

MEASURING PLANT INTERACTIONS: A NEW COMPARATIVE INDEX

CRISTINA ARMAS,¹ RAMÓN ORDIALES, AND FRANCISCO I. PUGNAIRE

*Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, General Segura 1,
04001 Almería, Spain*

Abstract. We propose an index to measure the relative interaction intensity in plants (RII) with strong mathematical and statistical properties which overcome problems shown by other frequently used indices. RII has defined limits $[-1, +1]$; is symmetrical around zero, with identical absolute values for competition and facilitation; is linear; and does not have discontinuities in its range. It is therefore safe to use in statistical and mathematical operations. RII distribution is approximately normal, with means equal to the true population index and a sampling variance that can be derived. Its strong statistical properties make RII proper for use in parametric meta-analyses. It can be applied to any kind of interaction (from competitive exclusion to symbiosis) and in commonly published ranges of interaction intensity it offers the most consistent results. Because RII uses basic arithmetical operators, it can be scaled up and used to measure multispecific interactions at the community level.

Key words: competition; facilitation; interaction indices; interaction intensity.

INTRODUCTION

Interaction among species is central to community ecology (e.g., Connell 1983, Schoener 1983, Bruno et al. 2003), but accurate quantification of species interactions is hotly debated (Reynolds 1999, Weigelt and Jolliffe 2003). Testing hypotheses in community ecology often requires quantification of the magnitude of interactions between species so that these magnitudes can be compared among groups of taxa or of environments (Goldberg et al. 1999).

In plant communities, the result of an interaction is frequently measured as the ratio of some performance variables, usually biomass, between individuals with experimentally removed neighbors and control plants with neighbors left intact. However, plant mass and other measurements only render the net balance of the interaction, i.e., the sum of all direct and indirect, positive and negative factors that influence plant growth (Goldberg et al. 1999). Because complex combinations of competition and facilitation operate simultaneously in plant communities (Callaway and Walker 1997, Holmgren et al. 1997, Holzapfel and Mahall 1999, Pugnaire and Luque 2001) their effects are difficult to distinguish.

Several indices have been used over the years to explore the net balance of plant interactions (Reynolds 1999, Weigelt and Jolliffe 2003). These include the relative competition index (RCI) of Wilson and Keddy (1986) used for measuring diffuse competition (e.g., Paine 1992); the log response ratio (lnRR) of Hedges et al. (1999); and the relative neighbor effect (RNE), which is RCI modified to account for facilitative effects (Markham and Chanway 1996). However, these and

other indices may be misleading because of their lack of symmetry, their poor statistical properties, or because they produce artifacts under some circumstances (Hedges et al. 1999).

Indices used to measure the net balance of an interaction should meet several basic properties. They must be symmetrical, i.e., for a given interaction intensity the index should provide the same result for competition and for facilitation but with opposite signs. The numerical range must be limited, otherwise it could not be applied when the interaction intensity is extreme (i.e., competitive exclusion and obligate symbiosis) and therefore the results of an experiment could be biased.

Another important property of an interaction index is that it should be relative, so that it could be used to compare different experiments, species or environments. This is of special importance for testing conceptual models and theories in community ecology through meta-analyses. For this purpose, the sampling distribution and sampling error of an index must be able to be derived and its statistical properties must be known. For example, the failure of meta-analyses to detect facilitation among plants may have been due to flaws in the indices used (see Goldberg et al. 1999, Hedges et al. 1999, Osenberg et al. 1999).

Here we propose an index with strong mathematical and statistical properties that overcomes many problems of other indices. We first explain and justify the derivation of the index and then make a comparison of its properties with those of the most frequently used indices in plant community dynamics. We also derive its sampling distribution and a way to obtain its sampling error, and make a comparison with the properties of lnRR, the index with the best statistical properties to date (Hedges et al. 1999).

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¹ E-mail: cris@eeza.csic.es

RATIONALE

The interaction between two plants—either conspecific or not—is typically derived from differences between individuals growing alone vs. growing with other plants. For convenience, we will hereafter refer only to the biomass of such individuals, but interactions may also be derived from other metrics of plant growth or reproduction. The biomass of individuals growing alone will reach a maximum size determined by the genotype and the environment. Individuals will be smaller if competing with other plants and larger if the presence of other plants is facilitative.

