NImp}_C$  tend to zero in such a system (Fig S4). This is a consequence of the standardization for size, which weighs the impact of small neighbour effects with respect to the maximum performance of the target plant (see Fig. S5 and Appendix S2 for further details). As a consequence,  $\text{NImp}_S$  standardization is a step forward towards solving the issue of spurious patterns possibly emerging in the importance indices (see Appendix S2).

Overall, Neighbour-effect Importance indices share the same properties as their associated intensity indices.  $\text{NImp}_A$  and  $\text{NImp}_C$  display additive and commutative symmetry (see Appendix S1), respectively. As a consequence of their symmetries, they have uneven (see Appendix S2) and even boundaries, respectively.

We should acknowledge that it may be difficult to assess the theoretical maximum performance of the species with standard experimental set-ups, and thus these values should be assessed using all available information (including other data sets or previously published literature) to find their best proxy. For most relevant experimental designs on plant–plant interactions, the optimal performance without neighbours is also the superior limit for the performance with neighbours ( $P_{+N} \leq MP_{-N}$ ) and  $MP_{-N}$  can be estimated using also the maximum performance, regardless of the presence or absence of neighbours (following Seifan *et al.* 2010). For example, when facilitation is mediated by the same resource whose availability defines the stress treatment, and the study includes non-stressed conditions, the maximum performance along a gradient always occurs without neighbours, although it might not be experimentally observed. However, this 'practical' upper limit of additive importance indices can be surpassed if the performance with neighbour exceeds the optimal performance without neighbours ( $P_{+N} > MP_{-N}$ ). The absolute boundaries



and the upper ‘practical’ boundary of the additive importance index (see Appendix S2 for details) are reported in Table 3.

### Recommendation and guidelines

We strongly recommend using indices that fulfil all four mathematical properties as previously discussed. Therefore, we cannot recommend the use of indices outside the NInd<sub>s</sub> family (with the exception of RII), as they fail to show these basic properties. Most importantly, none of the currently used importance indices is standardized, significantly hindering cross-species or cross-studies comparisons. We also recommend for the first time to use pair of indices with the same symmetry for intensity and importance, to avoid spurious effects in the comparison: NInt<sub>A</sub> with NImp<sub>A</sub> and NInt<sub>C</sub> with NImp<sub>C</sub> (see also Appendix S2 for a standardized commutative importance index related to the intensity index RII). We thus discourage the common practice of using together commutative intensity and additive importance indices (Armas, Rodríguez-Echeverría & Pugnaire 2011; Anthelme & Dangles 2012; Anthelme *et al.* 2012; Howard, Eldridge & Soliveres 2012; Maalouf *et al.* 2012; Soliveres, Torices & Maestre 2012; le Bagousse-Pinguet *et al.* 2014; Bulleri & Piazzi 2015; de Castanho *et al.* 2015).

Furthermore, in general, we advise to use additive indices (NInt<sub>A</sub> and NImp<sub>A</sub>). In the following, we will motivate this preference, discussing in details how to choose between the two types of symmetry and between NInt<sub>C</sub> and RII. We will focus on comparing across the intensity indices because they are generally easier to understand (although their properties are shared by their importance counterparts).

To illustrate the relevance of symmetry, we compare NInt<sub>A</sub> (eqn 2), NInt<sub>C</sub> (eqn 3) and RII for a fixed control performance ( $P_{-N}$ ) and a variable impact of a neighbour-adding treatment, ranging from competitive to facilitative neighbours (Fig. 4, from left to right on the horizontal axis). From this visual comparison it is apparent that if the facilitative neighbour impact is within the (additive) range of symmetry (which we define as  $|\Delta P| \leq P_{-N}$ , grey area in Fig. 4), the additive NInt<sub>A</sub> reports symmetrical values for equal competitive or facilitative effects (as it descends from its definition). Within this range, the two commutative indices are more (RII) or less (NInt<sub>C</sub>) far from NInt<sub>A</sub> (see Appendix S3 for a mathematical calculation of this distance). In other words, the commutative indices, and especially RII, tend to underestimate facilitation with respect to equivalent values of competition. This effect is especially relevant for  $|\Delta P|$  values larger than 10% of  $P_{-N}$  (Figs 4, S4 and Appendix S3). If a commutative index is chosen, we recommend using NInt<sub>C</sub> over RII.

