

## Associations between species and groups of sites: indices and statistical inference

MIQUEL DE CÁCERES<sup>1</sup> AND PIERRE LEGENDRE

*Département de Sciences Biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec H3C 3J7 Canada*

**Abstract.** Ecologists often face the task of studying the association between single species and one or several groups of sites representing habitat types, community types, or other categories. Besides characterizing the ecological preference of the species, the strength of the association usually presents a lot of interest for conservation biology, landscape mapping and management, and natural reserve design, among other applications. The indices most frequently employed to assess these relationships are the phi coefficient of association and the indicator value index (IndVal). We compare these two approaches by putting them into a broader framework of related measures, which includes several new indices. We present permutation tests to assess the statistical significance of species–site group associations and bootstrap methods for obtaining confidence intervals. Correlation measures, such as the phi coefficient, are more context-dependent than indicator values but allow focusing on the preference of the species. In contrast, the two components of an indicator value index directly assess the value of the species as a bioindicator because they can be interpreted as its positive predictive value and sensitivity. Ecologists should select the most appropriate index of association strength according to their objective and then compute confidence intervals to determine the precision of the estimate.

**Key words:** *community types; fidelity measure; indicator value; phi coefficient of association.*

### INTRODUCTION

In many ecological studies, researchers analyze the relationship between single species and one or more groups of sites. The classification of sites into groups (hereafter called “site groups”) may have been derived from the similarities in environmental conditions among sites (e.g., habitat types, disturbance states), or in species composition (i.e., community types); it may also have been given by the study design (e.g., comparison of geographic regions or sampling years) or obtained using other criteria. With respect to the species, the analysis of its strength of association with site groups provides a characterization of its ecological preferences (e.g., Harms et al. 2001). With respect to the site group, the list of species strongly associated to the site group has a lot of interest for predictive purposes. For example, in vegetation studies, plant species that preferably occur in a single or a few vegetation types are generally called “diagnostic species,” and are useful for the identification of vegetation types in field surveys (Chytrý et al. 2002*b*). A species restricted to one or a few habitat types potentially represents a better ecological indicator of environmental change than a habitat generalist, owing to the greater susceptibility of the specialist to local or regional extinction. Species of this kind are called “indicator species” by ecologists, and are used to

monitor environmental changes and assess the impacts of disturbances on an ecosystem (Carignan and Villard 2002). McGeoch (1998) suggested that indicator species could be used in three distinct ways: (1) to reflect the biotic or abiotic state of the environment; (2) to reveal evidence for the impact of environmental changes; and (3) to indicate the diversity of other species, taxa, or communities within an area. Both “diagnostic” and “indicator” species essentially refer to the same concept: using the preference of the species for predicting purposes. This concept is frequently applied in conservation, land management, and reserve design.

In European phytosociology, the study of species–site group associations has a long tradition. The strength of the association was called “fidelity,” which was defined as a measure of species concentration in vegetation units. The determination of diagnostic species is still an active research topic in vegetation science (e.g., Bruelheide 1995, 2000, Chytrý et al. 2002*a, b*, Tichý and Chytrý 2006, De Cáceres et al. 2008, Willner et al. 2009), where the most widely used index is the phi coefficient of association or modified forms of it (Chytrý et al. 2002*b*, Tichý and Chytrý 2006, Willner et al. 2009). In contrast, many ecologists prefer to determine indicator species using the IndVal index (Dufrene and Legendre 1997). Although some comparisons between the two approaches have been made (Tichý and Chytrý 2006, De Cáceres et al. 2008), ecologists still lack a thorough framework to help them understand the differences between the available indices and determine when to apply one or

Manuscript received 1 October 2008; revised 9 March 2009; accepted 10 March 2009. Corresponding Editor: H. H. Wagner.

<sup>1</sup> E-mail: miquelcaceres@gmail.com

TABLE 1. Non-equalized indices of association between a species and a group of sites.

Index type	Correlation indices	Indicator value indices
Presence-absence	$r_{\Phi} = \frac{N \times n_p - n \times N_p}{\sqrt{(N \times n - n^2) \times (N \times N_p - N_p^2)}}$ †	$\sqrt{\text{IndVal}_{pa}} = \sqrt{A_{pa} \times B_{pa}} = \sqrt{\frac{n_p}{n} \times \frac{N_p}{N_p}}$ †
General abundance	$r_{pb} = \frac{N \times a_p - a \times N_p}{\sqrt{(N \times l^2 - a^2) \times (N \times N_p - N_p^2)}}$ †	$s_{\cos} = \sqrt{\frac{a_p}{l^2} \times \frac{a_p}{N_p}}$
Individual-based (partial)		$\sqrt{\text{IndVal}_{ind}} = \sqrt{A_{ind} \times B_{pa}} = \sqrt{\frac{a_p}{a} \times \frac{N_p}{N_p}}$ †
Individual-based (full)	$r_{ind} = \frac{N \times a_p - a \times N_p}{\sqrt{(N \times c \times a - a^2) \times (N \times N_p - N_p^2)}}$	$s_{ind} = \sqrt{A_{ind} \times B_{ind}} = \sqrt{\frac{a_p}{a} \times \frac{a_p}{c \times N_p}}$

Notes: IndVal is the indicator value of a species, which is the product of two quantities,  $A$  and  $B$ , and  $r$  is the correlation index. See *Indices for assessing species-site group associations* for details. For the presence-absence case, we follow the notation used in previous works (Bruehlheide 2000, Chytrý et al. 2002b, Tichý and Chytrý 2006, De Cáceres et al. 2008):  $N$ , total number of sites;  $N_p$ , number of sites belonging to the target site group;  $n$ , number of occurrences of the species among all sites;  $n_p$ , number of occurrences of the species within the target site group. Indices for species abundance data require the following values:  $a_p$ , sum of the abundance values of the species within the target site group;  $a$ , sum of the abundance values of the species over all sites;  $l$ , norm of the vector abundances of the species;  $c$ , constant representing the total number of individuals or the total biomass per site.

† Recommended indices.

another. With the aim of improving the statistical practices of ecologists regarding species-site group associations, in the present work we compare the phi coefficient and indicator value approaches by integrating them into a broader algebraic framework of indices. We also address methods of inference for this kind of ecological relationships, specifically covering permutation tests of hypotheses and confidence intervals derived from bootstrap methods.

INDICES FOR ASSESSING SPECIES-SITE GROUP ASSOCIATIONS

In this section, we present several species-site group association indices and elaborate their mathematical relationships. Some of these indices are well known to ecologists, but others are less known or have never been used before. All of them share the following properties:

(1) the association with a site group is calculated for each species independently; unlike the TWINSPAN method (Hill 1979), the pattern observed for a given species does not influence the association value of another species to a site group; (2) the strength (not the statistical significance) of the association is independent of the number of observations; (3) the strength of the association is bounded, i.e., there is a maximum and a minimum value; (4) in the case of indices for species abundance data, the strength of the association is invariant to multiplication of species abundance values by a constant. To follow the description of the indices, readers should refer to Tables 1 and 2, which present the formulas of all indices, as well as Fig. 1, which displays the mathematical relationships between indices.

TABLE 2. Group-equalized indices of association between a species and a group of sites.

Index type	Correlation indices	Indicator value indices
Presence-absence	$r_{\Phi}^g = \frac{N \times n_p^g - n^g \times N_p^g}{\sqrt{(N \times n^g - n^{g2}) \times (N \times N_p^g - N_p^{g2})}}$ †	$\sqrt{\text{IndVal}_{pa}^g} = \sqrt{A_{pa}^g \times B_{pa}^g} = \sqrt{\frac{n_p/N_p}{\sum_{k=1}^K n_k/N_k} \times \frac{N_p}{N_p}}$ †
General abundance	$r_{pb}^g = \frac{N \times a_p^g - a^g \times N_p^g}{\sqrt{(N \times l^{g2} - a^{g2}) \times (N \times N_p^g - N_p^{g2})}}$ †	$s_{\cos}^g = \sqrt{\frac{a_p/N_p}{\sum_{k=1}^K l_k^2/N_k} \times \frac{a_p}{N_p}}$
Individual-based (partial)		$\sqrt{\text{IndVal}_{ind}^g} = \sqrt{A_{ind}^g \times B_{pa}^g} = \sqrt{\frac{a_p/N_p}{\sum_{k=1}^K a_k/N_k} \times \frac{N_p}{N_p}}$ †
Individual-based (full)	$r_{ind}^g = \frac{N \times a_p^g - a^g \times N_p^g}{\sqrt{(N \times c \times a^g - a^{g2}) \times (N \times N_p^g - N_p^{g2})}}$	$s_{ind}^g = \sqrt{A_{ind}^g \times B_{ind}^g} = \sqrt{\frac{a_p/N_p}{\sum_{k=1}^K a_k/N_k} \times \frac{a_p}{c \times N_p}}$

Notes: In addition to the quantities defined in Table 1, the following symbols are used:  $K$ , number of site groups;  $N_k$ , number of sites belonging to the  $k$ th site group;  $n_k$ , number of occurrences of the species in the  $k$ th site group;  $a_p$ , sum of the abundance values of the species in the  $k$ th site group. Quantities to use as substitutes in correlation indices are computed as  $N_p^g = N/K$ ,  $n_p^g = N_p/N_p$ ,  $n^g = N_p^g \times \sum_{k=1}^K (n_k/N_k)$ ,  $a_p^g = N_p^g(a_p/N_p)$ ,  $a^g = N_p^g \times \sum_{k=1}^K (a_k/N_k)$ , and  $l^{g2} = N_p^g \times \sum_{k=1}^K (l_k^2/N)$ .

