Integrating importance and intensity: a novel approach to normalize measurement of neighbour effects

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Abstract: An intense debate is underway on the different approaches to measuring the importance of neighbour interaction. Both the ecological meaning and the statistical suitability of one of the most popular indices have been seriously questioned, but no simpler and practical alternative tools have been proposed up to now. This paper proposes a novel approach based on the use of new normalized indices which scale the effects of neighbours and environment to the maximum target-plant potential. Two indices related to environmental suitability and size-asymmetry are suggested as tools to stratify data in homogeneous subsets before analysis, and an index of normalized neighbour effect \( N_{imp} \) is proposed to integrate the measuring of neighbour importance and intensity. When tested on literature data, \( N_{imp} \) index proves to be very highly correlated to the most currently used importance index. At the same time, it is moderately but significantly correlated to the intensity index. Yet, an accurate reanalysis of three published datasets proves that several detected trends are predictable on the basis of the inherent properties of the used indices. This is inextricably linked to the use of the same phytometers at different productivity levels. Thus, a glimpse is proposed towards the opportunity to use groups of equivalent competitors, each one working at a different point of the gradient, but all in a comparable range of environmental suitability and potential size-asymmetry relative to neighbours. Once defined these equivalence conditions, the normalized \( N_{imp} \) metric is suited to measure how the relative weight of neighbour impact changes along the productivity gradient.

Introduction

Choosing a suitable index for measuring the effect size in plant-to-plant interactions has long been recognized as one of the most crucial steps for studying neighbour interactions along productivity gradients (Grace 1991, 1993, 1995, Goldberg et al. 1999, Weigelt and Jolliffe 2003). The attempt to assess whether competition importance increases with standing crop (Grime 1973) or is independent from it (Newman 1973, Tilman 1982) has become a kind of never-ending controversy in plant ecology (Craine 2005), and the need to clarify what is to be meant for competition importance and which is the best index for measuring it, has recently raised intense debate (Welden and Slauson 1986, Brooker et al. 2008). Most of the experiments dealing with competition along productivity gradients are analyzed in terms of intensity, whereas importance should be the appropriate variable to be tested. Hence, they propose to use a more suitable measure, the index of competition importance \( C_{imp} \), which scales the impact of competition to the total impact of competition plus environmental stress (Brooker et al. 2005, Brooker and Kikvidze 2008):

\[
C_{imp} = \frac{(Y_{iso}-Y_{mix})}{(\max(Y_{iso})-\min(Y_{mix},Y_{iso}))} \quad (1)
\]

where \( Y_{mix} \) and \( Y_{iso} \) are the performances of target-plants grown with and without neighbours respectively, \( \max(Y_{iso}) \) stands for the maximum performance reached by the isolated target-plant along the whole gradient, and \( \min(Y_{mix},Y_{iso}) \) indicates, for each pairs of replicates, the lower value between the target-plant growing in isolation and the one growing in mixed stand. It should be noted that in the present paper the indices have been set to get positive and negative values for competition and facilitation respectively, as in Brooker and Kikvidze (2008), Kikvidze et al. (2011a), Bennett and Cahill (2012).

Further debate on this index has been addressed to improve the measuring of facilitative interactions (Kikvidze and Armas 2010, Seifan et al. 2010). A more general interaction
importance index (I_{imp}) has been recently proposed by Seifan et al. (2010):
\[ I_{imp} = \frac{(Y_{iso} - Y_{mix})}{|Y_{iso} - Y_{max}| + |Y_{iso} - Y_{mix}|} \]  
(2)

where \(Y_{max}\) differs from the previous definition of \(\text{MAX}(Y_{iso})\), since it represents the maximum performance expressed by the target-plant along the whole gradient, either in presence or in absence of neighbours (not only in isolation, as in \(C_{imp}\)). In that particular case in which the denominator is equal to 0, this index is set to 0 by definition.

A novel approach to normalize the measuring of neighbour effects

Importance indices, in spite of being promptly adopted by several authors, have been criticized both for their mathematical and conceptual approach (Freckleton et al. 2009, Freckleton and Rees 2011, Rees et al. 2012). In particular, an inherent tendency to increase with productivity has been attributed to these indices (Rees et al. 2012). Most of these arguments are based on the implicit assumption that single target species are used to measure the level of competition along productivity gradient. This indeed is the most widely used way to analyze neighbour interaction trends, but it is not the only possible approach. The underlying idea of this paper is that neighbour interaction trends could be better studied by using different groups of phytometers, each one accounting for only a limited range of the gradient. This approach firstly implies that neighbour effects are compared on an appropriate scale, and secondly that the different target species are in equivalent conditions as for their relationships with environment and neighbours.