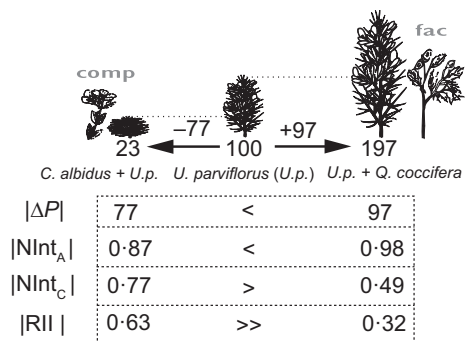
These differences between indices can influence the conclusions extracted from quantitative analysis of experimental data. All the indices will correctly identify the same sign for the neighbour effects (facilitation or competition), and they will order the index values from low to high neighbour effects in the same way (as they all show an increase from left to right, see Fig. 4). However, when averaging several experiments or treatments, including both competitive and facilitative

situations, the average net outcome can be biased towards competition when using commutative indices, as a consequence of the abovementioned underestimation of facilitation (especially large for RII). See Appendix S3 for such an example with real data (Metz & Tielbörger 2016).

Although we generally recommend additive indices, commutative indices can still be used outside the range of symmetry, when there is a much larger facilitative than competitive effect ( $\Delta P \leq P_{-N}$ ). The use of additive indices is instead the only advisable option when the effect of facilitation is within the same order of magnitude as the effect of competition ( $|\Delta P| \leq P_{-N}$ ). In the following, we illustrate these two cases with the help of real examples.

#### ADDITIVE SYMMETRY FOR INTERACTIONS INSIDE THE ADDITIVE RANGE OF SYMMETRY

When  $|\Delta P| \leq P_{-N}$ , we strictly recommend the use of additively symmetric indices (NInt<sub>A</sub> and NImp<sub>A</sub>) because in this range there is a correspondence between competitive and facilitative values and, arguably, because additive symmetry is more intuitive and easier to interpret than commutative symmetry. This is apparent by, for instance, re-examining the results of Montès *et al.* (2008) who recorded the performance of four dominant species in Mediterranean shrublands and evaluated the effect of pairwise interactions by measuring their productivity in monoculture and in mixture with each of the other species. We use their results to establish which of two neighbours, namely,



**Fig. 5.** The effect of symmetry when comparing competitive and facilitative treatments on a control species in an illustrative experimental setup. The illustrations represent the experimental design and show the performance of the target species growing with and without neighbours. The table below contains the magnitudes of the total impact of neighbours,  $|\Delta P|$ , and the corresponding value for three intensity indices,  $|NInt_A|$ ,  $|NInt_C|$  and  $|RII|$ . The target plant is *Ulex parviflorus*, with performance when alone ( $P_{-N} = 100$ ). In absolute terms ( $|\Delta P|$ ) the facilitative (‘fac’) impact of *Quercus coccifera* is larger than the competitive (‘comp’) impact of *Cistus albidus* ( $97 > 77$ ). However, the only index which provides larger strength for facilitative effect of *Q. coccifera* is the additive index NInt<sub>A</sub>, whereas commutative indices ( $|NInt_C|$ , and  $|RII|$ ) indicate a larger competitive than facilitative effect (contrary to the expectations from  $\Delta P$ ). The performance values have been calculated from the values of RII obtained through digitalization of Fig. 3 in Montès *et al.* (2008); all performance values are given by a multiplicatively constant arbitrarily fixed as  $P_{-N} = 100$  units, whose value does not influence the results shown.

the competitor *Cistus albidus* and the facilitator *Quercus coccifera*, has the largest impact on the productivity of the target species, *Ulex parviflorus*. When looking at the total effect ( $\Delta P$ ), using the performance of *U. parviflorus* alone as the reference (i.e. we fix  $P_{-N} = 100$  units) the change induced by *Q. coccifera* (increase of 97 units) is larger than the change due to *C. albidus* (decrease of 77, units, see Fig. 5). Noticeably, this relationship is captured only by  $\text{NInt}_A$  ( $|\text{NInt}_A|$  equal to 0.98 and 0.87 for *Q. coccifera* and *C. albidus*, respectively), whereas it is reversed by commutative indices, with a particularly large difference when using RII (with  $|\text{RII}|$  equal to 0.32 and 0.63 for *Q. coccifera* and *C. albidus*, respectively; Fig. 5). Commutative indices, and especially RII, can thus be a misleading choice when competition and facilitation cases are comparable in terms of absolute total impacts ( $|\Delta P|$ ).