† Recommended indices.

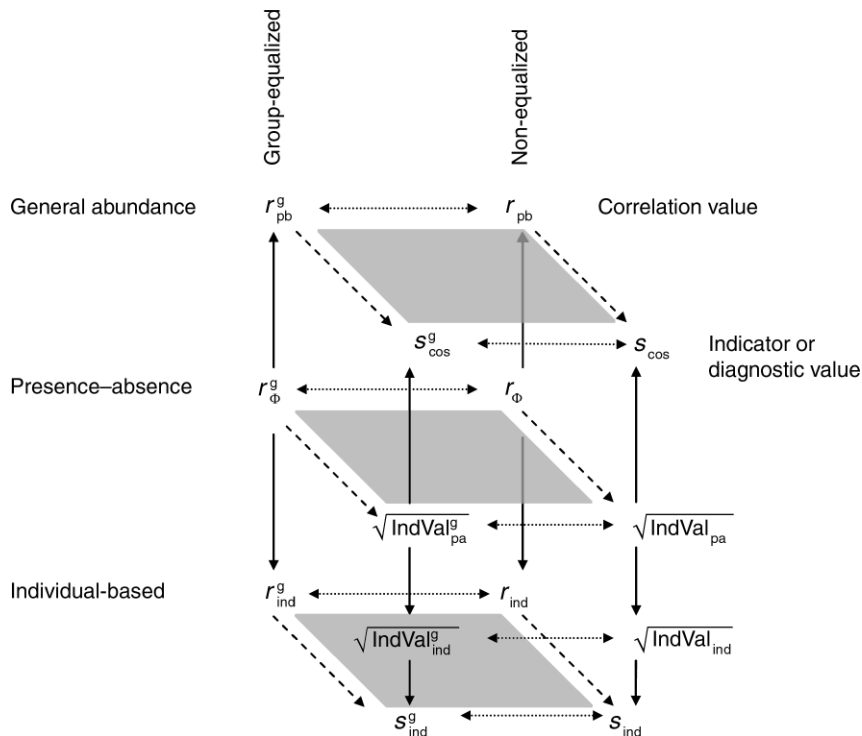


FIG. 1. Representation of the relationships among the 14 association indices considered in this study. Dotted horizontal arrows indicate equal values when groups have the same relative size. Downward/upward arrows indicate generalizations from presence/absence to abundance data. Dashed diagonal arrows indicate the limit value on data sets encompassing a large ecological range. Notation is as in Tables 1 and 2.

Correlation indices

We begin with species presence–absence data and the phi coefficient of association ( $r_{\Phi}$ ). This well-known index is the Pearson correlation computed using two binary vectors: a vector containing “1” for sites where the species is present and “0” for those where it is absent, and a vector with “1” for sites belonging to the group of interest and “0” for sites belonging to other groups. There are at least two possible generalizations of  $r_{\Phi}$  to species abundance data. One is the point-biserial correlation coefficient ( $r_{pb}$ ), which is the Pearson correlation computed between a quantitative vector (i.e., the vector containing the species abundance values at the various sites) and a binary vector (i.e., the vector of site membership values). The second generalization is intended to be used with individual count data, and it is equivalent to the one proposed by Chao et al. (2006) for site similarity measures. This latter generalization consists in computing  $r_{\Phi}$  on the presence-absence of individuals instead of the presence–absence of the species (see Legendre and Legendre 1998:463 for more information). Unfortunately, this approach requires knowing the total number of sampled individuals in a site, and hence it uses information from species other than the species of interest. In order to fulfill the first above-mentioned requirement, we need to assume that the total number of individuals per site is constant for all sites. The resulting individual-based correlation index

( $r_{ind}$ ) is rather similar to  $r_{pb}$  (see Table 1). In order to avoid setting the total number of individuals to an arbitrary value one can transform the species data table by dividing each abundance value by the sum of the abundances at the corresponding site, and then set the constant  $c$  equal to one. Willner et al. (2009) suggested a very similar generalization of the phi coefficient, in which they used percentages of cover as abundance values; they did not explicitly assume that all sites should have a sum of covers equal to 100%.

A disadvantage of the three correlation measures is that they are dependent on the relative size of the target site group (i.e., the proportion of sites in the data set that belong to the target site group,  $N_p/N$ ), and this precludes comparisons between values corresponding to site groups of different relative sizes. Tichý and Chytrý (2006) recognized this limitation in  $r_{\Phi}$  and suggested a modification to allow such comparisons. The modification consists in equalizing the relative sizes of all site groups. Several of the quantities used to compute  $r_{\Phi}$  are affected by this modification (see Table 2 for details). The group-equalized phi coefficient ( $r_{\Phi}^g$ ) is obtained by substituting the original quantities in  $r_{\Phi}$  by the modified ones. We can similarly define group-equalized counterparts for  $r_{pb}$  and  $r_{ind}$ , obtaining two new indices  $r_{pb}^g$  and  $r_{ind}^g$  (see Table 2). If all site groups originally have the same size (i.e., the same number of sites) then the following equalities hold:  $r_{\Phi} = r_{\Phi}^g$ ,  $r_{pb} = r_{pb}^g$  and  $r_{ind} = r_{ind}^g$ .

An alternative modification of  $r_{\Phi}$ , which we will not include in our framework, consists in fixing the relative size of the target group to an arbitrary user-defined parameter (Knollová et al. 2005, Tichý and Chytrý 2006).

#### *Indicator value indices*

Dufrêne and Legendre (1997:350) defined the indicator value (IndVal) of a species as the product of two quantities, called *A* and *B*. For species abundance data, (IndVal<sub>ind</sub><sup>g</sup> in Table 2), quantity *A* was defined as the mean abundance of the species in the target site group divided by the sum of the mean abundance values over all groups ( $A_{\text{ind}}^g$ ). The sum of the mean abundances over all groups was used, instead of the sum of the actual abundances over all groups, in order to control for the effect of unequal sizes of the site groups. Quantity *B* was defined as the relative frequency of occurrence (presence-absence) of the species inside the target site group ( $B_{\text{pa}}$ ). Note that the original definition of IndVal was based on the number of individuals to assess *A* but on presence-absence data to assess *B*. If *A* was also based on presence-absence data, we would have  $A_{\text{pa}}^g$ , the relative frequency of the species in the target site group divided by the sum of relative frequencies over all groups, and the resulting indicator value index would be IndVal<sub>pa</sub><sup>g</sup> (Table 2). However, instead of using this latter index, Dufrêne and Legendre (1997:363) proposed that for species presence-absence data, indicator values should be calculated using IndVal<sub>pa</sub> (Table 1), where quantity *A* is the absolute frequency of the species inside the target group divided by the sum of absolute frequencies ( $A_{\text{pa}}$ ). Hence, Dufrêne and Legendre did not control for the effect of unequal sizes of the site groups when defining their IndVal index for presence-absence data. The abundance-based counterpart of IndVal<sub>pa</sub> is IndVal<sub>ind</sub> (Table 1), which is obtained by defining *A* as the sum of abundances of the species within the target site group divided by the sum of abundances of the species over all sites ( $A_{\text{ind}}$ ). Analogously to correlation measures, we can see that  $A_{\text{pa}}^g$  and  $A_{\text{ind}}^g$  are the group-equalized counterparts of  $A_{\text{pa}}$  and  $A_{\text{ind}}$ , respectively. If all site groups originally have the same size then the following two equalities hold: IndVal<sub>pa</sub><sup>g</sup> = IndVal<sub>pa</sub>, IndVal<sub>ind</sub><sup>g</sup> = IndVal<sub>ind</sub>.

#### *Relationships between correlation and indicator values for presence-absence data*

With species presence-absence data, the correlation and indicator value approaches may yield similar results when computed on a data set with very high beta diversity. This happens because in that case there are a large number of zeros for many species and site groups (i.e., many double zeros). The limit of  $r_{\Phi}$  when adding an infinite amount of double zeros is the Ochiai (1957) similarity coefficient, which is the square root of IndVal<sub>pa</sub> (Janson and Vegelius 1981, De Cáceres et al. 2008). The Ochiai coefficient is closely related to two

distance measures commonly used in community ecology, namely the chord (Orlói 1967) and Hellinger (Rao 1995) distances (Legendre and Legendre 1998). Moreover, suppose that the first groups in a data set contain occurrences of the species of interest while the remaining groups do not. The limit of  $r_{\Phi}^g$  when adding an infinite amount of site groups with no occurrences of the species is the square root of IndVal<sub>pa</sub><sup>g</sup>. These relationships are the reasons why indicator value indices appear as the square roots of the original indices in Tables 1 and 2. We will hereafter follow this convention.