Target-plant maximum potential (\(Y_{max}\)) provides a measure of plant performance in optimum biotic and abiotic conditions (Seifan et al. 2010). In most of the real conditions, plant size is limited by different factors, each accounting for a different portion of the total plant potential (Fig. 1). The difference between plant performance in isolation and in mixed stand expresses the absolute impact of neighbours (\(N_{a}\) in Fig. 1). This value, scaled to the maximum plant size, expresses the relative weight of neighbour impact regard to the total plant potential:
\[ N_{n} = \frac{(Y_{iso} - Y_{mix})}{Y_{max}} \]  
(3)

where \(N_{n}\) is a new index of normalized neighbour effect. This very simple measure allows to make comparisons among differently sized target-plants on a common scale. Since its scaling parameter behaves as a constant along the whole gradient, this index does not encounter most of the statistical problems associated with ratio-based indices. Moreover, this index is scaled between -1 and 1 and it is well suited to measure facilitation as well. Given its simplicity, this index could be used to reanalyze several previous studies in which absolute competition intensity was the tested index, since it simply requires the available data be rescaled to the maximum target-plant potential (\(Y_{max}\)), either as recorded on the dataset or as deduced by modelistic approaches.

The next step is to define the conditions for equivalence among phytometers. Two main items are addressed here: the relative environmental suitability and the size asymmetry relative to neighbours. Standing biomass increases with

<table>
<thead>
<tr>
<th>Suitability</th>
<th>Absolute impact</th>
<th>Importance</th>
<th>Normalized indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>(S_{a} = \frac{Y_{iso}}{Y_{max}})</td>
<td>(S_{a} = Y_{max} - Y_{iso})</td>
<td>(S_{imp} = \frac{S_{a}}{OC})</td>
<td>(S_{n} = \frac{S_{a}}{Y_{max}})</td>
</tr>
<tr>
<td>(E_{s} = \frac{Y_{iso}}{Y_{max}})</td>
<td>(N_{a} = Y_{iso} - Y_{mix})</td>
<td>(C_{imp} = \frac{N_{a}}{OC})</td>
<td>(N_{n} = \frac{N_{a}}{Y_{max}})</td>
</tr>
<tr>
<td>(O_{s} = \frac{Y_{mix}}{Y_{max}})</td>
<td>(OC = S_{a} + N_{a})</td>
<td>(S_{imp} + C_{imp} = 1)</td>
<td>(S_{n} + N_{n} + O_{s} = 1)</td>
</tr>
</tbody>
</table>

Figure 1. The similarities and the differences between the “importance” and the “normalizing” approach are outlined by referring to a purely competitive interaction. The indices of “suitability” are obtained by normalizing the performance of the target-plant to its maximum potential (\(Y_{max}\)). They may be calculated as well for the performance in isolation (\(Y_{iso}\) → environmental suitability, \(E_{s}\)) as for that in mixed stand (\(Y_{mix}\) → overall suitability, \(O_{s}\)). An index of neighbour suitability (\(N_{s}\)) is also proposed as the difference between the overall and the environmental suitability. \(N_{a}\) and \(S_{a}\) stand for the absolute impacts of neighbours and environmental stress, respectively. Their sum represents the overall constraints (\(OC\)). In purely competitive interactions the index of competition importance (\(C_{imp}\)) is defined as the ratio of \(N_{a}\) to the overall constraints. Its complement to unity, suggested as \(S_{imp}\), might represent an index of the importance of stress. \(N_{n}\) and \(S_{n}\) stand for the normalized impacts of neighbours and environmental stress, respectively.
Table 1. Three different approaches to measuring neighbour effects are compared by referring to a purely competitive interaction. The three main indices (CI: relative competition intensity; Cimp: competition importance; Nmax: normalized neighbour effect) have the same numerator (N, the absolute impact of neighbours). They differ for which components of the target-plant maximum potential (Ymax) are included in their denominators (S: environmental stress; N: neighbour impact; O: overall performance). Yiso and Ymix represent the target-plant performances in isolation and in mixed stand respectively.

<table>
<thead>
<tr>
<th>Description</th>
<th>Relative intensity (CI)</th>
<th>Importance (Cimp)</th>
<th>Normalized index (Nmax)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Description</td>
<td>It standardizes the impact of competition to the performance in isolation</td>
<td>It measures the importance of neighbour impact relative to the overall constraints</td>
<td>It measures the weight of neighbour impact relative to the total plant potential</td>
</tr>
<tr>
<td>Denominator</td>
<td>Yiso</td>
<td>Ymax – Ymix</td>
<td>Ymax</td>
</tr>
<tr>
<td>It excludes</td>
<td>- Stress (Ymax – Yiso)</td>
<td>- Overall performance (Ymix)</td>
<td>-</td>
</tr>
<tr>
<td>It includes</td>
<td>- Neighbour impact (Yiso–Ymix)</td>
<td>- Stress (Ymax–Yiso)</td>
<td>All the three components of target-plant potential</td>
</tr>
<tr>
<td>Expression</td>
<td>N/(N+O)</td>
<td>N/(S+N)</td>
<td>N/(S+N+O)</td>
</tr>
</tbody>
</table>

resource availability, but each phytometer gets its maximum size in a different range of the gradient. In most of the tested environments the target-plant will not express its full potential, even if grown in isolation, since habitat conditions do not fulfil its optimal requirements. The extent to which Yiso is lower than Ymax (Si in Fig. 1) accounts for how much the environment limits the expression of plant potential. The ratio between them may be kept as an index of relative environmental suitability (Es):

\[ E_s = \frac{Y_{iso}}{Y_{max}} \] (4)