We define the effect of one plant on another in relative terms taking the mass potentially achieved by the target plant growing in absence of inter- or intraspecific interactions (B_o) and the mass observed when growing with other plants (B_w). In the latter case plant mass is potentially subject to the effects of competition and facilitation, which results in an increase of biomass produced by facilitation (ΔB_F , where $0 \leq \Delta B_F \leq +\infty$) and a decrease caused by competition (ΔB_C , where $0 \leq \Delta B_C \leq B_o$). For simplicity, we assume that both phenomena are independent and have additive and antagonistic effects on plant performance, so mass of B_w can be represented by the following expression:

$$B_w = B_o + \Delta B_F - \Delta B_C. \quad (1)$$

Because it is not possible to separate the potential effects of competition and facilitation in the observed, final size of a plant (Goldberg et al. 1999), we assign the observed, actual value, to ΔB_{FC} , so that

$$\Delta B_{FC} = \Delta B_F - \Delta B_C. \quad (2)$$

Therefore

$$B_w - B_o = \Delta B_{FC} \quad (3)$$

where

$$-B_o \leq \Delta B_{FC} \leq +\infty \quad (4)$$

with ΔB_{FC} being the absolute effect of the interaction. The interaction index should be relative and hence non-dimensional. A common procedure is to obtain a ratio of the absolute effect (ΔB_{FC}) related to the plant biomass (B_w or B_o). For example, a relative interaction index could be expressed as

$$\frac{\Delta B_{FC}}{B_w} = \frac{\Delta B_{FC}}{(\Delta B_{FC} + B_o)}. \quad (5)$$

If there is only facilitation ΔB_{FC} is always positive and has a finite range [0,1]:

$$|\Delta B_{FC}| \leq |\Delta B_{FC} + B_o|. \quad (6)$$

However if there is only competition, ΔB_{FC} is always negative and Eq. 6 may not be true, as the index has an unlimited range $[-\infty, 0]$ and facilitation and competition intensities would not be comparable using Eq.

5. A similar approach with B_o in the denominator has similar flaws.

We propose a new relative interaction index (RII) defined as follows:

$$\begin{aligned} \text{RII} &= \frac{\Delta B_F + (-\Delta B_C)}{(\Delta B_F + B_o) + [(-\Delta B_C) + B_o]} \\ &= \frac{\Delta B_{FC}}{\Delta B_{FC} + 2B_o} \end{aligned} \quad (7)$$

where the absolute value of the denominator is always greater than the absolute value of the numerator and hence has a finite range.

This index represents the ratio of the net mass loss/gain due to the interaction (numerator) relative to the mass affected by only facilitative interaction and only competitive interactions (denominator), simultaneously. RII has values ranging from -1 to 1 , is symmetrical around zero and is negative for competition and positive for facilitation. Taking into account Eqs. 1 and 3, RII also can be expressed as

$$\text{RII} = \frac{B_w - B_o}{B_w + B_o}. \quad (8)$$

Similar equations such as the normalized difference vegetation index (NDVI) or the Ivlev index (1955, cited in Netwing 1980) have been used for other purposes, including remote sensing or fisheries and predator-prey interactions (Netwing 1980).

Interaction experiments usually compare the mass of isolated individuals with neighbors removed to control plants with neighbors left intact. In our expression, B_o is the mass of isolated individuals and B_w the mass of plants with neighbors (both ranging from 0 to infinity).

For simplicity in the statistical and mathematical calculations and analysis, we use B_o and B_w in this paper as the mean value of each distribution, assuming non-paired field experiments.

COMPARATIVE ANALYSIS

We analyzed the range and symmetry of RCI, RNE, and lnRR in comparison with RII. For simplicity, we derived equations expressing the interaction as $B_w = \alpha B_o$, with α being a proportionality interaction factor which ranges from 0 to $+\infty$ (it has to be positive because biomass cannot be negative). When $\alpha < 1$, competition prevails, while when $\alpha > 1$ (to $+\infty$) facilitation prevails. When $\alpha = 1$, the interaction outcome is neutral.

