

METHODOLOGICAL INSIGHTS

Increasing the utility of Indicator Species Analysis

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Summary

1. The identification of species associated with or indicative of groups of samples is a common aspect of ecological research, including studies of environmental management. Indicator Species Analysis (ISA) permits statistically rigorous assessments of these indicator species, but its usage is currently restricted to simple designs.

2. I describe three improvements that greatly increase the utility of ISA. First, exact permutation tests require that the correct exchangeable units be permuted; these exchangeable units may vary among factors. Secondly, the consistency of indicators can be assessed using meta-analytic techniques to combine the results from multiple sites. Thirdly, while ISAs are classically conducted using abundance data, a simplified ISA can be conducted using binary (presence/absence) data.

3. These improvements are illustrated by identifying indicators of grazing treatment (inside or outside exclosure) at three sites in a southwestern ponderosa pine *Pinus ponderosa* forest. Most indicators were consistent among sites, and the number of significant indicators was reduced 37–40% by combining results from multiple sites. Species that occurred at multiple sites were more likely to be indicators than those present at a single site.

4. Simplified ISAs produced very similar results to classical ISAs: both methods identified the same group as having the maximum Indicator Value in > 93% of tests. Compared to abundance data, however, the presence/absence data used in a simplified ISA are easily collected and efficiently published in data tables or appendices.

5. *Synthesis and applications.* Meta-analytic techniques and simplified Indicator Species Analyses can increase the ability to analyse new or previously published data, and permit rigorous assessments of the consistency of indicator status spatially or temporally. Other recommendations to improve the utility of ISA include identifying organisms to as fine a taxonomic resolution as possible, providing detailed descriptions of groups and typologies, ensuring adequate sample sizes within groups, reporting the sample size and frequency of all species in all groups, and publishing data for all species – whether or not they are significant indicators – to prevent publication bias in future meta-analyses.

Key-words: Arizona (USA), Coconino National Forest, grazing, Hill plots, meta-analysis, permutation tests, ponderosa pine forests

Introduction

Diversity indices and other community-level variables can indicate broad ecological patterns (Magurran 2004) but may mask interspecific differences (Weiss & Reice 2005). Similarly, most multivariate methods permit analyses of the response of the entire community (e.g. Laughlin *et al.* 2004) but do not clarify whether responses are driven by all or a subset of species in the community. In-depth analyses are often required to identify species indicative of particular groups.

The identification of species associated with, or indicative of, particular habitats or ecological conditions has a long ecological history (e.g. Korstian 1917), and is a common feature of ecological research, including studies of environmental management (e.g. Bustos-Baez & Frid 2003; Laughlin *et al.* 2004; Pöyry *et al.* 2005; Rentch *et al.* 2005). Nonetheless, the indicator species concept is broad and poorly defined (Zacharias & Roff 2001). Zacharias & Roff (2001) distinguish between indicators of the presence of a particular habitat, community, or ecosystem ('composition indicators') and indicators of the condition of a habitat, community, or ecosystem ('condition indicators'). This distinction is largely a

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function of the scale of the comparisons: are samples being compared between habitats (composition) or within a habitat (condition)? The example presented in this study is a condition indicator but, for simplicity and clarity, I use the term 'indicator' throughout this paper.

By definition, the identification of indicator species requires comparisons between two or more groups. Groups can be defined in many ways, including experimental treatments within a site, different sites, or measurements of the same site at different times. When multiple groups are sampled, the identification of significant indicators will depend on the scale in the typology at which comparisons are conducted (Dufrêne & Legendre 1997; Hess *et al.* 2006).

To have broad relevance, indicators should be associated with the same group at multiple sites. However, few studies have investigated the consistency of indicator species. Studies of benthic communities and Lepidoptera have concluded that actual indicator taxa are of limited applicability due to strong spatio-temporal heterogeneity (Zacharias & Roff 2001; Bustos-Baez & Frid 2003; Pöyry *et al.* 2005; Weiss & Reice 2005), although McGeoch, Van Rensburg & Botes (2002) found that dung beetles are reliable indicators of habitat. Terrestrial plants may be more likely to be consistent indicators due to the widespread distribution of many plant species and their sessile growth habit. To my knowledge, however, their consistency as indicators has not been assessed.