This index is similar to the species-specific site-quality index adopted by Berkowitz et al. (1995) in a field experiment. Es is scaled between 0 and 1, where 0 represents the most unsuitable and 1 the best suitable environment for the target species. In the particular case in which Ymax is achieved in mixed stand, Es will always be lower than 1, pointing out that even in the most suitable abiotic environment the target-plant cannot express its maximum potential if grown in isolation. This index is proposed here as a tool for stratifying data prior to analysis, in order to compare interaction effects only among phytometers working in homogeneous conditions as for their relation with the habitat. Blocking data for relative environment suitability would prevent individual responses to the environment to be confounded with the global effect of productivity on neighbour interaction trends.

The second equivalence criterion addressed in this paper is size-asymmetry regarding neighbours. Species replacement generally occurs along the gradient (Peltzer et al. 1998), since the less productive species tend to be substituted by more productive ones when resource availability increases. Consequently, neighbour size may virtually increase with no limit along the gradient, whereas phytometer plasticity is intrinsically limited by its maximum potential size. Wilson (2007) proposed an index of relative crowding (D) as a measure of the abundance of neighbours relative to the target-plant, obtained as the ratio of neighbour abundance (Zmix) to the isolated target-plant size (see also Appendix 1 in supplementary materials). If using Ymax as the scaling factor, this index can be adopted to express the potential size-asymmetry of the interaction:

\[ rD_i = \frac{Z_{mix}}{Y_{max}} \] (5)

where rDi is a new index of potential crowding. This index measures the extent to which the interaction is matched inside the range of target-plant potential plasticity, and may be applied to any plant-trait correlated with competitive ability (e.g., aboveground biomass, plant height, canopy area) (Gaudet and Keddy 1988, Keddy et al. 2002, Navas and Violle 2009). Its use, either as a blocking variable during data analysis, or as a tool to design balanced interaction experiments, would allow to rule out the effects of neighbour replacement along productivity gradient by setting a corresponding turnover of appropriately sized phytometers.

Integrating importance and intensity

The normalized neighbour index (Nmax) expresses the weight of neighbour impact relative to the total plant potential. It substantially differs from both the intensity and the importance indices. In operational terms, the distinction between importance and intensity (Welden and Slauson 1986, Grace 1991, Brooker et al. 2005, Brooker and Kikvidze 2008, Kikvidze et al. 2011a) mainly relies on the different role assigned to the effects of environmental constraints. Importance indices scale the impact of neighbours to the effects of environmental constraints, or as a tool to design balanced interaction experiments, would allow to rule out the effects of neighbour replacement along productivity gradient by setting a corresponding turnover of appropriately sized phytometers.

The normalized neighbour index (Nmax) expresses the weight of neighbour impact relative to the total plant potential. It substantially differs from both the intensity and the importance indices. In operational terms, the distinction between importance and intensity (Welden and Slauson 1986, Grace 1991, Brooker et al. 2005, Brooker and Kikvidze 2008, Kikvidze et al. 2011a) mainly relies on the different role assigned to the effects of environmental constraints. Importance indices scale the impact of neighbours to the effects of neighbours plus abiotic stress (N + S) (Table 1). Intensity indices, on the contrary, either ignore the abiotic stress (as in the absolute competition intensity index, CI) or deliberately exclude it from their denominator. Most of the relative intensity indices standardize the absolute impact of competition to the performance of the isolated target-plants, so they measure neighbour impact independently of any environmental effect (Grace 1995). Their denominator excludes the abiotic stress, whereas it intrinsically includes both neighbour effects and the overall plant performance (N + O) (Table 1). Some authors have corrected the intensity index denominator, in order to limit its range in facilitative interactions (Markham and
Chanway 1996, Armas et al. 2004), but in no case intensity indices include the maximum plant potential in their denominator. The normalized index \( (N_{imp}) \) is intrinsically scaled to all the three ideal components of \( Y_{max} \) \((N + S + O)\). Hence, it can neither be considered an intensity index, since it includes the stress component in its denominator, nor an importance index, since it is not strictly scaled to the two selecting forces \((N, S)\) originally addressed by Welden and Slauson (1986). However, looking from a wider perspective, the target-plant overall performance may be viewed as the result of several other hidden impacts, whose relative weight could be dissected by appropriate experimental approaches. The original concept of "overall constraints" (Welden and Slauson 1986) has been already extended in the recent literature with the use of the "total magnitude of factors" (Seifan et al. 2010), which sums the absolute values of the counteracting positive and negative impacts on plant performance. Kikvidze et al. (2011a) have recently proposed that the formalized concept of importance could be usefully extended to determine the relative share of any overall effect experienced by the target organisms. In this wider context, the normalized framework could represent a very simple and general approach to quantifying the relative weight of the concurring selective forces acting on individuals and communities.