#### *Indicator value alternatives for abundance data*

At this point we may wonder what the limits of correlation indices in the case of species abundance data are. The limit of  $r_{\text{pb}}$  when adding double zeros is the cosine of the angle formed by the two vectors ( $s_{\text{cos}}$ ). The cosine cannot take negative values because the species abundance values are always nonnegative. When computed with presence-absence data,  $s_{\text{cos}}$  is equal to the Ochiai index, and like its presence-absence counterpart it is closely related to the chord distance. Accordingly, the limit of  $r_{\text{pb}}^g$  when adding an infinite number of site groups with no occurrence of the species is  $s_{\text{cos}}^g$ , the group-equalized counterpart of  $s_{\text{cos}}$ . If we conduct the same limit operations on  $r_{\text{ind}}$  and  $r_{\text{ind}}^g$  we obtain two new indicator value indices,  $s_{\text{ind}}$  and  $s_{\text{ind}}^g$ , which allow us to understand how the indicator value measures for species abundance data fit into the general framework. Unlike  $\sqrt{\text{IndVal}_{\text{ind}}^g}$  and  $\sqrt{\text{IndVal}_{\text{ind}}}$ , which are partial generalizations to species abundances,  $s_{\text{ind}}^g$  and  $s_{\text{ind}}$  are full generalizations following the individual-based approach (see Tables 1 and 2).

#### *Synthetic data examples*

We will use synthetic data to illustrate the differences between the four indices for presence-absence data described above (see Table 3). In all scenarios the species occurs in 50% of the sites belonging to Group 1, which is the target site group. In the basic scenario (scenario a, to which the other scenarios will be compared) the species is found in 25% of the sites belonging to Group 2. As the two site groups do not have the same relative sizes,  $\sqrt{\text{IndVal}_{\text{pa}}}$  and  $\sqrt{\text{IndVal}_{\text{pa}}^g}$  do not produce the same value; the same happens with the ( $r_{\Phi}$ ,  $r_{\Phi}^g$ ) pair. Equalizing the relative sizes of the groups while keeping the same frequency of the species within each group solves the disagreement within index pairs (scenario b). If one modifies the classification of the sites not belonging to the target site group (scenarios c and d)  $\sqrt{\text{IndVal}_{\text{pa}}}$  and  $r_{\Phi}$  remain unaltered compared to scenario a, but  $\sqrt{\text{IndVal}_{\text{pa}}^g}$  and  $r_{\Phi}^g$  both change their values. If sites with the target species absent are added to the nontarget group of sites (scenario e)  $r_{\Phi}$ ,  $\sqrt{\text{IndVal}_{\text{pa}}^g}$  and  $r_{\Phi}^g$  increase their values but not  $\sqrt{\text{IndVal}_{\text{pa}}}$ . Both indicator value indices are unaffected by the consider-

TABLE 3. Values obtained with presence–absence association indices for a set of synthetic scenarios (a–g).

Scenario	Site								$\sqrt{\text{IndVal}_{pa}^g}$	$\sqrt{\text{IndVal}_{pa}}$	$r_{\Phi}^g$	$r_{\Phi}$
	A	B	C	D	E	F	G	H				
a												
Group	1	1	2	2	2	2			0.577	0.500	0.258	0.250
Species	1	0	0	0	1	0						
b												
Group	1	1	1	1	2	2	2	2	0.577	0.577	0.258	0.258
Species	1	1	0	0	0	1	0	0				
c												
Group	1	1	2	2	2	3			0.548	0.500	0.351	0.250
Species	1	0	0	0	1	0						
d												
Group	1	1	2	2	2	3			0.408	0.500	0.000	0.250
Species	1	0	0	0	0	1						
e												
Group	1	1	2	2	2	2	2		0.598	0.500	0.314	0.300
Species	1	0	0	0	1	0	0					
f												
Group	1	1	2	2	2	2	3	3	0.577	0.500	0.408	0.333
Species	1	0	0	0	1	0	0	0				
g												
Group	1	1	2	2	2	2			0.447	0.354	-0.258	-0.250
Species	1	0	1	1	0	1						

Notes: The group to which each site A–H belongs is indicated by a nominal variable “Group,” whereas “Species” is a binary variable indicating the presence or absence of the species in each site. The index values measure the association of the species to target group 1. Scenario a is the scenario to which all others are compared. Differences between scenarios are described in *Interpretation of association indices: Correlation vs. indicator value indices*.

ation of an additional group of sites where the species is absent (scenario f), whereas the  $r_{\Phi}$  and  $r_{\Phi}^g$  values change. Finally, in scenario g, the species occurs in 75% of the Group 2 sites. Two correlation indices return negative values whereas the two indicator values are lower but remain positive.

INTERPRETATION OF ASSOCIATION INDICES

In this section we address the ecological interpretation of the indices introduced in the previous section.

*Correlation vs. indicator value indices*

A careful look at the first column of Tables 1 and 2 reveals that the numerator of correlation indices is essentially a difference between the observed occurrence (or abundance) of species in the target site group and the expected occurrence (or abundance) under the hypothesis of no association. Negative correlation values tell us when a species “avoids” the target site group (scenario g in Table 3), a situation where traditional phytosociologists would say that the species shows “negative fidelity.” Such ecological behavior could also be tested with IndVal by interchanging the role of presence and absence, but at the expense of having to recompute the association value (Duf rene and Legendre 1997, McGeoch and Chown 1998).

Another important difference between the correlation and indicator value approaches is their treatment of absences of the species outside the target site group

(scenarios e and f in Table 3). Correlation indices take into account absences outside the target site group, and these absences contribute to increase the strength of the association as much as the presences inside that group. In contrast, indicator value indices do not treat species absences in the same way in the target site group and in its complementary set. Indicator value indices assume that the species can be absent from many conceivable habitats, and having fewer or more absences in the complementary set of sites is irrelevant and not taken into account. This makes correlation indices more context dependent than indicator value indices. Nevertheless, the ecological and geographical context surrounding the assessment of species–site group relationships is always crucial and should be explicitly stated in all applications (e.g., Chytr y et al. 2002a, Willner et al. 2009). In short, correlation indices indicate the degree of preference for the target site group compared to the other groups, whereas indicator value indices assess how much the target site-group matches the set of sites where the species is found.

*Components of the indicator value*

Duf rene and Legendre (1997) used the terms “specificity” and “fidelity” for quantities *A* and *B*, respectively, but we avoid this terminology here because it differs from the traditional phytosociological concept of fidelity (Tich y and Chytr y 2006, Willner et al. 2009). Instead, we prefer to use terms that relate to the contribution of *A*

and  $B$  to bioindication. The interpretation of  $A$  depends on whether species presence-absence or abundance data are considered:  $A_{pa}$  is the probability that a site belongs to the target site group, given the fact that the species has been found. It is therefore the positive predicting value of the species as indicator of the site group (Murtaugh 1996).  $A_{ind}$  is the probability of the target site group given the fact that an individual of the species has been found, so it has nearly the same interpretation as  $A_{pa}$ , but based on individuals. Group-equalized versions of these quantities do not change their basic interpretation. Quantity  $B_{pa}$  is the probability of finding the species when the site belongs to the target site group, thus expressing the sensitivity of the species as a bioindicator (Murtaugh 1996). A very high  $B_{pa}$  value for a site group means that if the species is not found at a given site the probability that the site belongs to that site group is low. The practical usefulness of  $B_{pa}$  comes from the fact that high values indicate species that are easier to detect in habitats belonging to the target site group. Note that  $B_{pa}$  could be adapted to quantify how easily the species is detected not only in space but also in time. Species whose phenology and/or behavior makes them visible during a short portion of the year may be present at all sites belonging to a site group when one pools survey data for the whole year. However, they will not be good indicators of that site group if seasons are treated as different observations because they cannot be observed during most of the year. One of the reasons why the indicator value approach is not very popular among vegetation scientists is that the  $B$  component gives too much weight to common species compared to rare species (e.g., Chytrý et al. 2002b, Tichý and Chytrý 2006). Rare plant species are often considered good indicators of vegetation types. That is, a species may be difficult to detect, but once found it is its positive predictive value that is of interest. Alternatively, Wagner and Edwards (2001) use  $A$ , and not  $IndVal$ , in order to assess the indicator value of a species without taking its rarity into account. Other combinations of  $A$  and  $B$  may be of interest (see McGeoch et al. 2002). A species with high values in both quantities has a good positive predictive value and is easy to find, so it becomes a very good species to be used as a bioindicator. Dufrêne and Legendre (1997) referred to species with either high  $A$  or high  $B$  values, but not both, as asymmetrical indicator species. This terminology conceptually matches the traditional phytosociology concept of asymmetrical fidelity (Juhász-Nagy 1964, De Cáceres et al. 2008).

The alternative quantitative indicator value indices present some problems regarding the interpretation of their components. The components in cosine measures ( $s_{cos}$  and  $s_{cos}^g$ ) cannot be interpreted as positive predictive power or sensitivity (see Tables 1 and 2). Full generalizations following the individual-based approach ( $s_{ind}$  and  $s_{ind}^g$ ) may not be recommendable either, because the interpretation of quantity  $B$  changes when computed with abundances instead of presence-absence data.  $B_{ind}$

is the average relative abundance of individuals of the species at a site that belongs to the target site group. It is hence measuring the dominance of the species in the community rather than its frequency, and it is less useful as a sensitivity measure. As an example, consider a species that is always found at sites belonging to the target site group, but occurs in low abundance compared to other species in the community. In that case,  $B_{pa}$  is one whereas  $B_{ind}$  has a low value.