Although the four indices have very similar results over much of their range (Fig. 1) there are some crucial differences among them. RII and RNE are the only indices with upper and lower limits, that are symmetrical for facilitation and competition, and that are balanced around zero (Table 1, Fig. 1). lnRR has no limits ($-\infty \leq \lnRR \leq +\infty$) but equations for facilitation and competition are symmetrical and balanced around zero (Table 1, Fig. 1). RCI is the most statistically troubled

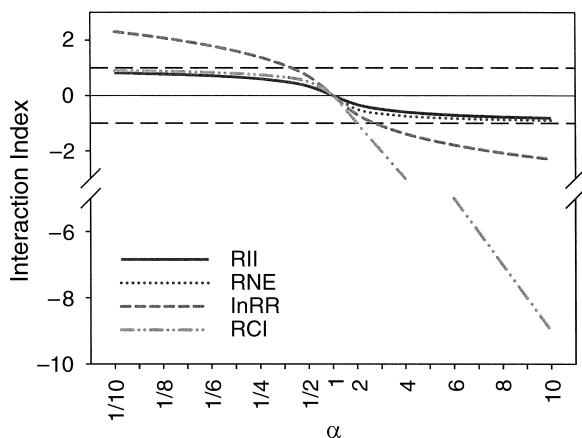


FIG. 1. Graphical representation of the indices' symmetry and limits for a set of values of the interaction factor α . To facilitate the graphic comparison, the sign of RII has been changed (negative for facilitation, positive for competition).

index because it has no lower limit ($-\infty \leq \text{RCI} \leq +1$) and equations for facilitation and competition are neither symmetrical nor balanced around zero; for these reasons the facilitation and competition sides of the curve are not comparable (Table 1, Fig. 1).

The lack of upper or lower limits do not allow for the calculation of lnRR and RCI in some particular cases (e.g., when variables measuring plant performance are zero). For example, Hedges et al. (1999) examined field data on the effects of competition and found that nine out of 77 experiments had zero biomass in the control group (B_w). For these cases, computing the log response ratio is not possible ($B_w = 0$ in the denominator), but RCI, RNE, and RII could be used. In the opposite case, when plants growing alone die during the experiment ($B_o = 0$), RCI and lnRR have B_o as the unique denominator or numerator, respectively, and neither index can be calculated. Therefore,

lnRR and RCI may produce biased results in a particular experiment or in a meta-analysis, as their use will require the elimination of cases with very intense interactions (i.e., competitive exclusion or obligate symbiosis).

RNE has an undesirable mathematical characteristic because its denominator is a MAX function—there are two possible solutions depending on which type of interaction prevails (Table 1). This is of particular importance in modeling, because the denominator is not known a priori (i.e., we cannot anticipate the result of the MAX function).

The statistical properties of RCI and similar indices (e.g., RNE) have been already compared to lnRR (Hedges et al. 1999), showing that the distributions of the former are highly skewed and biased, while lnRR shows strong statistical properties which have been derived for use in meta-analysis. We compared the sampling distribution and error of RII and lnRR and showed they have similar properties (Appendices A and B).

These indices are also similar because lnRR could be considered as a derived function of RII. If $\ln\text{RR} = -\ln(\alpha)$ and $\text{RII} = (\alpha - 1)/(\alpha + 1)$ (applying equations from Table 1),

$$\ln(\alpha) = 2 \left[\left(\frac{\alpha - 1}{\alpha + 1} \right) + \frac{1}{3} \left(\frac{\alpha - 1}{\alpha + 1} \right)^3 + \frac{1}{5} \left(\frac{\alpha - 1}{\alpha + 1} \right)^5 + \dots \right] \quad (9)$$

(solved by Taylor's series). When the interaction factor (α) is smaller than 2, the values after the second term of the polynomial tend to zero. In these cases, lnRR is approximately two times the value of RII but with opposite sign because $\ln\text{RR} = -\ln(\alpha)$. For larger values of α , lnRR differs from RII, growing to infinity. Thus, for mathematical and statistical purposes, lnRR is similar to RII but adds an unpractical function complexity

TABLE 1. Mathematical properties of four indices of interaction: RII (relative interaction index), RCI (relative competition index), RNE (relative neighbor effect), and lnRR (log response ratio).