An analytical comparison of \( N_{imp} \) with importance and intensity indices may be worked out by considering their respective algebraic relationships. In a purely competitive interaction, the relationship between \( N_{imp} \) and \( C_{imp} \) is the following:

\[
N_{imp} = C_{imp} \times (Y_{max} - Y_{mix})/Y_{max}
\]

(6)

Since the expression \((Y_{max} - Y_{mix})\) represents the amount of the overall constraints on target-plant performance \((OC\) in Fig. 1), in competitive interactions the two indices tend to be equal if \( OC \rightarrow Y_{max}\), that is when the target-plant in mixed stand experiences the maximum possible constraints. On the contrary, they tend to diverge when \( OC \rightarrow 0\), that is when the target-plant approaches its optimal biotic and abiotic environment. Both indices tend to approximate \( E_{i} \) when \( Y_{mix} \rightarrow 0\). Thus, when the overall suitability for target-plants in mixed stand \((O_{s}\) in Fig. 1) is low or null, the two indices tend to reflect the normalized response of the isolated target-plant to productivity.

A quite different behaviour may be deduced with regard to the relations between \( N_{imp} \) and \( CI_{r} \):

\[
N_{imp} = CI_{r} \times Y_{iso}/Y_{max} = CI_{r} \times E_{i}
\]

(7)

\( N_{imp} \) tends to be equal to \( CI_{r} \) when \( E_{i} \rightarrow 1\), i.e., when approaching the optimal phytometer environmental range, whereas it diverges from \( CI_{r} \) when \( E_{i} \rightarrow 0\), that is in the most stressful environments. In this latter case, both \( C_{imp} \) and \( N_{imp} \) always assume low values (Fig. 2), because the relative impact of competition is low, with regard either to the overall constraints (in the case of \( C_{imp} \)) or to the maximum target-plant potential (in the case of \( N_{imp} \)). Yet \( CI_{r} \) can assume very high values if the impact of competition relative to the performance of the isolated target-plant is high. However, in this case the risk is high that falsely significant results are detected (Jasienski and Bazza 1999), since this ratio is highly sensitive to the slightest difference between severely stressed individuals. Looking at the upper end of the gradient, in the extent to which \( E_{i} \) approaches its maximum value, \( N_{imp} \) and \( CI_{r} \) will tend to converge around values that are proportional to the absolute size of competitive impact. On the contrary, \( CI_{r} \) tends to assume its maximum possible value independently of neighbour effect-size, since competitive impact accounts for almost the totality of the constraints experienced by the target-plant. Definitely, \( N_{imp} \) assumes values that are always lower than both \( CI_{r} \) and \( C_{imp} \) and tends to approach \( C_{imp} \) in the most unsuited and \( CI_{r} \) in the most suited environments. Synthetically, it could be described as an index which integrates the concepts of intensity and importance in a more conservative approach.

**Trends along the gradient: the importance of a null hypothesis**

Rees et al. (2012) highlighted the problematic statistical interpretation of any trend detected by using either \( C_{imp} \) or \( I_{imp} \) to measure competition importance along productivity gradients, since they always get the highest values in the target-plant optimal range, whereas they have limited values outside this range. Hence, their increasing trend along the gradient could depend on the inherent properties of the indices rather than on the underlying biology. Importance and intensity are not necessarily correlated (Brooker et al. 2005): \( C_{imp} \) may strongly increase even in presence of a linear decrease of competition intensity along the gradient (Fig. 2c, 2f), and this pattern could be hardly differentiated from the corresponding trends obtained when either a decreasing (Fig. 2a, 2b) or a constant (Fig. 2c, 2d) trend of competition intensity is set. The improved \( I_{imp} \) index behaves similarly and, if the interaction shifts to positive, it symmetrically returns an opposite increasing facilitative pattern towards the optimal environmental range (Fig. 3). Both importance indices show a marked tendency to be correlated to the isolated target-plant response to productivity. Thus, whenever \( Y_{iso} \) is correlated to productivity, importance indices will tend to be correlated to standing crop.

This makes very hard to imagine what the null hypothesis should be for testing any prediction about neighbour importance along the gradient. No doubt, the use of \( N_{imp} \) as the index to quantify the weight of neighbour impact relative to the other components of target-plant fitness would meet lower difficulties relative to \( I_{imp} \): the theoretical range of possible variation of \( N_{imp} \) is sufficiently diversified, both for patterns and effect size (Fig. 2, Fig. 3), to allow any predicted trend to be tested against alternative hypothesis on the basis of model error comparison.