Terrestrial vegetation can be sampled relatively easily, and the collection of multiple samples per site permits the use of statistically rigorous procedures such as Indicator Species Analysis (ISA; Dufrêne & Legendre 1997). One way to assess indicator consistency is to compare the results of a study against other published studies. However, most published studies and data repositories contain summary statistics (e.g. mean cover) about each species. This confounds the most common ('classical') type of ISA, which requires actual abundance values on individual sample units.

In this study, I describe three improvements to ISA: how to correctly permute data for ISA, assess the consistency of indicators by combining results from multiple sites, and conduct a simplified ISA based on binary (presence/absence) data. I illustrate these concepts by identifying indicators of grazing treatments in southwestern ponderosa pine forests.

Indicator Species Analysis

Although several other methods of identifying indicator species have been proposed (e.g. Hill 1979; Carleton, Stitt & Nieppola 1996), the ISA method proposed by Dufrêne & Legendre (1997) is one of the most appealing. Advantages of ISA are that it accounts for both the abundance and frequency of species, is calculated independently for each species in the assemblage, and can be applied to any typology, including a priori classifications such as the levels of an experimental factor (Dufrêne & Legendre 1997; McGeoch & Chown 1998).

ISA involves the calculation of an Indicator Value (*IV*) for species *i* in group *j*. The classical *IV_{ij}* is the product of the

relative abundance (specificity; *A_{ij}*) and relative frequency (fidelity; *B_{ij}*):

$$A_{ij} = \frac{\bar{x}_{ij}}{\sum_j \bar{x}_i} \quad \text{eqn 1}$$

$$B_{ij} = \frac{n_{ij}}{n_j} \quad \text{eqn 2}$$

$$IV_{ij} = A_{ij} \times B_{ij} \times 100, \quad \text{eqn 3}$$

where \bar{x}_{ij} is the mean cover of species *i* within group *j*, $\sum_j \bar{x}_i$ is the sum of the mean cover of species *i* in all groups, n_{ij} is the number of samples in group *j* occupied by species *i*, and n_j is the total number of samples in group *j*. Formulas are described in more detail by Dufrêne & Legendre (1997) and McCune & Grace (2002). In this study, a sample refers to an individual sample unit, a group to a set of samples within a site, and a site to a physical area containing two or more groups.

IV_{ij} ranges between 0 (species *i* is absent from group *j*) and 100 (species *i* occurs in all samples within group *j* and does not occur in other groups). Uncommon species will have low *B_{ij}* values and therefore low *IV_{ij}* values. Ubiquitous species have high *B_{ij}* values and therefore higher *IV_{ij}* values, but are unlikely to be statistically significant as permutations of the data will also yield high *B_{ij}* values. Species that are ubiquitous only within a single group are most likely to have large, significant *IV_{ij}* values for that group. Dufrêne & Legendre (1997) suggest that species *i* be considered a 'strong' indicator of group *j* if *IV_{ij}* > 25, although they note that this threshold level is arbitrary. As described below, all *IV_{ij}* values need to be considered when combining results from multiple sites.

PERMUTATION TESTS AND EXCHANGEABLE UNITS

The statistical significance of *IV_{ij}* is assessed via Monte Carlo randomizations. Computer-intensive permutation tests are increasingly popular (Manly 1997) but, as with all statistical methods, can be used incorrectly. Incorrect permutation tests may result in incorrect partitioning of sources of variability, particularly for complex designs. Exact permutation tests for multi-factorial analysis of variance require that the correct exchangeable units be permuted, and that permutations be restricted to occur within levels of terms of smaller or equal order as the term being tested (Anderson & ter Braak 2003). The correct exchangeable units in a permutation test are identified by the term that would form the denominator mean-square of the *F*-ratio to test that factor in an ANOVA.

This logic can also be applied to permutation tests of *IV_{ij}*. For example, if a single data vector is obtained from each sample within each group, the samples form the error term for the analysis of the factor and, therefore, are the correct exchangeable units. However, if samples are subsampled, the subsamples must either be permuted together or pooled to yield a single data vector per sample (e.g. Peterson & McCune 2001).