#### STATISTICAL INFERENCE FOR SPECIES-SITE GROUP ASSOCIATIONS

The study of the relationship between a species and a site group is not complete after computing the value of an index. It is also important to assess (1) whether the species is significantly preferring (or avoiding) the environmental conditions of the sites in the target site group and (2) the precision of the estimated association strength. Since many of the indices compared here have neither exact nor approximate known statistical distributions, statistical methods that randomize the observed data should be used to answer these questions. In this section we discuss the application of permutation tests to answer the first question and bootstrap confidence intervals for the second.

#### *Significance tests for the association between a species and a site group*

In order to determine if a species is associated with a site group, we must conduct a statistical test of the null hypothesis that there is no such relationship. Under this null hypothesis, the fact that the species was observed at a site belonging to the target site group is due to chance only. A permutation test is a procedure that involves comparing an observed test statistic with a distribution obtained by randomly reordering (i.e., permuting) the data. If the null hypothesis of no association is true, the association value computed after randomly reassigning species occurrence or abundance values to sites will be similar or very close to that observed for unpermuted data. The  $P$  value of the permutation test of positive (negative) species preference is the proportion of permutations that yielded the same or higher (lower) association values than that observed for the unpermuted data.

Any of the 14 association indices can be used in a permutation test. We list in Table 4 four distinct one-tailed tests that have a clear ecological interpretation of the null and alternative hypotheses. The first two address differences in frequency, whereas the other two focus on differences in relative abundance. Each case is duplicated depending on whether a non-equalized measure or a group-equalized measure is used as test statistic. The difference in interpretation of the null hypothesis is that group-equalized indices make explicit reference to the relative abundance (or frequency) of the species in each of the nontarget site groups, whereas non-equalized measures do not. Sometimes different statistics can be found that yield the same  $P$  value in

TABLE 4. Summary of the recommended and equivalent statistics for testing the significance of association by means of permutation tests.

Null ecological hypothesis	Recommended statistic	Equivalent statistics
Differences in frequency		
The species is not more (less) frequently found at sites belonging to the site group than at sites not belonging to it.	$n_p$	$r_\Theta, \sqrt{\text{IndVal}_{pa}}$
The frequency of the species in the target site group is not higher (lower) than the frequency in the other site groups	$A_{pa}^g$	$r_\Phi^g, \sqrt{\text{IndVal}_{pa}^g}$
Differences in abundance		
The abundance of the species in sites belonging to the site group is not higher (lower) than its abundance in sites not belonging to it	$a_p$	$r_{pb}, r_{ind}, s_{ind}, s_{cos}$
The average abundance of the species in the target site group is not higher (lower) than the average abundance in the other site groups	$A_{ind}^g$	

Notes: Notation follows Tables 1 and 2. In addition,  $s_{cos}$  is the cosine between the species abundance vector and the vector of membership to the site-group;  $s_{ind}$  is the full generalization of  $\sqrt{\text{IndVal}_{pa}}$  following the individual-based approach.

permutation tests. The statistics are then said to be equivalent for the permutation testing (Edgington 1995). For example, when using species presence-absence data, the only quantity that is affected by the permutation of the values is the number of occurrences of the species within the target site group. This makes  $r_\Phi$  and  $\sqrt{\text{IndVal}_{pa}}$  equivalent statistics for testing whether the species is more frequently found among sites belonging to the target site group than at other sites. The number of occurrences of the species within the target group is also an equivalent statistic to  $r_\Phi$  and  $\sqrt{\text{IndVal}_{pa}}$ , and it is the preferred statistic because it is the fastest to calculate. We report in the Appendix some power and type I error simulation results for this specific test.

The permutation test described in Dufrêne and Legendre (1997) deserves a special comment due to its widespread use. Regarding the interpretation of the results, looking at Table 4 we can see the ecological hypothesis being tested when using  $\sqrt{\text{IndVal}_{pa}^g}$  or  $\sqrt{\text{IndVal}_{pa}}$  as test statistics. Since  $\sqrt{\text{IndVal}_{ind}}$  and  $\sqrt{\text{IndVal}_{ind}^g}$  are partial generalizations to species abundance values, their corresponding null hypotheses are more difficult to interpret ecologically because they combine frequency and abundance values (but see Mouillot et al. 2002). Significance tests can be used, to study the association of a species to any one or all of the site groups. However, the number of simultaneous tests has to be taken into account when reporting the results. Regardless of the index used, testing multiple species-site group associations will require a correction for multiple testing and is likely to result in fewer significant species-site group associations. The recommendation of Dufrêne and Legendre (1997) was to test only the significance of the association with the group for which the indicator value was the highest. Moreover, they avoided the problem of multiple testing by using the maximum indicator value among the site groups as test statistic (i.e., the maximum value was recomputed after each permutation). The same approach can be adopted with other association indices in order to avoid corrections for multiple testing.

Some additional recommendations are in order with permutation tests. First, the statistical null model assumed in an unrestricted permutation approach (such as the one described above) may be very ecologically unlikely, to the extent that testing it may become irrelevant. Falsifying null hypotheses generated from more restricted null models of association (e.g., Gotelli 2000) may provide more interesting ecological information. Second, users should be aware that autocorrelation in the data could make permutation tests too liberal. One way to solve that problem in a grid of observations of rectangular shape is by restricting the possible permutations to those allowed by a toroidal shift (Harms et al. 2001, Fortin and Dale 2005) or by simulating random autocorrelated patterns (Roxburgh and Chesson 1998). Finally, practitioners should keep in mind that if the classification of the sites has been obtained from the species composition itself (for example by *K*-means partitioning), the site groups would not be completely independent of the species data. In such a case of circularity, we can expect more significantly associated species than expected by chance only.

*Confidence intervals for species-site group associations*

Like all measurements that imply statistical uncertainty, it is important to complement the measured strength of association along with an indication of the precision of the assessment. In the case of indicator values, we recommend computing confidence intervals not only for the indicator value index but also for quantities *A* and *B*, as suggested by De Cáceres et al. (2008). Many of the above-mentioned association indices do not allow deriving confidence intervals using parametric methods; therefore we recommend using bootstrap confidence intervals. Bootstrapping is the practice of estimating properties of an estimator by measuring those properties when sampling from an approximating distribution, usually the empirical distribution of the observed data. Efron's simple percentile bootstrap method (Efron 1979, Manly 1997) obtains the limits of the confidence interval for an estimator from the percentiles of the distribution of values generated by resampling the observed data with replacement. Using

simulated data we studied the performance of bootstrap confidence intervals for the four presence–absence association indices. Asymptotic parametric methods were also evaluated when available. Details of the simulation methods and results are given in the Appendix. In practical applications, bootstrap confidence intervals can be trusted for indicator values between 0.1 and 0.9 when the sample size is not small (i.e.,  $N > 100$  sites) and at least 30–50 sites belong to the target site group. Larger samples may be needed to obtain valid confidence intervals for indicator values near 0 or 1. The same rule can be used for correlation measures, and in this case it applies analogously for negative correlation values.

#### FINAL REMARKS

We discussed here the properties of several related indices measuring the association between species and groups of sites. Although both the correlation and indicator value approaches can be successful in many applications, they have been developed with slightly different purposes. (1) For determining the ecological preference of a given species among a set of alternative site groups, the correlation approach is probably more useful than the indicator value approach, because the former naturally allows the detection of negative preferences. An example would be the determination of species–habitat associations (Harms et al. 2001, Gunatilleke et al. 2006). The phytosociological concept of “differential species” (a species whose pattern of occurrence in a particular community type can be used to differentiate between that type and closely related types) also matches this purpose (De Cáceres et al. 2008). For species abundance data, we believe that the point-biserial coefficients ( $r_{pb}$  or  $r_{pb}^s$ ) generally seem to be a better choice than the individual-based indices ( $r_{ind}$  or  $r_{ind}^s$ ). The reason is that assuming a constant total number of sampled individuals (or biomass) for all sites may be very unrealistic, especially in animal communities. (2) For assessing species predictive values (e.g., for field determination of community types or ecological monitoring), one should preferably compute indicator values (McGeoch and Chown 1998), because they are decomposable into components that are interpretable as probabilities. In addition, we believe the indicator value approach is well suited for analyzing species–habitat associations based on large biological record databases because it provides potentially unique values (De Cáceres et al. 2008). For example, we may want to assess the strength of the association between the nesting sites of a bird species and a given forest type. If the entire geographical distributions of the bird species and the forest type are considered and the sample of observation points can be assumed to be random, the indicator value will provide a single population value regardless of the beta-diversity range of the database. This is not true for the correlation approach even if the previous two conditions are met. The symmetric

treatment of absences in correlation indices has the effect that any inclusion of new habitat types into the database leads to a different population value.

In order to compare association values for a species across site groups, the association index must be independent of the relative sizes of the groups. Non-equalized indices give the same weight to individual sites, whereas group-equalized indices give equal weights to all site groups. Using group-equalized measures can be considered similar to performing a group-based stratified re-sampling with the aim of ensuring that no site groups are over-sampled with respect to others. Therefore, the decision whether to use group-equalized indices is related to how the sampling was conducted.

We presented here permutation tests to assess the statistical significance of species–site group associations and bootstrap methods for obtaining confidence intervals. Permutation tests allow discarding species with no preference but do not allow selecting species with high association values. Therefore, we encourage ecologists to use confidence intervals in order to use them to evaluate the likeliness of arbitrary population association values. The behavior of inference methods with group-equalized indices is a topic that deserves further research. The main problem is that groups with small number of sites are very influential when randomizing or bootstrapping data. In the meanwhile, we recommend using group-equalized measures when all groups should contain a reasonable number of sites (i.e., at least 10).