However, \( N_{imp} \) cannot be considered an importance index by its definition. Moreover, its use would not immediately solve the problems highlighted by Rees et al. (2012). Indeed, this index follows the pattern of an absolute competition intensity index \( (CI_{r}) \), and the latter may tend to increase with the isolated target-plant performance, since the range of its
Figure 2. Simulated trends (b, d, f) of the indices of relative competition intensity (Cl), competition importance (Cimp) and normalized-neighbour effect (Nn), calculated on the basis of the simulated growth responses represented in sub-fig. a, c, e. The response of isolated target-plants (Yiso) to productivity was supposed to respond to a logistic model with a maximum ceiling value (Ymax) of 100 conventional units (see appendix 3 for details on model parameters). The performance of the target-plant in mixed stand (Ymix) was modelled as a fraction (relative yield - RY) of the isolated target-plant performance. Three simulations are presented: (a, b) linear decrease of RY, from 100% at a 0 level of productivity to 0% at a productivity level of 100 conventional units; (c, d) constant (40%) RY; (e, f) linear increase of RY, from 0% at a 0 level of productivity to 99.9% at a productivity level of 100 conventional units.

Figure 3. The trends of the index of importance (Iimp) and of the normalized-neighbour effect index (Nn) are represented in the sub-figures (b, e) and (c, f) respectively, as calculated on the basis of the simulated growth responses of sub-fig. (a) and (d). The response of isolated target-plants (Yiso; thick black line) to productivity was supposed to respond either to a logistic (a, b, c) or to a peak model (d, e, f) (see appendix 3 for details on model parameters). The performance of the target-plant in mixed stand (Ymix; tiny gray lines) was modelled as a fraction (relative yield - RY) of the isolated target-plant performance, either as a facilitative (empty symbols) or as a competitive interaction (filled symbols). RY values were set as follows: filled circle 0%; filled triangle 50%; filled rhombus 80%; filled square 95%; empty square 105%; empty rhombus 120%; empty triangle 150% empty circle 200%.
possible values is lower in the unsuitable compared to the optimal environments. This reasoning however is strictly referred to the response of a single phytometer to increasing productivity levels, since it depends on the inherent properties of the target species response to resource availability. On the contrary, no inherent trend would be found if the competition level was measured across habitats by using different phytometers, each ideally representative of just one of the studied habitats. Thus, a glimpse towards a different possible approach is proposed here: rather than looking at single phytometers as the tools for measuring relative neighbour impact along productivity gradients, it would be meaningful to select groups of target species, each for any range of the gradient, and to keep their average responses as the measure for that range of productivity.

There are several examples of multispecies approach to measuring neighbour interaction trends (e.g., Wilson and Keddy 1986, Wilson and Tilman 1995, Callaway et al. 2002, Lamb and Cahill 2008, Bennett and Cahill 2012). The arguments proposed in this paper may contribute to improve this approach by defining two basic rules for equivalence among phytometers. Firstly, using the index of environmental suitability (E) as a blocking parameter in order to allow the different phytometers to work under the same relative impact of the stress component. Secondly, the use of the index of relative crowding (rD) as a tool to select the target species on the basis of their size, so that they work as equivalent competitors relative to neighbour size, with a constant degree of potential size-asymmetry in all the ranges of the gradient. Once ideally fixed these two conditions, the different approaches to measuring competition would converge as for their trend along the gradient. A linear dependence would link the index of normalized neighbour effect (N) to CI index, if E is set constant. Similarly, it may be verified that N and I would be positively correlated over a wide range of constant values of E (see Appendix 2 in supplementary materials).

In the following section it will be shown that I and N get very close values and trends over a significant selection of published datasets, only differing when a relatively higher performance of the target-plants in mixed stand is found.

Applications to literature data

The behaviour of the new proposed indices has been tested on real data by reanalyzing three published datasets that Brooker and Kikvidze (2008) used to compare the competition importance index with other interaction indices. Previously, the same datasets were used by Wilson (2007) to test two other indices, the interaction strength index (I) and the relative crowding index (D) (see Appendix 1 in supplementary materials). The three datasets include: i) an extensive intercontinental study with *Poa pratensis* across differently productive grasslands (Reader et al. 1994); ii) an experiment focused on the components of competition intensity along a soil depth gradient, with *Trichostema brachiatum* as phytometer (Belcher et al. 1995); iii) a test aimed to evaluate the effects of fluctuating resource availability within both natural and artificial gradients, with the desert annual *Stipa capensis* as phytometer (Kadmon and Schmida 1990, Kadmon 1995). Wilson (2007) evidenced on these datasets some significant patterns that do not correspond to the current theories on competition: a positive correlation with standing crop was always found for relative crowding, whereas a negative correlation was found for interaction strength in all but Belcher et al. (1995) dataset. Brooker and Kikvidze (2008) reanalyzed the three datasets and found a general increase of interaction importance with productivity; the only exception was represented by Belcher et al. (1995) dataset, in which a peaking pattern of competition importance was found.

Materials and methods

Data were obtained from the original papers, when directly available. Otherwise they were extracted through digitizing procedures, if plotted in figures (see Appendix 3 in supplementary materials). Reference was also made to the metadata of Goldberg et al. (1999) (http://esapubs.org/archive/ecol/E080/006/), except when some discrepancies were reported in literature.

After recalculating the indices, correlations with standing crop and cross-correlations among indices were tested through a Pearson correlation analysis. If any different test and/or transformation was applied in the original papers, the same criteria were adopted. The studied indices included the normalized index of neighbour effect (N), the two Wilson's indices (D, I), an index of importance (I), an index of intensity (RNE, Markham and Chanway 1996) and the index of environmental suitability (E).