COMBINING RESULTS FROM MULTIPLE SITES

Dufrène & Legendre (1997) suggest identifying the group j in which IV_i is at its maximum and assessing the significance of this maximum IV_i via a permutation test. The hypothesis being tested might be summarized as ‘What is the probability of obtaining, in any group, an IV_i equal to or greater than the calculated value?’ This approach is implemented in IndVal (version 2.1; Dufrène 2004) and PC-ORD (version 5.12; McCune & Mefford 1999). However, while it correctly identifies significant indicators at a single site, it cannot be extended to multiple sites because the maximum IV_i may not occur in group j at all sites.

A more specific hypothesis is: ‘What is the probability of obtaining, in group j , an IV_{ij} equal to or greater than the calculated value?’ A key advantage of this hypothesis is that, while identifying the same significant indicators at a single site as the earlier hypothesis, it is also easily extended to multiple sites. This approach is available in an Indicator Value function (see Supporting Information Appendix S1) written for R software (R Development Core Team 2007).

For species i in group j , the IV_{ij} at each site k can be combined into a weighted mean IV (\bar{IV}_{ij}), weighting each site by its sample size. Sites where species i does not occur are not included in the calculation for that species. Statistical significance can be assessed through a weighted Z-transform (Whitlock 2005), which is particularly appropriate for combining multiple tests of the same hypothesis (Rice 1990). The P value for species i in group j at site k is converted to a Z-score using normal distribution theory, and the Z-scores are combined:

$$Z_{ij}^w = \frac{\sum_{k=1}^s w_{jk} Z_{ijk}}{\sqrt{\sum_{k=1}^s w_{jk}^2}}, \quad \text{eqn 4}$$

where w_{jk} is the weight (degrees of freedom) for group j at site k , and s is the total number of sites at which species i was present. Z_{ij}^w is then converted back to a P value for the combined effect. The group with the maximum \bar{IV}_{ij} ($\bar{IV}_{i..}$) is identified, and the associated P value determines the statistical significance of species i as an indicator of this group. An example of this procedure is presented in Supporting Information Appendix S2.

ANALYSIS OF PRESENCE/ABSENCE DATA

The classical ISA described above has been used in numerous studies (e.g. Peterson & McCune 2001; Pöyry *et al.* 2005). However, Dufrène & Legendre (1997, p. 363) also proposed a simplified ISA based on presence/absence data. For the simplified ISA, the formula for specificity (A_{ij}) is modified to:

$$A_{ij} = \frac{n_{ij}}{n_i}, \quad \text{eqn 5}$$

where n_{ij} is the number of samples in group j occupied by species i , and n_i is the total number of samples occupied by

species i . B_{ij} and IV_{ij} are calculated as above. In practice, a simplified ISA can be implemented by transforming the data to binary data (0 = absence, 1 = presence) and calculating a classical ISA on the transformed data. To my knowledge, the classical and simplified ISAs have not been rigorously compared. However, the simplified ISA would be advantageous because the data requirements are greatly reduced: analyses can be conducted from tabular data summaries. Data requirements and IV calculations for classical and simplified ISAs are compared in Supporting Information Appendix S3.

Methods

FIELD SAMPLING

Field work was conducted on the Hill plots, a series of exclosures in northern Arizona that were established in 1912 to prevent livestock grazing. Data from inside and outside exclosures at three sites are reported here. The vegetation inside and outside each exclosure was sampled in 2004 using the line transect method (Canfield 1941), as had been used in 1941 (Bakker & Moore 2007). Areas subject to localized disturbances (powerline right-of-ways, etc) were omitted from analyses. Additional details about the sites, exclosures, and grazing histories are provided by Bakker & Moore (2007).

In total, 389 line transects (hereafter, lines) were included in this analysis. For herbaceous plants (graminoids and forbs), the rooted portions of live plants directly underneath the line were measured. For shrubs, the plant canopy was projected down onto the line and this distance was measured. Distances were recorded to the nearest 0.25 cm. The recorded distances were summed and divided by the line length [15.24 m (50 ft)] to yield the percentage cover of each species on each line. All nomenclature is based on the USDA NRCS plants database (2004), and species nativity follows USDA NRCS (2004) and Kearney & Peebles (1942). In total, 130 species were identified (Supporting Information Table S1), including 15 exotics. Table S1 also summarizes the distribution of lines among grazing treatments and sites.