Although this recommendation is generally valid, the researchers should check that the equivalence between symmetric values of facilitation and competition is sensible in their experiment. For example, the additive symmetric indices are the right choice if complete displacement of the target species by the neighbour is not expected, or if this total displacement is considered as relevant as a facilitative effect that doubles the target species performance, but not as relevant as an obligate facilitative effect (if observed).

#### ADDITIVE OR COMMUTATIVE SYMMETRY FOR INTERACTIONS OUTSIDE THE ADDITIVE RANGE OF SYMMETRY

In studies with large differences between plants growing alone and with a neighbour, i.e. when  $\Delta P > P_{-N}$ , commutative indices can substitute, or to use in combination with, additive indices. We show this with an example of cushion plants in alpine environments, which can display a largely facilitative effect on other plants (Cavieres *et al.* 2014). The nurse plants can increase the abundance of other species even ninefold with respect to open sites ( $\text{RII} \sim 0.8$ ) (Cavieres *et al.* 2014) and can increase richness up to 2.9 times (Cavieres & Badano 2009). The additively symmetric  $\text{NInt}_A$  assigns impact values close to 2 for the very large facilitative effects found for cushion plants, which is twice the magnitude it would assign to exclusive competition (i.e. disappearance of the target species). Using the additive index in this case implies that alpine conditions are highly severe for non-cushion species in the open, and competition has a much smaller range than facilitation. On the other hand, the use of a commutative index, such as  $\text{NInt}_C$  or RII (which both have a maximum facilitation value of 1), implies that the total removal of the target species is considered as equivalent to extremely large facilitative impacts and to obligate facilitation. Also, commutative indices might be applied in experiments where different performance estimators rather than biomass are used, such as count data (e.g. seed production, Cavieres *et al.* 2014), which can span different orders of magnitude. For this type of variable, an increase from 10 to 40 seeds and a decrease from 10 to 2.5 seeds might be considered as equivalent, if they have, for example, similar and

opposite impacts on species survival, and thus a commutative symmetric index could be used.

Finally, we note that our family of indices with the same mathematical properties allows also for impartial comparisons of the impact of different index symmetries as, for example,  $\text{NInt}_A$  and  $\text{NInt}_C$  differ only in their symmetry.

## Conclusions

As standardized importance indices and properly defined additively symmetric intensity indices are lacking, we filled these gaps introducing a new family of Neighbour-effect Indices, encompassing standardized intensity and importance indices, with additive ( $\text{NInt}_A$  and  $\text{NImp}_A$ ) and commutative ( $\text{NInt}_C$  and  $\text{NImp}_C$ ) symmetry. We recommend a widespread use of these additively symmetric indices, as their correspondence between competition and facilitation with equal net effect matches common experimental set-ups studying plant interactions. In most of these cases, current commutative intensity indices (mostly RII) are inappropriately applied, and RII underestimates the strength of facilitation when compared to the additive intensity index,  $\text{NInt}_A$ . The use of  $\text{NInt}_A$  will thus help clarifying the actual strength of positive net effects in plant communities. The standardization introduced in the neighbour-effect importance indices makes them a robust tool for studying plant neighbour effects along stress gradient and for cross-study comparisons, solving most of the statistical problems of previous importance indices (Rees, Childs & Freckleton 2012; but see also Brooker *et al.* 2013), although whether or not  $\text{NImp}_S$  allow the formulation of null models to test plant neighbour effects (Mingo 2014a) is still an open question.

Our family of indices allows for unbiased comparisons of different index symmetries, and of intensity and importance, which then need to be chosen with the same symmetry within the family.

Concluding, the methodological definition of a common family of Neighbour-effect Indices introduced in this study provides a general framework to organize and compare the different measurements devised for net effects among plants. We expect that this precise methodological design will strongly help the development of new perspectives in the field, by overcoming the limitations of the current tools.

## Authors' contributions

R.D.S. conceived the study; R.D.S. and M.B. designed the analysis, which R.D.S. performed; R.D.S., M.B. and M.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Data accessibility

This manuscript does not include any data.

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** Formal definition of the mathematical properties of Neighbour-effect Indices.

**Appendix S2.** Additional comments on Importance Indices.

**Appendix S3.** Comparison and different effects of additive and commutative intensity indices.