Subsequently, for exploratory purpose, the responses of target-plants to productivity were interpolated to non linear models, separately for the target-plants growing in isolation (Y) and in mixed stand (Y). Starting from the predicted target-plant performances, derived models were elaborated for each of the studied indices and fitted to the index values obtained from the real data. Details on modelling criteria are provided in Appendix 3 (supplementary materials).

Results and discussion

Correlation analysis broadly confirms the relationships already detected by Brooker et al. (2005), Wilson (2007), and Brooker and Kikvidze (2008) (Table 2), with just some small differences that could depend on data selection criteria. N shows a positive significant correlation with standing crop in both Reader et al. (1994) and Kadmon (1995) datasets, whereas no significant relation is found in Belcher et al. (1995) dataset, similarly to what already found for C by Brooker and Kikvidze (2008). N always shows a significant positive correlation with I and to a lower extent with RNE. The correlation between N and I is higher in Kadmon (1995) and Belcher et al. (1995) relative to Reader et al. (1994) dataset. Both N and I always result to be very highly correlated with the index of relative environmental suitability (E), with slightly lower correlation values found in Reader et al. (1994) dataset. It is interesting to note that E is...
Measuring neighbour effects

is positively and significantly correlated with standing crop in all but Belcher et al. (1995) dataset. By a cross-comparison of these correlation patterns it may be argued that the high correlations found for both $N_n$ and $I_{imp}$ with standing crop in the two other datasets strongly reflect their correlation with the environment suitability, i.e., with the response of the isolated target-plants to productivity.

The index of environmental suitability ($E_s$) is also positively correlated with RNE in the datasets of Kadmon (1995) and Belcher et al. (1995). This pattern, however, is not linear as in the case of $N_n$ and $I_{imp}$ indices, but it rather seems to respond to an hyperbolic trend (Fig. 4). Interestingly, this trend might be compared to a similar pattern proposed by Berkowitz et al. (1995) as a null model for the response of competitive intensity to the species-specific site suitability (details in appendix 2, supplementary materials). The intensity of competition tends to approach such model in the extent to which the variability of the overall suitability along the gradient is low, as it is partly verified in the two mentioned datasets (Fig 4a and 4b). On the contrary, no correlated pattern between competitive intensity and environmental suitability is found in Reader et al. (1994) dataset, since in this case the overall suitability for plants in mixed stand is quite more variable along the gradient (Fig 4c). Looking at Wilson’s indices, $N_n$ results to be highly and positively correlated with $I$ index in Belcher et al. (1995), whereas no correlation is found in Kadmon’s dataset. $D_r$ only shows a significant negative correlation with $N_n$ in Reader et al. (1994) dataset.

Table 2. Pearson correlation values among six indices related to neighbour interaction (RNE: relative neighbour effect; $I_{imp}$: interaction importance index; $D_r$: index of crowding; $I$: index of interaction strength; $N_n$: normalized neighbour effect index; $E_s$: index of environmental suitability. The analysis was conducted on three competition experiments extracted from literature data. Bold and italic characters point out significance levels of $P < 0.001$ and $P < 0.01$ respectively.

Belcher et al. (1995)

<table>
<thead>
<tr>
<th></th>
<th>Standing crop</th>
<th>$E_s$</th>
<th>$N_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_<em>$ (</em>)</td>
<td>$P$</td>
<td>$r$</td>
</tr>
<tr>
<td>RNE</td>
<td>0.229</td>
<td>0.332</td>
<td>0.486</td>
</tr>
<tr>
<td>$I_{imp}$</td>
<td>0.113</td>
<td>0.636</td>
<td>0.995</td>
</tr>
<tr>
<td>$D_r$</td>
<td>0.636</td>
<td><strong>0.003</strong></td>
<td>-0.381</td>
</tr>
<tr>
<td>$I$</td>
<td>0.159</td>
<td>0.502</td>
<td>0.943</td>
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<tr>
<td>$N_n$</td>
<td>0.113</td>
<td>0.636</td>
<td>0.995</td>
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<tr>
<td>$E_s$</td>
<td>-0.150</td>
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Kadmon (1995)

<table>
<thead>
<tr>
<th></th>
<th>Log standing crop</th>
<th>$E_s$</th>
<th>$N_n$</th>
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<tr>
<td></td>
<td>$r$</td>
<td>$P$</td>
<td>$r$</td>
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<tr>
<td>RNE (**)</td>
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<td><strong>0.000</strong></td>
<td>0.669</td>
</tr>
<tr>
<td>$I_{imp}$</td>
<td>0.659</td>
<td><strong>0.008</strong></td>
<td>1.000</td>
</tr>
<tr>
<td>$D_r$</td>
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<td>0.013</td>
<td>0.046</td>
</tr>
<tr>
<td>$I$</td>
<td>-0.389</td>
<td>0.152</td>
<td>-0.161</td>
</tr>
<tr>
<td>$N_n$</td>
<td>0.659</td>
<td><strong>0.008</strong></td>
<td>1.000</td>
</tr>
<tr>
<td>$E_s$</td>
<td>0.661</td>
<td><strong>0.007</strong></td>
<td></td>
</tr>
</tbody>
</table>