CALCULATION OF INDICATOR VALUES

In this study, each line transect is a sample, each grazing treatment at a site is a group, and each site refers to a physical area containing grazed and ungrazed grazing treatments. Classical and simplified ISAs were conducted for each species at each site using the Indicator Value function (Supporting Information Appendix S1). Calculated IV s were assessed for statistical significance using Monte Carlo randomizations with 9999 permutations. Each site was analysed separately so that permutations were restricted to occur within sites. Indicator species were identified by calculating the weighted mean IV (\bar{IV}_{ij}) for each group (grazing treatment) across sites, and by using the weighted Z-transform to combine P values from that group. For each species, the group in which \bar{IV}_{ij} was largest ($\bar{IV}_{i..}$) was identified. The indicator status of species i with respect to this group was then assessed by examining the statistical significance of $\bar{IV}_{i..}$, its magnitude, and the consistency of the species as an indicator of that group across sites. Statistical significance was assessed using $\alpha = 0.05$. Species were considered to be ‘strong’ indicators if $\bar{IV}_{i..} > 25$.

Indicator consistency was assessed by noting whether species that were indicators of a grazing treatment at one site were indicators of the opposite treatment at another site. I also compared the number of species that were indicators of grazing treatments at individual

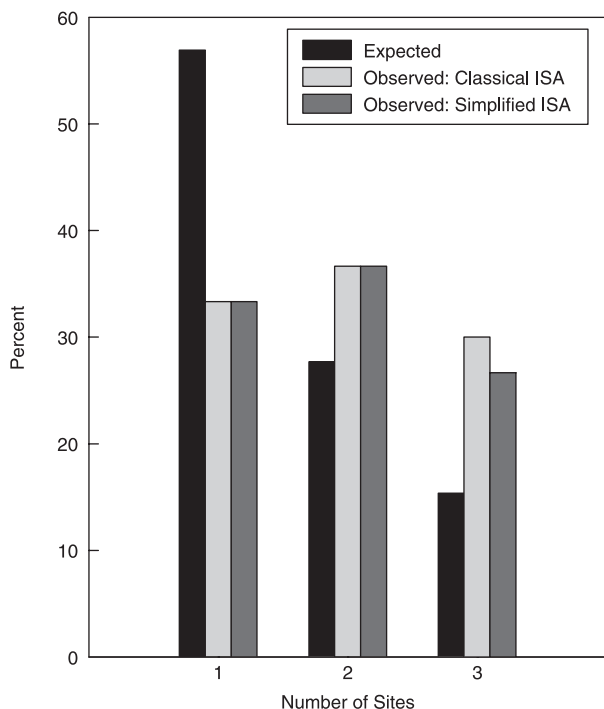


Fig. 1. Percentage of species occurring at one, two, or all three sites. 'Expected' is the percentage of all species, and 'Observed' is the percentage of all significant and consistent indicators as identified by classical and simplified ISAs.

sites with the number that were indicators once data from all sites were combined. Finally, I used contingency analysis to assess the relationship between the number of sites a species occurred at, and the likelihood it was a significant and consistent indicator overall.

Classical and simplified ISAs were compared by assessing whether they identified the same group as having the maximum *IV* for each species, by tallying the number of species that were identified as statistically significant indicators by one or both methods, and by comparing the magnitude of the calculated *IV*s. These comparisons were conducted using individual tests (each species at each site; 206 tests total) and combined tests (each species, all sites combined; 130 tests total).

Results

CONSISTENCY OF INDICATOR SPECIES

The classical ISA identified 50 species as indicators of grazing treatments at one or more sites. Seven species were inconsistent indicators, meaning that they were significant indicators of conditions inside exclosures at one site but of conditions outside exclosures at another site. Combining the results from all sites reduced the number of indicators to 30 (Supporting Information Table S2), including 10 indicators of conditions inside exclosures and 20 of conditions outside exclosures. Two species (*Erigeron divergens* and *Muhlenbergia montana*) remained significant but inconsistent indicators after the results from all sites were combined. Species that occurred at multiple sites were more likely than expected to be indicators of grazing treatment ($\chi^2 = 26.57$, $P < 0.0001$; Fig. 1).

The simplified ISA identified 46 species as indicators of grazing treatments at one or more sites; five species were inconsistent indicators. Combining the results from all sites reduced the number of indicators to 29, including 10 of conditions inside exclosures and 19 of conditions outside exclosures (Supporting Information Table S2). *E. divergens* and *M. montana* remained significant but inconsistent indicators after the results from all sites were combined. Species that occurred at multiple sites were more likely than expected to be indicators of grazing treatment ($\chi^2 = 20.96$, $P < 0.0001$; Fig. 1).