Some other topics could not be covered in this paper. For example, species niche preferences may involve more than one group of sites, and this ecological situation is not properly addressed with the current analysis approach. Moreover, the results of species–site group association analyses have been suggested to be used in order to choose among competing partitions of the same set of sites, either representing hierarchical levels of a nested classification, or being the result of different partitioning methods (e.g., Dufrêne and Legendre 1997:362–363, Tuomisto et al. 2003). We believe these questions need further development and deserve to be addressed in future works.

#### AVAILABLE SOFTWARE

Some of the association measures cited in this manuscript are already available in computer programs, such as Marc Dufrêne’s IndVal (*available online*),<sup>2</sup> PC-ORD (McCune and Mefford 1999), JUICE (Tichý 2002), or GINKGO (Bouxin 2005). The original (group-equalized) IndVal can also be computed using the “duleg” function of the R language package “labdsv” (Roberts 2006). We provide a Supplement with an R package containing functions to compute all the association measures discussed in this manuscript, including options for calculating simple bootstrap

<sup>2</sup> (<http://biodiversite.wallonie.be/outils/indval/home.html>)



confidence intervals, and a function to perform the tests listed in Table 4.

#### ACKNOWLEDGMENTS

The manuscript was substantially improved using comments provided by Melodie McGeoch and an anonymous reviewer. The authors are also grateful to Francesc Oliva for his useful recommendations on bootstrap methods, to Marco Moretti for pointing out interesting applied issues, and to Sapna Sharma for the revision of the English style. This research was funded by NSERC grant no. 7738 to P. Legendre.

#### LITERATURE CITED

- Bruehlheide, H. 1995. Die Grünlandgesellschaften des Harzes und ihre Standortbedingungen. *Dissertationes Botanicae* 244: 1–338.
- Bruehlheide, H. 2000. A new measure of fidelity and its application to defining species groups. *Journal of Vegetation Science* 11:167–178.
- Bouxin, G. 2005. Ginkgo, a multivariate analysis package. *Journal of Vegetation Science* 16:355–359.
- Carignan, V., and M. Villard. 2002. Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment* 78:45–61.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T. J. Shen. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62:361–371.
- Chytrý, M., A. Exner, R. Hrivnák, K. Ujházy, M. Valachovič, and W. Willner. 2002a. Context-dependence of diagnostic species: a case study of the Central European spruce forests. *Folia Geobotanica* 37:403–417.
- Chytrý, M., L. Tichý, J. Holt, and Z. Botta-Dukát. 2002b. Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13:79–90.
- De Cáceres, M., X. Font, and F. Oliva. 2008. Assessing species diagnostic value in large data sets: a comparison between phi coefficient and Ochiai index. *Journal of Vegetation Science* 19:779–788.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Edgington, E. S. 1995. Randomization tests. CRC Press, Boca Raton, Florida, USA.
- Efron, B. 1979. Bootstrap methods: another look at the jackknife. *Annals of Statistics* 7:1–26.
- Fortin, M. J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, UK.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81:2606–2621.
- Gunatilleke, C. V. S., I. Gunatilleke, S. Esufali, K. E. Harms, P. M. S. Ashton, D. Burslem, and P. S. Ashton. 2006. Species–habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology* 22:371–384.
- Harms, K. E., R. Condit, S. P. Hubbell, and R. B. Foster. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89:947–959.
- Hill, M. O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York, USA.
- Janson, S., and J. Vegelius. 1981. Measures of ecological association. *Oecologia* 49:371–376.
- Juhász-Nagy, P. 1964. Some theoretical models of cenological fidelity I. *Acta Botanica Debrecina* 3:33–43.
- Knollová, I., M. Chytrý, L. Tichý, and O. Hajek. 2005. Stratified resampling of phytosociological databases: some strategies for obtaining more representative data sets for classification studies. *Journal of Vegetation Science* 16:479–486.
- Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier, New York, New York, USA.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, Boca Raton, Florida, USA.
- McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.
- McGeogh, M. A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73: 181–201.
- McGeoch, M. A., and S. L. Chown. 1998. Scaling up the value of bioindicators. *Trends in Ecology and Evolution* 13:46–47.
- McGeoch, M. A., B. J. Van Rensburg, and A. Botes. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology* 39:661–672.
- Mouillot, D., J. M. Culioli, and T. D. Chi. 2002. Indicator species analysis as a test of non-random distribution of species in the context of marine protected areas. *Environmental Conservation* 29:385–390.
- Murtaugh, P. A. 1996. The statistical evaluation of ecological indicators. *Ecological Applications* 6:132–139.
- Ochiai, A. 1957. Zoogeographic studies on the soleoid fishes found in Japan and its neighbouring regions. *Bulletin of the Japanese Society of Scientific Fisheries* 22:526–530.
- Orlóci, L. 1967. An agglomerative method for classification of plant communities. *Journal of Ecology* 55:193–206.
- Rao, C. R. 1995. A review of canonical coordinates and an alternative to correspondence analysis using Hellinger distance. *Questiò (Quaderns d'Estadística i Investigació Operativa)* 19:23–63.
- Roberts, D. W. 2006. LABDSV: laboratory for dynamic synthetic vegetation phenology. R package version 1.2–2. (<http://cran.r-project.org/>)
- Roxburgh, S. H., and P. Chesson. 1998. A new method for detecting species associations with spatially autocorrelated data. *Ecology* 79:2180–2192.
- Tichý, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13:451–453.
- Tichý, L., and M. Chytrý. 2006. Statistical determination of diagnostic species for site groups of unequal size. *Journal of Vegetation Science* 17:809–818.
- Tuomisto, H., K. Ruokolainen, M. Aguilar, and A. Sarmiento. 2003. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology* 91:743–756.
- Wagner, H. H., and P. J. Edwards. 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology* 16:121–131.
- Willner, W., L. Tichý, and M. Chytrý. 2009. Effects of different fidelity measures and contexts on the determination of diagnostic species. *Journal of Vegetation Science* 20:130–137.

#### APPENDIX

Inference for species–site group association indices (*Ecological Archives* E090-250-A1).

#### SUPPLEMENT

R package for performing indicator species analyses (*Ecological Archives* E090-250-S1).

## APPENDIX

### *Ecological Archives E090-250-A1*

#### INFERENCE FOR SPECIES-SITE GROUP ASSOCIATION INDICES

We present here a simulation study that we carried out in order to assess the performance of statistical inference methods on species-site group associations. We restricted our attention to the four indices based on presence-absence species data:  $\sqrt{IndVal_{pa}}$ ,  $\sqrt{IndVal_{pa}^g}$ ,  $r^g$  and  $r_{\phi}^g$ . We specifically evaluated (1) the type I error and power of permutation tests, and (2) the performance of confidence intervals derived from parametric and bootstrap approaches. The mathematical notation follows essentially that of Table 1 of the main text.

#### *Simulated data*

We started by creating a set of finite but large (100,000 sites) populations describing different species occurrence patterns and different two-group classifications of sites (one of the groups being the target site group). The populations were specified by setting three parameters:  $A$ , the proportion of species presences in sites belonging to the target site group,  $B$ , the proportion of species presences in sites not belonging to the target site group, and  $C$ , the relative size of the target site group. We then randomly sampled sites from the populations. We chose those sample sizes that yielded specific expected values of the number of sites belonging to the target group:  $E(N_p)=5, 10$  and  $50$ . We obtained 1000 samples for each population and each sample size. We include the average characteristics (i.e. the expected values of species occurrence patterns) of samples in Table A.1, which we used to help interpreting the results of inference methods.

#### *Power and type I error of permutation tests*

We mentioned, in Table 4 of the main text, four permutation tests with easy ecological interpretation. We studied here the power and type I error for the first one, which uses the number of species presences in the target site group ( $n_p$ ) as test statistic. Although it also deals with presence-absence species data, we did not evaluate permutation tests using  $A_{pa}^g$  as test statistic, because the simulated scenarios involve two groups only, and in this situation the two statistics are equivalent under permutations of the data. We report in Table A.2 the percentages of null hypothesis rejection when  $\alpha=0.05$  is used as significance level. As expected, the rate of null hypothesis rejection was higher for higher differences between population frequencies  $A$  and  $B$ . However, the power of the test also depended on the expected number of sites belonging to the target site group. For the same sample size, a smaller relative size of the target group decreased the power of the tests. For situations of equal frequency of the species (that is, when the null hypothesis was true in the population), the test had a rate of type I error that was always lower or equal than the nominal level. Therefore, the permutation test is statistically valid.