Reader et al. (1994)

<table>
<thead>
<tr>
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<th>Standing crop</th>
<th>$E_s$</th>
<th>$N_n$</th>
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<td>$r$</td>
<td>$P$</td>
<td>$r$</td>
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<td>-0.045</td>
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<tr>
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<tr>
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<tr>
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<td><strong>0.001</strong></td>
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</tr>
<tr>
<td>$E_s$</td>
<td>0.676</td>
<td><strong>0.000</strong></td>
<td></td>
</tr>
</tbody>
</table>

(*) Spearman correlation analysis has been applied to this dataset, as in the original paper
(**) In Kadmon’s dataset the intensity index has been arcsin square-root transformed prior to analysis, as done by the author in his paper


When looking at the trends in response to productivity, the dataset of Belcher et al. (1995) appears to be characterized by a peak of \( Y_{\text{mix}} \) performance in the middle of the gradient, with very low values in the two extremes (Fig. 5a). This pattern strongly determines the trend of competition indices, since \( Y_{\text{mix}} \) performance is constantly low along the whole gradient, except for a small facilitative peak detected at very low productivity level. As predicted, in these conditions (very low values of the overall suitability all over the gradient) \( N_{\text{r}} \) tends to behave exactly as \( I_{\text{imp}} \) index (Fig. 5e and 5f), and both reflect the response of the isolated target-plant. Also the \( I \) index shows a quite evident response to the peaking pattern of the isolated target-plants (Fig 5c), so resulting highly correlated to both \( N_{\text{r}} \) and \( I_{\text{imp}} \) indices (Table 2). This peak of competition importance at intermediate productivity was expressly observed by Brooker and Kikvidze (2008), who hypothesized a possible role of other factors, for example facilitation, which could have limited the impact of competition at a higher productivity. However, if looking at target-plant biomass, and not just at the indices which derive from it, this peak seems definitely to depend on the response of the isolated target to productivity. RNE index shows a less clear pattern, with both highly positive and highly negative values dispersed on both sides of the gradient, though it could be described to some extent by the same peaking behaviour (Fig. 5d), consistently with the positive significant correlation that have been found among RNE and both \( N_{\text{r}} \) and \( I_{\text{imp}} \) indices (Table 2).

Kadmon's dataset is also characterized by very low values of the target-plant performance in mixed stand. On the contrary, the target-plants in isolation respond to productivity with a linearly increasing pattern (Fig. 6a). As predicted, also in this dataset \( N_{\text{r}} \) and \( I_{\text{imp}} \) are strongly inter-correlated (Table 2), and both present a positive trend in response to productivity (Fig. 6e and 6f). RNE index (Fig. 6d) responds to productivity with a pattern that closely resembles the null model proposed in Fig. 4b. Hence, its trend along the gradient could be associated to the combined effect of the constantly low \( O_{\text{r}} \) and the high correlation between \( E_{\text{r}} \) and standing crop.

Wilson's indices evidence a globally increasing pattern of \( D_{\text{r}} \), though this pattern is not clearly evidenced by the curve-predicted model (Fig. 6b). The \( I \) index appears to respond to a hyperbolically decreasing pattern (Fig. 6c).

In the experiment of Reader et al. (1994), \( Y_{\text{iso}} \) is well fitted by a logistic-type model, whereas \( Y_{\text{mix}} \) is better fitted by a peak model (Fig. 7a). In this dataset, the overall suitability is not so low as in the others, and it tends to peak in the middle of the gradient (Berkowitz et al. 1995) (see also appendix 2 in supplementary materials). This model fits quite well the first two datasets analyzed, where the overall suitability \( O_{\text{r}} \) is constantly low, whereas no such pattern is found for the third dataset, where the performance in mixed stand is highly variable along the gradient. Note that in Reader et al. (1994) dataset negative values could be assumed by the target-plant performance, because of the variable measured (RGR), so RNE index results to be outscaled relative to its predicted range. See Table 2 for correlation values.

![Figure 4](https://example.com/figure4.png)