CLASSICAL VS. SIMPLIFIED ISA

The classical and simplified ISAs identified the same grazing treatment as having the maximum *IV* in 93.7% of individual tests (193 of 206). In no test did the two methods identify opposite grazing treatments as statistically significant indicators (Fig. 2A). *IV*s were generally equal or slightly lower for the simplified than the classical method. Species were identified as significant indicators by both methods in 53 tests, by the classical ISA alone in eight tests, and by the simplified ISA alone in one test.

When the results from all sites were combined, the classical and simplified ISA methods identified the same grazing treatment as having the maximum *IV* in 95.4% of tests (124 of 130). Once again, in no test did the two methods identify opposite grazing treatments as statistically significant indicators (Fig. 2B). Species were identified as significant indicators by both methods in 29 tests, by the classical ISA alone in one test, and by the simplified ISA alone in no tests (Supporting Information Table S2).

Discussion

CONSISTENCY OF INDICATOR SPECIES

Unlike studies with other taxa (Bustos-Baez & Frid 2003; Pöyry *et al.* 2005), this study found considerable consistency in the indicator status of vascular plants. Although the number of significant indicators was reduced by 37–40% when the results from multiple sites were combined, species that occurred at multiple sites remained more likely than expected to be indicators. These widespread species are more likely to have broad relevance and be generalizable to other studies than species found at a single site (Zacharias & Roff 2001). Furthermore, this consistency suggests that the detected patterns are robust; distributions of these species were affected by grazing treatments.

Consistency obviously could not be assessed for species that occurred at a single site; the indicator status of these species should be regarded as tentative unless supported by published data or future studies. However, these species were also less likely than expected to be indicators, possibly because they were sampled at lower intensities than species that occurred at multiple sites or because they were responding to unique aspects of that site rather than to the grazing treatment *per se*.

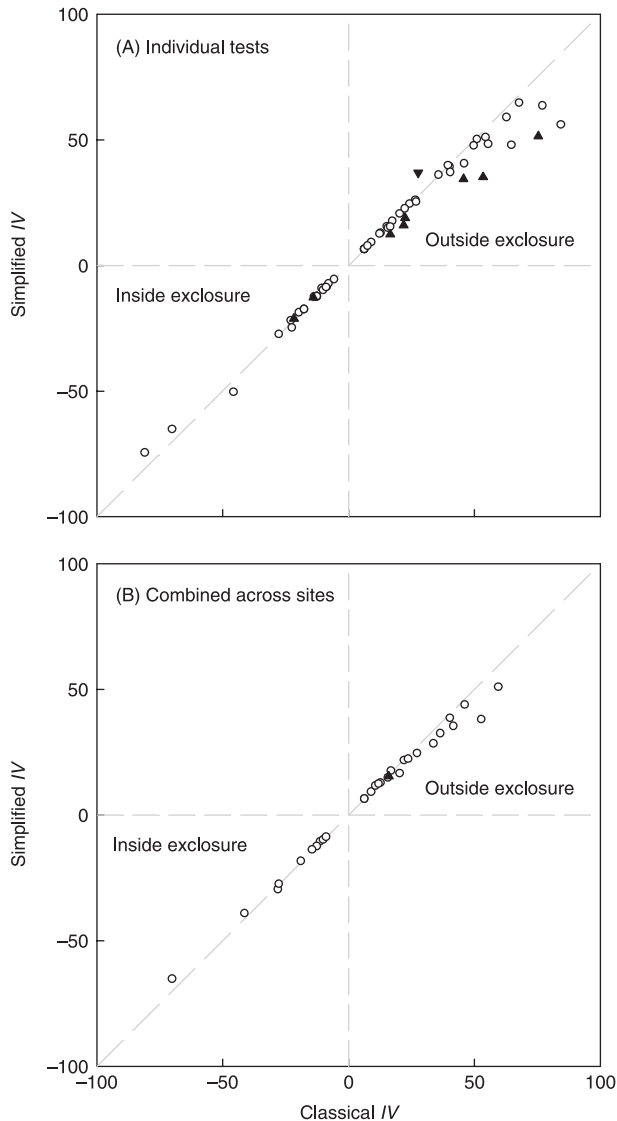


Fig. 2. Relationship between Indicator Values (*IV*) obtained using classical ISA and simplified ISA based on (A) tests conducted separately for each species at each site, and (B) tests combined across all sites. For simplicity, results are only shown for species identified as statistically significant indicators by the classical ISA (▲), simplified ISA (▼), or both methods (○). Indicators of conditions inside exclosures have been expressed as negative values to distinguish them from indicators of conditions outside grazing exclosures. All indicator species are listed in Supporting Information Table S2. Dashed horizontal, vertical, and 1:1 lines are shown for reference.