#### *Performance of bootstrap and parametric confidence intervals*

Statistical methods for deriving confidence intervals can be empirically evaluated by calculating intervals from random samples. The proportion of intervals including the true population value provides an assessment of the actual confidence level of the intervals, and therefore informs of the reliability of the method used to derive them. In our case, we calculated the population values for the four indices studied, and we determined the actual confidence level of 95% confidence intervals using the above mentioned random samples. In the case of  $r_{\phi}$  and

$\sqrt{IndVal_{pa}}$ , we could evaluate the performance of parametric confidence intervals because these indices are asymptotically normally distributed. Specifically, we computed an estimation of the asymptotic variance and used it to build a Wald 95% confidence interval (i.e. the sample statistic  $\pm 1.96$  times the standard deviation). We calculated the asymptotic variance of  $r_\phi$  by using the formula in Bishop et al. (1975: 381):

$$s_\infty^2(r_\phi) = \frac{1}{N} \left\{ 1 - r_\phi^2 + \left( r_\phi + \frac{1}{2} r_\phi^3 \right) \cdot \frac{(N-2n) \cdot (N-2N_p)}{\sqrt{n \cdot (N-n) \cdot N_p \cdot (N-N_p)}} \right. \\ \left. - \frac{3}{4} r_\phi^2 \cdot \left[ \frac{(N-2n)^2}{n \cdot (N-n)} + \frac{(N-2N_p)^2}{N_p \cdot (N-N_p)} \right] \right\}$$

We took the formula from Janson and Vegelius (1981) for  $\sqrt{IndVal_{pa}}$ :

$$s_\infty^2(\sqrt{IndVal_{pa}}) = \frac{n_p^2 \cdot (n - n_p) + n_p^2 \cdot (N_p - n_p) + 4n_p \cdot (n - n_p) \cdot (N_p - n_p)}{4N_p^2 \cdot n^2}$$

Unlike their non-equalized counterparts,  $\sqrt{IndVal_{pa}^g}$  and  $r_\phi^g$ , do not have either exact or approximate known distributions. Therefore, we decided to use the Efron's simple percentile bootstrap method (Efron 1979, Manly 1997), which assumes that a monotone transformation of the original variable that yields a normal distribution exists (even if it is not known). Following this method, we calculated 95% confidence intervals by taking the distribution of values obtained from 100 bootstrap samples and determining the 2% and 97% percentiles. We used a small number of bootstrap samples for computational reasons, but at least 1000 samples should be used in practical applications. We assessed the performance of the bootstrap percentile method on the four binary indices.

The results for bootstrap  $\sqrt{IndVal_{pa}}$  intervals are presented in Tables A.3. The actual confidence level of bootstrap  $\sqrt{IndVal_{pa}}$  intervals, like the index itself, does not depend on the sample size directly. However, the bootstrapped distribution needs to include enough distinct values to produce reliable percentiles that lead to actual confidence levels close to the nominal 95%. The number of distinct bootstrap samples is not enough when either the total number of species presences or the number of sites in the target site group is small (i.e. when  $n < 5$  or  $N_p < 5$ ). Even if these conditions are met, the overlap between the pattern of the species and the pattern of site group must not be too small (i.e. when  $n_p < 2.5$ ) or too big (i.e. when  $N_p - n_p < 2.5$  and  $n - n_p < 2.5$ ). In other words, bootstrap intervals are less successful when  $\sqrt{IndVal_{pa}}$  values are close to 0 or 1. Generally speaking, the actual confidence level of parametric intervals was very similar to that of bootstrap intervals (see Table A.4), but bootstrap intervals seem to perform slightly better for small sizes of the target site group. Presumably, parametric confidence intervals usually failed for indicator values close to 0 or 1 because the distribution of the statistic becomes more asymmetric in these cases and therefore the approximation to the normal distribution becomes poorer. The performance of confidence intervals for the phi coefficient of association (see Tables A.5 and A.6), was very similar to those of  $\sqrt{IndVal_{pa}}$ . Again, intervals usually had actual confidence levels below the nominal level for correlation values close to 0 or 1 (following the symmetry of  $r_\phi$ , the same must happen for correlation values close to -1). However, the results were affected by the fact that samples without species occurrences or with all sites occupied

preclude the calculation of correlation coefficients. The performance of bootstrap intervals for  $\sqrt{IndVal_{pa}^g}$  and two equally-sized groups was similar to that of  $\sqrt{IndVal_{pa}}$ , but not for unequally sized groups (Table A.7). Group-equalized indices are not sensible to differences in size of the site groups. Thus, we observed no increase in the actual confidence level of the intervals when  $N_p$  was kept constant and we increased the size of the non-target site group. Moreover, bootstrap samples give equal  $\sqrt{IndVal_{pa}^g}$  values when the species is present in all sites, which makes bootstrap intervals to have lower actual confidence levels in this situation. We obtained similar results for the group-equalized phi coefficient,  $r_{\phi}^g$  (Table A.8).

With the aim of providing a practical rule, we recommend trusting confidence intervals for association values between 0.1 and 0.9 (also between -0.1 and -0.9 for correlation measures) when at least 30-50 sites belong to the target site group.

#### LITERATURE CITED

- Bishop, Y. M. M., P. W. Holland, and S. E. Fienberg. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Mass.
- Efron, B. 1979. Bootstrap methods: Another look at the jackknife. *The Annals of Statistics* 7:1-26.
- Janson, S. and J. Vegelius. 1981. Measures of ecological association. *Oecologia* 49:371-376.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall texts in statistical science series.





**Table A3.** Actual confidence level of *simple percentile bootstrap*  $\sqrt{IndVal_{pa}}$  intervals of 95% nominal confidence. Results are displayed for different populations and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>C=0.5</i>			<i>N=10 E(N<sub>p</sub>)=5</i>			<i>N=20 E(N<sub>p</sub>)=10</i>			<i>N=100 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.071	5	0	95	10	0	91	55	0	45
0.1	0.01	0.302	42	0	58	64	0	36	90	2	8
0.5	0.01	0.700	89	4	7	94	4	2	93	3	4
0.9	0.01	0.943	54	45	1	67	31	2	93	5	2
0.99	0.01	0.990	23	77	0	19	81	0	62	37	0
0.1	0.1	0.224	40	0	60	65	1	35	93	1	6
0.5	0.1	0.645	88	4	8	94	2	4	93	2	5
0.9	0.1	0.900	67	30	3	86	12	2	93	4	3
0.99	0.1	0.948	48	51	1	66	33	1	94	4	2
0.5	0.5	0.500	92	2	6	92	3	6	94	3	4
0.9	0.5	0.761	91	4	5	93	4	4	93	3	5
0.99	0.5	0.811	91	6	3	93	4	4	94	3	3
0.9	0.9	0.671	90	4	6	92	3	5	93	3	4
0.99	0.9	0.720	90	4	6	93	2	5	92	2	6
0.99	0.99	0.704	92	5	3	93	4	4	94	2	4

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.032	5	0	96	10	0	90	38	0	62
0.1	0.01	0.229	39	0	61	63	1	36	93	1	6
0.5	0.01	0.651	90	2	8	94	2	4	92	3	5
0.9	0.01	0.905	76	22	2	84	14	2	93	5	3
0.99	0.01	0.953	59	40	0	63	36	1	93	5	3
0.1	0.1	0.100	41	0	59	59	0	41	91	1	8
0.5	0.1	0.423	88	2	10	92	2	6	94	2	4
0.9	0.1	0.671	92	2	6	93	3	5	94	2	4
0.99	0.1	0.720	91	2	7	93	3	5	94	2	4
0.5	0.5	0.224	90	0	9	92	1	7	93	1	5
0.9	0.5	0.387	89	1	10	93	1	6	93	1	6
0.99	0.5	0.423	91	1	8	93	1	6	92	1	7
0.9	0.9	0.300	91	2	7	92	1	7	95	2	3
0.99	0.9	0.328	92	1	7	93	2	5	95	1	4
0.99	0.99	0.315	94	2	5	93	1	6	94	2	5

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.010	6	0	95	10	0	91	41	0	59
0.1	0.01	0.096	41	0	59	62	0	38	92	1	7
0.5	0.01	0.410	88	1	11	93	1	5	94	1	5
0.9	0.01	0.655	93	2	5	95	2	4	94	2	4
0.99	0.01	0.704	92	5	3	94	2	4	93	2	5
0.1	0.1	0.032	35	0	65	64	1	36	91	1	9
0.5	0.1	0.155	90	1	9	92	1	7	94	2	4
0.9	0.1	0.274	94	1	6	92	1	6	95	2	3
0.99	0.1	0.300	92	1	8	92	1	7	95	1	4
0.5	0.5	0.071	91	1	8	89	2	9	94	1	5
0.9	0.5	0.127	93	1	7	92	1	6	92	2	6
0.99	0.5	0.139	90	1	10	90	1	8	92	2	6
0.9	0.9	0.095	91	1	8	92	1	7	94	2	4
0.99	0.9	0.104	92	2	7	92	1	7	92	2	6
0.99	0.99	0.099	93	1	6	92	1	6	92	2	6

**Table A4.** Actual confidence level of *asymptotic parametric*  $\sqrt{IndVal_{pa}}$  intervals of 95% nominal confidence. Results are displayed for different populations and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>C=0.5</i>			<i>N=10 E(N<sub>p</sub>)=5</i>			<i>N=20 E(N<sub>p</sub>)=10</i>			<i>N=100 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.071	4	1	95	10	0	90	41	1	58
0.1	0.01	0.302	38	2	60	64	2	34	93	4	3
0.5	0.01	0.700	87	8	5	95	4	2	94	4	2
0.9	0.01	0.943	43	57	1	66	34	0	91	9	0
0.99	0.01	0.990	10	90	0	19	81	0	64	36	0
0.1	0.1	0.224	38	6	57	61	3	36	91	3	6
0.5	0.1	0.645	86	8	6	90	8	2	94	4	2
0.9	0.1	0.900	66	34	0	86	13	1	92	7	0
0.99	0.1	0.948	44	56	0	68	32	0	92	7	1
0.5	0.5	0.500	85	9	6	94	3	3	95	3	2
0.9	0.5	0.761	88	11	1	91	8	1	95	4	1
0.99	0.5	0.811	86	13	2	91	8	2	95	4	1
0.9	0.9	0.671	92	5	2	93	6	1	95	3	2
0.99	0.9	0.720	91	9	1	95	4	1	94	4	2
0.99	0.99	0.704	93	6	2	92	6	2	94	4	2