Condition	RII	RCI	RNE	lnRR
Limits				
Competition (limit when $B_w \rightarrow 0$)	-1	+1	+1	$\ln\text{RR} \rightarrow +\infty$
Neutral	0	0	0	0
Facilitation (limit when $B_w \rightarrow +\infty$)	+1	$\text{RCI} \rightarrow -\infty$	-1	$\ln\text{RR} \rightarrow -\infty$
Symmetry	yes	no	yes	yes
Indices as a function of α ($\forall \alpha \geq 0$ and $B_w = \alpha B_o$)	$\frac{\alpha B_o - B_o}{\alpha B_o + B_o} = \frac{\alpha - 1}{\alpha + 1}$	$\frac{B_o - \alpha B_o}{B_o} = 1 - \alpha$	$\frac{B_o - \alpha B_o}{\text{Max}(B_o; \alpha B_o)} = \begin{cases} 1 - \alpha & (\forall 0 \leq \alpha < 1) \\ \frac{1 - \alpha}{\alpha} & (\forall \alpha > 1) \end{cases}$	$\ln\left(\frac{B_o}{\alpha B_o}\right) = -\ln(\alpha)$

Notes: The table shows limits, symmetry, and indices as a function of interaction factor α , $\forall B_w = \alpha B_o$. B_o is the mass of isolated individuals, and B_w is the mass of plants with neighbors $\forall 0 < B_o < +\infty$ and $0 \leq B_w < +\infty$. Competition prevails when $0 \leq B_w < B_o < +\infty$ or $0 \leq \alpha < 1$, while facilitation prevails when $0 \leq B_o < B_w < +\infty$ or $\alpha > 1$. When there is no interaction or the outcome is neutral, $B_w = B_o$ or $\alpha = 1$. Equations for the four indices of interaction are: $\text{RII} = (B_w - B_o)/(B_w + B_o)$; $\text{RCI} = (B_o - B_w)/B_o$; $\text{RNE} = (B_o - B_w)/(\text{max}[B_o; B_w])$; $\ln\text{RR} = \ln(B_o/B_w)$.

to RII and therefore the latter is a simpler and preferable index.

A practical, but not serious, inconvenience of both RII and lnRR is that their results are not as intuitive for competition as RCI or RNE, nor for facilitation when compared to RNE. For example, if there is a 50% reduction in performance in the presence of competitors (e.g., $B_o = 12$, $B_w = 6$), both RCI and RNE yield 0.5, which is equivalent to the biomass reduction, but RII yields -0.33 and lnRR 0.69. In the opposite case (i.e., when there is facilitation and $B_o = 6$, $B_w = 12$), the indices produce a set of results similar to those of competition but with opposite sign, except RCI that gives -1 . Therefore, RNE results are more intuitive than the others irrespective of the interaction intensity, while both RII and lnRR have a “logarithm” behavior (RII being asymptotic to y lines 1 and -1 as a sigmoid function, and lnRR being asymptotic in the y -axis) with no inconvenience for anyone familiar with the log scale. Nevertheless, the stronger mathematical and statistical properties of RII and lnRR, as compared to RCI and RNE, prevail over intuitive advantage of the latter.

SENSITIVITY ANALYSIS

Sensitivity is the impact of a small change in the interaction factor (α) on the actual value of the index; i.e., an indirect measure of the response of the index to small changes in interaction intensity. It is also a measure of the dispersion of data in the sample, because the more sensitive the index the greater the range and scatter of values. This is of considerable importance when the interaction between species is weak: an unbalanced and oversensitive index can lead to wrong conclusions, showing competition when the net balance would be facilitation and vice-versa.

We compared the standardized sensitivity of the four indices (see Appendix C for details). The graphical expression of the index sensitivity shows their symmetry around 1, or the lack of it (Fig. 2A). The sensitivity analysis shows that when α tends to 1 (neutral interaction) RCI has a discontinuity because of its lack of symmetry. For $\alpha \rightarrow 1^-$ (i.e., α values approaching 1 but less than 1) RCI sensitivity has a limit of 2, while for $\alpha \rightarrow 1^+$ (i.e., slightly greater than 1) the limit is 1. This lack of symmetry causes two times greater dispersion of RCI values when $B_o \geq \sim B_w$ than when $B_o \leq \sim B_w$ (Fig. 2B), but because of its asymmetry, values may be biased toward facilitation at weak intensity interactions. On the other hand, RII, lnRR, and RNE show the same sensitivity in each side ($\alpha \rightarrow 1^-$ and $\alpha \rightarrow 1^+$) and then are unbiased at low intensity interactions. Nevertheless, for α values tending to 1 ($\alpha \rightarrow 1^-$ or $\alpha \rightarrow 1^+$), RNE is the most sensitive index, i.e., it is most likely to reflect small changes when α is near 1 (Fig. 2B).