How groups are defined can affect the conclusions of an ISA. For example, the few species that were inconsistent indicators of grazing treatments may have been affected by inter-site differences in grazing treatments, such as the type of livestock or grazing intensity. Data from additional sites would be required to better understand the responses of these species to the grazing treatments. However, combining the results from multiple sites eliminated most of these species as significant indicators.

One of the intriguing benefits of this method is the ability to rigorously assess the spatial and temporal consistency of

indicator status. For example, consistency of indicator status may depend on the spatial scale of analysis and the ecological amplitudes of a species; since ISAs are conducted independently for each species, consistency can be assessed by analysing responses across the distributional range of a species. Furthermore, these responses can be extracted from published studies and analysed using simplified ISAs. For example, this study found that *Elymus elymoides* was a strong indicator of conditions outside exclosures in ponderosa pine forests (Supporting Information Table S2). A literature search uncovered two other studies reporting the frequency of *E. elymoides* inside and outside grazing exclosures. Results from another ponderosa pine forest agree with this study: *E. elymoides* was a significant indicator of conditions outside exclosures ($IV = 21.5$; $P = 0.0061$; data from Table II, Gardner & Hubbell 1943). However, results from a salt-desert shrubland show the opposite pattern: *E. elymoides* was a significant indicator of conditions inside exclosures ($IV = 13.3$; $P = 0.0047$; data from Table 3, Turner 1971). Clearly, further research is necessary to determine whether species are more appropriately identified as indicators at a regional or ecosystem level rather than across their entire range.

Numerous ecological and environmental management studies have sampled two or more groups at each of a number of sites but combined them into a single statistical analysis. Examples of such analyses include faunal responses to agricultural intensification (Pocock & Jennings 2008), lichen communities (Rogers, Rosentreter & Ryel 2007), roadside vegetation (Rentch *et al.* 2005), and parasites (Foata *et al.* 2006). Use of the meta-analytical techniques outlined here might clarify and strengthen the conclusions of these studies. For example, a conventional analysis often assumes that a species has an abundance of zero at sites where it does not occur. This reduces the likelihood that that species will be identified as an indicator of one group, although its absence may be related to biogeographic constraints or other factors unrelated to the groups being analysed. A more appropriate test of whether a species is an indicator of one group over another is to conduct an ISA at each site and then use meta-analytical techniques to combine the results from the sites where that species occurred.

CLASSICAL VS. SIMPLIFIED ISA

This study demonstrates the power of the simplified ISA. Its conclusions were very similar to those of the classical ISA, but it required much less data. Studies that use the simplified ISA could greatly simplify their data collection techniques by collecting presence/absence data rather than cover estimates or other measures of abundance. Also, these data are easily and efficiently published in data tables or appendices, permitting future analyses of published data.

One possible explanation for the correspondence between results from the simplified and classical ISAs in this study would be if the abundance and frequency data (A_{ij} and B_{ij}) were highly correlated. However, this was not the case: linear regression found low correlation between these data (classical

ISA; $F_{1,204} = 7.61$; $P = 0.006$; $r^2 = 0.031$; J.D. Bakker, unpublished data).

Nonetheless, the simplified ISA may not be appropriate in all situations, particularly for taxa with highly variable abundance among samples. The classical and simplified ISAs differ in how A_{ij} is calculated (equations 1 and 5). The degree of difference between these formulas is a function of the amount of variability among samples. In the simplest case, a species that is equally abundant on all samples where it occurs, these formulas yield identical results. If abundance differs among samples, the classical ISA gives differing weights to A_{ij} . This suggests that the magnitude of the difference between classical and simplified ISAs will be greatest for species with the most variability in abundance among samples. It is not clear how much variability is too much with respect to the simplified ISA: in this study, the coefficient of variation of abundance ranged from 0 to 200% (J.D. Bakker, unpublished data), yet the two methods yielded very similar results. Clearly, further work is needed to determine when the simplified ISA yields results comparable to the classical ISA, and thus, is preferred due to its lower data requirements, and when the variability among samples is so great that the classical ISA might be preferred. The effect of sample size also needs to be examined further.