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.032	3	3	94	7	1	92	39	0	60
0.1	0.01	0.229	35	5	60	63	3	34	92	3	5
0.5	0.01	0.651	82	10	8	93	6	2	94	4	2
0.9	0.01	0.905	62	37	1	84	16	0	92	7	1
0.99	0.01	0.953	42	57	1	64	36	0	92	8	0
0.1	0.1	0.100	37	1	62	65	1	34	91	1	8
0.5	0.1	0.423	86	6	8	90	5	6	93	3	4
0.9	0.1	0.671	91	7	3	93	6	2	95	4	2
0.99	0.1	0.720	89	9	3	94	5	2	94	3	2
0.5	0.5	0.224	89	3	9	92	3	6	95	2	3
0.9	0.5	0.387	94	3	4	95	2	3	95	3	2
0.99	0.5	0.423	93	3	4	95	2	3	95	2	3
0.9	0.9	0.300	93	3	4	94	3	3	95	3	2
0.99	0.9	0.328	95	2	2	95	2	3	95	3	2
0.99	0.99	0.315	94	2	4	95	2	3	94	3	2

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal_{pa}}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.010	4	0	96	10	0	91	38	0	62
0.1	0.01	0.096	36	2	63	65	1	34	92	0	8
0.5	0.01	0.410	85	6	9	93	3	4	96	2	2
0.9	0.01	0.655	90	7	3	93	6	2	96	3	1
0.99	0.01	0.704	91	7	2	94	5	2	96	2	2
0.1	0.1	0.032	39	0	60	65	0	35	90	0	9
0.5	0.1	0.155	88	2	10	92	2	6	96	2	3
0.9	0.1	0.274	92	3	5	94	2	4	94	3	3
0.99	0.1	0.300	94	2	4	95	2	3	97	1	3
0.5	0.5	0.071	88	3	9	91	3	6	96	2	3
0.9	0.5	0.127	93	2	4	95	3	3	95	2	3
0.99	0.5	0.139	93	2	5	95	3	2	96	2	3
0.9	0.9	0.095	91	3	6	95	2	3	94	2	4
0.99	0.9	0.104	94	1	4	95	3	2	95	3	3
0.99	0.99	0.099	95	1	4	94	2	4	95	3	3



**Table A5.** Actual confidence levels of *simple percentile bootstrap*  $r_\Phi$  intervals of 95% nominal confidence. Results are displayed for different populations, and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>C=0.5</i>			<i>N=10 E(N<sub>p</sub>)=5</i>			<i>N=20 E(N<sub>p</sub>)=10</i>			<i>N=100 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	9	91	0	20	80	0	64	36	0
0.1	0.01	0.197	39	0	61	62	1	37	91	2	7
0.5	0.01	0.562	88	3	10	92	4	4	94	3	3
0.9	0.01	0.894	61	37	2	68	32	1	91	6	3
0.99	0.01	0.980	42	58	0	18	82	0	60	39	1
0.1	0.1	0.000	64	36	0	84	14	2	95	2	3
0.5	0.1	0.436	87	4	9	92	5	4	95	3	3
0.9	0.1	0.800	75	24	1	84	14	2	93	4	3
0.99	0.1	0.894	61	38	1	65	35	1	92	6	2
0.5	0.5	0.000	96	2	3	93	2	4	95	2	4
0.9	0.5	0.436	90	2	8	91	5	4	94	2	4
0.99	0.5	0.562	89	2	9	93	2	5	94	3	4
0.9	0.9	0.000	65	35	0	85	14	2	92	3	4
0.99	0.9	0.197	42	0	58	64	0	36	91	3	7
0.99	0.99	0.000	10	90	0	18	82	0	63	37	1

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	4	0	96	10	0	90	41	0	59
0.1	0.01	0.198	41	0	59	65	1	35	93	2	6
0.5	0.01	0.624	88	2	10	94	2	4	94	3	3
0.9	0.01	0.894	74	23	2	84	14	2	94	4	2
0.99	0.01	0.947	61	39	1	66	32	1	93	5	2
0.1	0.1	0.000	41	0	59	64	1	35	91	1	8
0.5	0.1	0.346	89	2	9	92	2	6	93	2	5
0.9	0.1	0.625	92	4	4	92	4	4	95	2	4
0.99	0.1	0.682	92	4	4	93	2	5	96	2	3
0.5	0.5	0.000	91	3	7	92	2	5	94	2	4
0.9	0.5	0.241	93	3	4	92	3	4	94	3	3
0.99	0.5	0.295	92	1	7	92	2	6	94	1	5
0.9	0.9	0.000	78	19	3	63	36	1	93	5	2
0.99	0.9	0.094	90	1	9	95	1	3	93	5	2
0.99	0.99	0.000	5	95	0	11	89	0	40	60	0

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	6	0	94	11	0	89	40	0	60
0.1	0.01	0.086	40	0	60	64	1	36	92	1	8
0.5	0.01	0.402	89	2	10	93	2	6	95	2	3
0.9	0.01	0.605	92	3	5	94	2	4	95	2	3
0.99	0.01	0.700	93	3	4	93	4	4	94	2	4
0.1	0.1	0.000	43	0	57	63	0	37	90	1	10
0.5	0.1	0.130	90	1	9	92	1	7	94	1	5
0.9	0.1	0.256	92	1	7	92	2	6	94	1	5
0.99	0.1	0.284	90	1	9	93	1	6	94	2	4
0.5	0.5	0.000	93	3	4	94	2	3	95	2	3
0.9	0.5	0.080	92	2	6	93	3	4	95	2	2
0.99	0.5	0.098	92	1	7	95	1	4	93	1	5
0.9	0.9	0.000	67	31	2	62	37	1	93	5	2
0.99	0.9	0.030	93	2	5	94	4	2	88	11	1
0.99	0.99	0.000	66	32	2	15	85	0	41	59	1

**Table A6.** Actual confidence levels of *asymptotic parametric*  $r_\Phi$  intervals of 95% nominal confidence. Results are displayed for different populations, and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>C=0.5</i>			<i>N=10 E(N<sub>p</sub>)=5</i>			<i>N=20 E(N<sub>p</sub>)=10</i>			<i>N=100 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	7	92	1	11	86	3	15	62	23
0.1	0.01	0.197	41	1	58	63	3	34	93	4	3
0.5	0.01	0.562	84	7	10	90	7	4	93	5	3
0.9	0.01	0.894	43	55	2	65	35	0	90	10	1
0.99	0.01	0.980	10	90	0	19	82	0	61	39	0
0.1	0.1	0.000	43	11	46	60	14	26	88	5	7
0.5	0.1	0.436	83	11	6	90	8	2	95	3	2
0.9	0.1	0.800	67	33	1	87	12	1	94	6	1
0.99	0.1	0.894	41	57	2	69	31	0	89	10	1
0.5	0.5	0.000	81	10	10	92	5	4	94	3	3
0.9	0.5	0.436	83	11	6	91	8	2	94	4	2
0.99	0.5	0.562	83	6	11	91	5	4	95	4	2
0.9	0.9	0.000	44	45	12	57	28	16	90	4	6
0.99	0.9	0.197	39	1	59	63	2	35	93	5	2
0.99	0.99	0.000	8	91	1	11	85	3	16	59	25

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	28	3	69	40	5	55	39	1	60
0.1	0.01	0.198	36	4	60	59	4	37	92	3	6
0.5	0.01	0.624	79	12	9	91	7	2	95	3	2
0.9	0.01	0.894	58	41	1	84	16	0	91	8	1
0.99	0.01	0.947	39	60	1	66	34	0	91	9	0
0.1	0.1	0.000	43	2	55	58	1	41	92	1	7
0.5	0.1	0.346	85	5	10	92	4	5	94	3	3
0.9	0.1	0.625	91	6	3	93	5	2	94	4	3
0.99	0.1	0.682	89	8	3	94	5	2	94	4	2
0.5	0.5	0.000	82	9	8	91	5	4	96	2	3
0.9	0.5	0.241	94	4	2	95	4	1	94	4	2
0.99	0.5	0.295	93	2	4	95	2	3	95	2	3
0.9	0.9	0.000	43	55	2	62	37	1	92	7	1
0.99	0.9	0.094	94	1	5	94	4	3	92	8	0
0.99	0.99	0.000	30	67	4	40	57	3	40	59	1