There are two regions where all of the sensitivity functions cross (Fig. 2A). This occurs when $\alpha = 0.6 \pm 0.02$ and 1.67 ± 0.06 (but see Appendix C for the

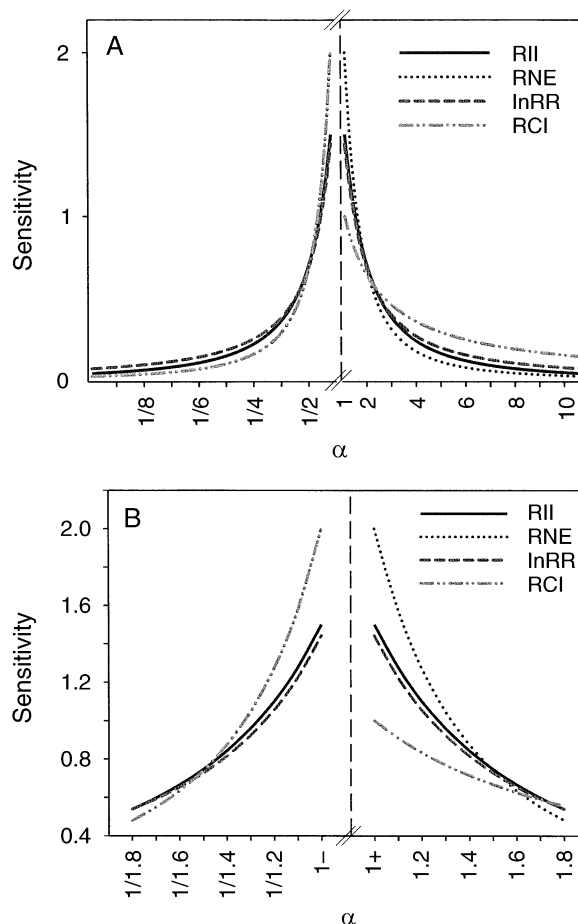


FIG. 2. (A) Sensitivity analysis of the four indices as a function of the interaction factor α , and (B) detail for the interval $0.56 < \alpha < 1.8$.

exact range of α -matching values). Within this range, sensitivity functions reveal the main differences among indices. RNE is the most sensitive index (for both competition and facilitation, Fig. 2B), although RCI is equally sensitive but only for competition (it has the same equation as RNE for competition, Table 1). Therefore, RNE will show the highest variability in this range of α values and RCI the lowest variability for facilitation, while lnRR and RII will show low variability for competition (Fig. 2B). Outside the mentioned range and in the facilitation region RNE, lnRR, and RII have approximately the same sensitivity (Fig. 2A). In case of competition, the four indices behave similarly, RNE and RCI being less sensitive (Fig. 2A).

CONCLUSIONS

The properties analyzed here point to RII as the most suitable index for analysis of plant interactions. RII has defined limits $[-1, +1]$, it is symmetrical around zero with identical absolute values for competition and facilitation, its sampling properties are known and ac-

curate (Appendix A), and it is safe to use in statistical and mathematical operations because it is linear and does not have discontinuities in its range. RII can be calculated for any type of net interaction (from competitive exclusion to symbiosis) and in the range of $0.6 \leq \alpha \leq 1.6$ it has the lowest variability, similar to lnRR. RII is easy to obtain and apply, and uses basic arithmetical operators, which make the index good for measuring multispecific interactions at the community level. Both lnRR and RNE also have good properties, along with some flaws. Since lnRR is a polynomial approach of RII (Eq. 9), it is similar to RII, but its unpractical mathematical complexity provides no advantage over RII. It also fails in the case of competitive exclusion or obligate symbiosis because its range values have no limits. We found that RNE has two different mathematical equations as a function of α , one in the case of facilitation and another in the case of competition. Hence, RNE is difficult to use in modeling or to perform mathematical operations and cannot be scaled up to multispecific interactions. In the range of $0.6 \leq \alpha \leq 1.6$, RNE shows more variability than RII and lnRR, although for stronger interactions (more intense facilitation or competition) it is the index with the least variability. RCI has the most conceptual and statistical problems. It is neither symmetrical nor balanced around zero; its facilitation and competition effects are not comparable, and when interaction intensity is weak, results of RCI can be biased toward the facilitation side of the curve because of its lack of symmetry. In addition, it has no lower limit and cannot be calculated when there is obligate symbiosis.

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APPENDIX A

A description of the estimation of sampling distribution and error of RII is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-082-A1.

APPENDIX B

A description of the RII function distribution is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-082-A2.

APPENDIX C

A description of sensitivity analysis is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-082-A3.