RECOMMENDATIONS

In closing, I offer some additional recommendations for using ISA:

1. Identify all organisms to as fine a taxonomic resolution as feasible. Congeneric species may differ in indicator status (Weiss & Reice 2005; Nahmani, Lavelle & Rossi 2006; Supporting Information Table S2), nativity, and other characteristics.
2. Consider the proper exchangeable units for permutations tests (Anderson & ter Braak 2003). Where appropriate, such as when a factor is nested within sites, analyse sites separately and combine the results using meta-analytic techniques.
3. Since the results of an ISA depend on the typology used (Dufrêne & Legendre 1997), comparisons among studies require that similar typologies be used. Groups included in the typology should be described in detail for the benefit of future researchers.
4. Ensure that sample sizes are sufficient to sample the vegetation within each group. Doing so will also provide enough samples to permit an adequate number of permutations. The number of possible permutations is:

$${}^nC_m = \frac{n!}{(n-m)!m!}, \quad \text{eqn 6}$$

where m is the number of samples per group and n is the total number of samples. In addition, the number of samples needs to be balanced with the physical dimensions of individual samples.

5. At a minimum, report the sample size and frequency of all species in all groups; simplified ISAs can be easily conducted with these data. This type of data summary used to be common (e.g. Gardner & Hubbell 1943; Turner 1971). Digital appendices and other repositories permit the archiving of

these data in an accessible manner (Parr & Cummings 2005).

6. When reporting the significance of an IV , report the actual P value rather than noting if the value is $< \alpha$ (e.g. $* < 0.05$). Small differences in P value make a large difference in the Z -scores inputted into the weighted Z -transform, particularly at the tails of the Z -distribution.
7. To prevent publication bias in future meta-analyses (Gurevitch & Hedges 2001), publish data for all species, regardless of whether or not they were significant indicators or were above a threshold IV (e.g. $IV_{ij} > 25$, as suggested by Dufrêne & Legendre 1997). The data for this study are reported in Supporting Information Table S1.

CONCLUSIONS

Indicator Species Analysis (ISA) was introduced to the ecological community by Dufrêne & Legendre (1997). It offers considerable improvements over prior techniques, notably its applicability to any typology and independent calculation for each species in an assemblage, but its utility has been limited to relatively simple designs. Consideration of the proper exchangeable units for permutation tests can ensure that analyses are conducted correctly. Meta-analytic techniques can be used to combine results from multiple sites, permitting an assessment of indicator consistency that has been absent to date. A simplified ISA based on presence/absence data yields very comparable results to the classical ISA based on abundance data but has much lower data requirements. One ecologically meaningful application of these techniques would be to rigorously assess the consistency of indicator status of a species across its range or over time.

Acknowledgements

I thank the Woolsey research team (M. Moore, D. Huffman, A. Sánchez Meador, D. Bell, P. Fulé, P. Parysow, W. Covington) for their support, and Coconino National Forest and the Northern Arizona University Centennial Forest for permission to sample study sites. Logistical support was provided by the Ecological Restoration Institute (ERI) and the University of Washington, and financial support by ERI and the National Research Initiative, USDA CSREES (grant 2003-35101-12919). Comments by M. Moore, W. Covington, L. DeWald, C. Gehring, N. Gotelli, M. Cadotte, and several anonymous reviewers greatly improved earlier versions of this article.

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Received 28 January 2008; accepted 5 September 2008

Handling Editor: Marc Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Indicator.Value function for R.

Appendix S2. Sample application of meta-analytical techniques to Indicator Species Analysis.

Appendix S3. Test case example from Dufrêne & Legendre (1997; Table 2) illustrating the data needs for classical and simplified Indicator Species Analyses and the calculation of Indicator Value by each method.

Table S1. Frequency of all plant species inside and outside grazing exclosures at three sites in northern Arizona in 2004.

Table S2. Significant indicators of grazing treatment as identified by classical and simplified Indicator Species Analyses.

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