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	<i>r<sub>Φ</sub></i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	10	0	90	10	0	90	41	0	60
0.1	0.01	0.086	36	1	63	60	1	39	92	0	8
0.5	0.01	0.402	86	6	8	92	4	4	95	3	3
0.9	0.01	0.605	91	7	2	93	5	2	95	3	3
0.99	0.01	0.700	94	5	1	93	5	2	95	3	2
0.1	0.1	0.000	40	2	59	64	0	36	92	0	7
0.5	0.1	0.130	88	3	10	92	3	6	95	2	3
0.9	0.1	0.256	93	2	4	95	2	3	95	3	2
0.99	0.1	0.284	94	2	5	95	2	3	95	2	3
0.5	0.5	0.000	82	9	10	92	3	5	94	3	3
0.9	0.5	0.080	93	5	2	93	6	1	95	3	2
0.99	0.5	0.098	95	1	4	95	1	4	95	3	3
0.9	0.9	0.000	40	58	2	66	34	1	92	8	1
0.99	0.9	0.030	94	4	2	92	6	2	87	13	0
0.99	0.99	0.000	11	88	2	8	92	0	40	60	0

**Table A7.** Actual confidence levels of *simple percentile bootstrap*  $\sqrt{IndVal}_{pa}^g$  intervals of 95% nominal confidence. Results are displayed for different populations and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>C=0.5</i>			<i>N=10 E(N<sub>p</sub>)=5</i>			<i>N=20 E(N<sub>p</sub>)=10</i>			<i>N=100 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal}_{pa}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.071	5	0	95	9	0	91	39	0	61
0.1	0.01	0.302	43	1	57	65	1	34	92	1	7
0.5	0.01	0.700	89	5	6	93	3	3	95	2	4
0.9	0.01	0.943	55	44	1	71	28	1	92	6	2
0.99	0.01	0.990	26	74	0	20	80	0	60	39	1
0.1	0.1	0.224	38	1	62	62	2	37	93	1	5
0.5	0.1	0.645	89	4	7	93	3	3	96	3	2
0.9	0.1	0.900	68	30	2	85	14	1	94	4	2
0.99	0.1	0.948	51	48	1	67	32	1	92	5	3
0.5	0.5	0.500	90	4	6	91	3	6	93	3	4
0.9	0.5	0.761	89	6	5	88	10	3	94	4	2
0.99	0.5	0.811	90	5	5	91	5	4	93	2	5
0.9	0.9	0.671	50	50	1	62	36	2	92	4	3
0.99	0.9	0.720	47	0	53	66	1	34	93	2	4
0.99	0.99	0.704	23	77	0	10	90	0	38	62	0

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal}_{pa}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.071	5	0	95	9	0	91	38	0	62
0.1	0.01	0.302	39	0	61	63	1	36	91	1	8
0.5	0.01	0.700	90	1	9	94	2	4	94	3	3
0.9	0.01	0.943	67	32	1	63	36	1	92	6	2
0.99	0.01	0.990	60	39	1	63	37	0	72	27	1
0.1	0.1	0.224	36	0	64	63	0	37	94	1	6
0.5	0.1	0.645	87	2	12	94	2	4	94	2	5
0.9	0.1	0.900	73	25	1	66	33	1	93	5	2
0.99	0.1	0.948	94	4	2	93	6	1	90	8	2
0.5	0.5	0.500	89	2	10	92	3	5	96	1	4
0.9	0.5	0.761	72	27	1	65	35	1	93	5	2
0.99	0.5	0.811	96	1	3	95	3	2	92	7	2
0.9	0.9	0.671	65	33	2	63	36	1	92	5	4
0.99	0.9	0.720	93	2	5	91	7	1	73	27	1
0.99	0.99	0.704	39	61	0	11	90	0	36	64	0

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$\sqrt{IndVal}_{pa}$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.071	5	0	95	10	0	90	41	0	59
0.1	0.01	0.302	41	0	59	63	0	37	93	1	6
0.5	0.01	0.700	87	3	10	94	2	4	95	2	3
0.9	0.01	0.943	66	33	1	64	36	1	93	5	2
0.99	0.01	0.990	72	28	0	31	69	0	40	60	0
0.1	0.1	0.224	39	0	61	63	0	37	92	1	7
0.5	0.1	0.645	89	2	10	92	4	5	96	1	3
0.9	0.1	0.900	68	31	2	66	33	1	94	5	2
0.99	0.1	0.948	91	8	1	81	19	0	54	46	0
0.5	0.5	0.500	87	2	11	93	3	4	95	1	4
0.9	0.5	0.761	66	33	2	65	34	1	94	4	2
0.99	0.5	0.811	94	4	1	83	17	0	57	43	0
0.9	0.9	0.671	69	29	2	65	35	0	93	6	1
0.99	0.9	0.720	73	27	0	29	71	0	41	59	1
0.99	0.99	0.704	42	57	1	15	85	0	41	59	0

**Table A8.** Actual confidence levels of *simple percentile bootstrap*  $r^g_\phi$  intervals of 95% nominal confidence. Results are displayed for different populations, and for different sample sizes. *Confid.*: Percentage of intervals containing the population value. *Err.L*: Percentage of intervals where the lower limit is higher than the population value. *Err.R*: Percentage of intervals where the upper limit is lower than the population value. Confidence levels equal or higher than 90% are highlighted.

<i>A</i>	<i>B</i>	$r^g_\phi$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	10	90	0	20	80	0	63	37	0
0.1	0.01	0.197	39	0	61	64	1	35	92	3	5
0.5	0.01	0.562	89	4	7	92	3	5	93	3	5
0.9	0.01	0.894	52	47	1	68	31	1	93	5	2
0.99	0.01	0.980	25	75	0	19	81	0	62	37	1
0.1	0.1	0.000	63	36	1	84	13	3	93	2	5
0.5	0.1	0.436	87	7	6	91	7	3	95	2	3
0.9	0.1	0.800	65	34	1	86	12	1	93	4	3
0.99	0.1	0.894	52	47	1	67	32	1	93	5	2
0.5	0.5	0.000	91	4	6	93	3	5	94	2	4
0.9	0.5	0.436	87	8	5	90	7	3	93	3	4
0.99	0.5	0.562	89	7	4	94	3	3	94	2	4
0.9	0.9	0.000	72	27	1	87	11	2	93	2	5
0.99	0.9	0.197	46	0	54	63	1	36	93	2	5
0.99	0.99	0.000	33	67	0	19	82	0	60	40	0

<i>C=0.1</i>			<i>N=50 E(N<sub>p</sub>)=5</i>			<i>N=100 E(N<sub>p</sub>)=10</i>			<i>N=500 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$r^g_\phi$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	41	59	0	60	38	2	58	1	41
0.1	0.01	0.197	36	0	63	62	0	37	93	1	7
0.5	0.01	0.562	86	3	11	92	3	5	93	2	5
0.9	0.01	0.894	65	34	1	64	35	1	92	6	2
0.99	0.01	0.980	58	41	1	65	34	1	70	29	1
0.1	0.1	0.000	56	1	44	62	0	37	92	1	7
0.5	0.1	0.436	89	3	8	94	2	4	95	2	3
0.9	0.1	0.800	78	20	2	69	30	1	93	5	2
0.99	0.1	0.894	93	5	2	91	7	2	91	7	2
0.5	0.5	0.000	87	2	11	93	2	5	95	2	4
0.9	0.5	0.436	80	19	1	67	32	1	94	4	2
0.99	0.5	0.562	94	2	4	94	3	2	92	7	1
0.9	0.9	0.000	82	17	1	66	34	1	93	5	3
0.99	0.9	0.197	92	3	6	91	7	2	80	20	1
0.99	0.99	0.000	60	39	1	66	34	0	67	33	1

<i>C=0.01</i>			<i>N=500 E(N<sub>p</sub>)=5</i>			<i>N=1000 E(N<sub>p</sub>)=10</i>			<i>N=5000 E(N<sub>p</sub>)=50</i>		
<i>A</i>	<i>B</i>	$r^g_\phi$	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>	<i>Confid.</i>	<i>Err.L</i>	<i>Err.R</i>
0.01	0.01	0.000	29	1	71	10	0	90	40	0	60
0.1	0.01	0.197	39	0	61	63	1	37	92	0	8
0.5	0.01	0.562	86	2	12	93	3	4	94	2	4
0.9	0.01	0.894	65	34	1	65	34	1	93	5	2
0.99	0.01	0.980	75	24	1	33	67	0	42	58	0
0.1	0.1	0.000	39	0	61	61	0	39	93	0	7
0.5	0.1	0.436	88	2	10	93	2	5	95	2	3
0.9	0.1	0.800	65	33	2	63	37	1	93	5	2
0.99	0.1	0.894	94	5	1	83	17	0	51	48	0
0.5	0.5	0.000	87	2	11	93	3	4	95	2	3
0.9	0.5	0.436	67	31	2	62	37	1	94	5	1
0.99	0.5	0.562	93	6	1	81	19	0	55	45	0
0.9	0.9	0.000	65	32	3	65	34	1	93	5	2
0.99	0.9	0.197	78	22	0	38	62	0	40	60	0
0.99	0.99	0.000	63	36	1	13	87	0	38	62	0

**SUPPLEMENT**

***Ecological Archives E090-250-S1***

**R PACKAGE FOR PERFORMING INDICATOR SPECIES ANALYSES**

The R package INDICSPECIES provides a set of functions to assess the strength of species–site group associations. It is also possible to check the statistical significance of such associations. Use function STRASSOC for assessing the strength of associations and generating bootstrap confidence intervals, and function SIGNASSOC to assess the statistical significance of the associations. A much more complete function is MULTIPATT. This package is available on the following Web pages:

<http://www.esapubs.org/archive/ecol/E090/250/suppl-1.htm>

<http://sites.google.com/site/miqueldecaceres/software>