**Figure 4.** The relationship between competitive intensity, measured as Relative Neighbour Effect (RNE), and environmental suitability \( E_{\text{r}} \), is represented as recorded on the datasets of (a) Belcher et al. (1995), (b) Kadmon (1995) and (c) Reader et al. (1994). The dotted lines in sub-figures (a) and (b) represent a null model obtained by calculating the competition intensity index in the hypothesis that the target-plant in mixed stand assumes its average value along the whole gradient (Berkowitz et al. 1995) (see also appendix 2 in supplementary materials). This model fits quite well the first two datasets analyzed, where the overall suitability \( O_{\text{r}} \) is constantly low, whereas no such pattern is found for the third dataset, where the performance in mixed stand is highly variable along the gradient. Note that in Reader et al. (1994) dataset negative values could be assumed by the target-plant performance, because of the variable measured (RGR), so RNE index results to be outscaled relative to its predicted range. See Table 2 for correlation values.
Figure 5. Results of the reanalysis of the dataset of Belcher et al. (1995). Sub-figure (a) shows the target-plant response to productivity, either in isolation ($Y_{iso}$ - filled circles) or in mixed stand ($Y_{mix}$ - empty circles), with non linear models interpolated to the two data-series. Five competition indices (relative crowding $D_r$; interaction strength $I$; relative neighbour effect $RNE$; importance index $I_{imp}$; normalized neighbour effect $N_n$) are shown in the sub-figures (b) to (f), as calculated on both real and model-predicted data. Fitting values of the derived models are reported in the sub-figures. For a better visualization, $D_r$ and $I$ indices were normalized to 1 as the maximum value prior to graph plotting. Details about model parameters in Appendix 3.

Figure 6. Results of the reanalysis of the dataset of Kadmon (1995). Captions as in Fig. 5. Pearson correlation of predicted vs real data in sub-fig. (a): $Y_{iso} \rightarrow r_{fit} = 0.851, P < 0.001; Y_{mix} \rightarrow r_{fit} = 0.437, P < 0.103; n = 15$. See Appendix 3, for details on model parameters.
7b), probably related to the decreasing rate of change of the isolated target-plant in response to productivity. Conclusions

The recent reaffirmation of the necessity to distinguish importance from intensity (Brooker et al. 2005) has opened a very interesting debate, aimed either to improve the indices (Kikvidze and Armas 2010, Seifan et al. 2010) or to propose alternative ways to address the same purpose (Damgaard and Fayolle 2010, Navas and Fayolle 2012). Nevertheless, the criticism to this approach has evidenced the existence of significant gaps which could limit its theoretical suitability (Freckleton et al. 2009, Freckleton and Rees 2011, Rees et al. 2012). The simulations proposed in this paper illustrated some of the most problematic issues with importance indices. A very simple measure, the normalized neighbour effect index (N\(n\)), has turned out to be a suitable index to integrate importance and intensity within the framework of a novel approach to measuring neighbour interactions. When tested on literature data, this index has resulted to be very highly correlated to the most currently used importance index, and in a lower extent to intensity index. However, in all the three studied cases, several detected trends appeared to be predictable on the basis of the inherent properties of the indices, and particularly on the basis of their inherent correlation with the response of the isolated target-plant to productivity.

Thus, the results of this paper definitely claim the necessity of looking towards a different approach: the trends of neighbour interaction in response to productivity cannot be studied correctly by using single target species, since in such conditions several detected trends could depend on the indices rather than on the interaction. The majority of the experiments with phytometers used single target-plants as a kind of neutral tool to measure the level of competition inside communities. However, a large amount of literature accounts for the general failure in finding clear patterns of plant competitive response to productivity by using such methods (Goldberg and Burton 1992, Gurevitch 1992, Goldberg 1996, Goldberg et al. 1999), and this issue does not seem to have an easier resolution with regard to the most recent debate on facilitative interactions (Maestre et al. 2005, Lortie and Callaway 2006). Perhaps, looking at the overall complexity of the processes involved in these interactions, there is actually no reason to expect monotonic trends to be expressed by single phytometers interacting with neighbours at increasing productivity. Rather, reconstructing the competitive response to productivity of selected target-plants should be considered the preliminary step to identify groups of functionally equivalent competitors to be used in the different points of the gradient. The use of a normalized index for measuring neighbour interaction, together with the adoption of criteria to stratify target-plant responses, would ideally fulfil the theoretical necessities of this new proposed approach.

Figure 7. Results of the reanalysis of the dataset of Reader et al. (1994). Captions as in Fig. 5. Pearson correlation of predicted vs real data in sub-fig. (a): \(Y_{iso} \rightarrow r_{fit} = 0.669, P < 0.001; Y_{mix} \rightarrow r_{fit} = 0.468, P < 0.001; n = 44\). It must be noted that the measured variable in this experiment (relative growth rate, RGR) may assume negative values as well, so RNE assumes values that exceed its predicted range. See Appendix 3, for details on model parameters.
Several studies used a multispecies approach to measuring the level of competition inside plant communities (e.g., Wilson and Keddy 1986, Wilson and Tilman 1995, Callaway et al. 2002, Lamb and Cahill 2008, Bennett and Cahill 2012), but, as far as I am aware, none of these works expressly considered any parameter related to environment importance and crowding as a possible blocking criterion. The natural prosecution of this research is to build up an opportune metadata to address the unresolved questions with this new methodological approach. Furthermore, the idea proposed in this paper could help to design new experiments, in which equivalent groups of phytometers are used to analyze how the relative weight of plant interaction changes with the changing productivity on the gradient.

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References


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Electronic Appendices

**Appendix 1.** Wilson’s indices and their relation with the normalized approach.

**Appendix 2.** Correlated trends among neighbour interaction indices.

**Appendix 3.** Details on reanalysis and modelling.

The file may be downloaded from the web site of the publisher at www.akademiai.com.