

Quantifying the Indicator Power of an Indicator Species

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Abstract: Biodiversity indicator species are needed for classifying biotopes and sites for conservation, and a number of methods have been developed for determining indicator species for this purpose. Nevertheless, in addition to site classification, there is sometimes a need to define an indicator species that indicates the occurrence of another species. For example, when a species of interest (target species) is difficult to detect or identify, a reliable indicator species can function as a tool that saves time and money. We derived a method that provides a quantitative measure of the indicator power (IP) of an indicator species for the target species or any species assemblage. We calculated the measure of IP from a presence-absence matrix that covered several sites. The method provided a list of indicator species, the presence of which reliably indicated the presence of another species (e.g., a threatened or rare species in a given area). The IP of the species was highest when the number of shared occurrences between the indicator species and the target species was high and, simultaneously, when the indicator species and the target species occurred separately in only a few cases. The IP was also positively influenced by the number of sites with no occurrences of either the indicator or the target species. Our method can also be used to quantify different types of species occurrence indications. We refer to these types as presence-presence, presence-absence, absence-presence, and absence-absence indications. To clarify the use of the method, we examined the situation with red-listed polypores in White-backed Woodpecker (*Dendrocopos leucotos*) habitats in Fennoscandia and found some suitable indicator species. Our method provides a new, objective way to evaluate the IP of an indicator species.

Keywords: biodiversity indicators, conservation value, *Dendrocopos leucotos*, indicator species, polypores, species inventories, surrogate species

Cuantificación del Poder Indicador de una Especie Indicadora

Resumen: Se requieren especies indicadoras de biodiversidad para la clasificación de biotopos y sitios para la conservación, y se han desarrollado varios métodos para determinar especies indicadoras para ese fin. Sin embargo, adicionalmente a la clasificación de sitios, a veces es necesario definir una especie indicadora que indique la ocurrencia de otra especie. Por ejemplo, cuando una especie de interés (especie blanco) es difícil de detectar o identificar, una especie indicadora confiable puede funcionar como una herramienta que ahorra tiempo y dinero. Derivamos un método que proporciona una medida cuantitativa del poder indicador de una especie indicadora para la especie blanco. Calculamos la medida del poder indicador a partir de una matriz de presencia-ausencia que cubría varios sitios. El método proporcionó una lista de especies indicadoras, cuya presencia indicaba confiablemente la presencia de otra especie (e.g., una especie amenazada o rara en un área determinada). El poder indicador (PI) de la especie fue más alta cuando el número de ocurrencias compartidas entre la especie indicadora y la especie blanco fue alto y, simultáneamente, cuando la especie indicadora y la especie blanco ocurrieron separadamente en solo unos cuantos casos. El poder indicador también fue influido positivamente por el número de sitios sin ocurrencia

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de la especie indicadora ni la especie blanco. Nuestro método también puede ser utilizado para cuantificar los diferentes tipos de indicación de la ocurrencia de especies. Nos referimos a esos tipos de indicación como presencia-presencia, presencia-ausencia, ausencia-presencia y ausencia-ausencia. Para clarificar el uso del método, examinamos la situación con poliporos en la lista roja en hábitats de *Dendrocopos leucotos* Fenoscandia y encontramos algunas especies indicadoras adecuadas. Nuestro método proporciona una forma nueva y objetiva de evaluación del poder indicador de una especie indicadora.

Palabras Clave: *Dendrocopos leucotos*, especies indicadoras, especies sustitutas, indicadores de biodiversidad, inventarios de especies, poliporos, valor de conservación

Introduction

Comprehensive species inventories are very expensive and, as a result, are often impossible to conduct, especially if the area of interest is large or even moderately sized (Kaiser 1997; Ricketts et al. 1999). Biodiversity indicators or surrogates provide a shortcut that may enable biodiversity estimates to be based on the knowledge of a smaller number of species or on species that are easier to detect or identify than the target species (McGeoch 1998; Pearman & Weber 2007; Rodrigues & Brooks 2007). Several statistical methods have been developed to define indicator species and other surrogates (reviewed in Caro & O'Doherty 1999 and Rodrigues & Brooks 2007). For example, there are methods for predicting the species richness of a species group based on the richness of another species group (Kerr et al. 2000; Mac Nally & Fleishman 2002; Williams et al. 2006), predicting the occurrences of species of interest based on biotope data (e.g., Woolf et al. 2002), and determining whether specific species can function as indicators of species richness or composition of a community (Nilsson et al. 1995; Chase et al. 2000). There are also several methods for determining the level of and reasons for the co-occurrence of two species, most of which have been developed to determine the reasons for nonrandom species distributions (Stone & Roberts 1990; Gotelli & McCabe 2002; Mackenzie et al. 2005). Nevertheless, no reliable methods have so far been developed for determining the indicator power (IP) of an indicator species for a specified target species. These kinds of indicator species are needed in situations in which biotope information does not exist or is inadequate to reveal the occurrences of some rare or threatened species or when the focus is on conserving a particular species instead of the total species richness.

Many empirical attempts to develop relevant biodiversity indicator species groups have focused on predicting the overall species richness or, for example, the richness of threatened species on the basis of the diversity of one or a few well-known species groups such as birds, vascular plants, or mosses (Prendergast & Eversham 1997; Jonsson & Jonsell 1999; Similä et al. 2006). Unfortunately this approach neglects species identities. Thus, for example, a community composed of native species can be

evaluated as equal to a community disturbed by humans that is composed of exotic species.

The use of biodiversity indicators as described above has been questioned (Simberloff 1998; Caro & O'Doherty 1999; Andelman & Fagan 2000). The approach is also thought to suffer from loosely defined and poorly targeted applications in which the actual indicator value may be poor or even misdirected (Failing & Gregory 2003). Many of the biodiversity indicator lists that are used, for example, to evaluate conservation values in forests (Kotiranta & Niemelä 1996; Thor 1998; Sverdrup-Thygeson & Lindenmayer 2003), are actually based on expert opinion. Even though expert opinions are derived from long experience in comprehensive fieldwork, the opinions tend to suffer from a lack of empirical evidence and statistical analysis to support and verify the expert judgments.

We derived a method that provides a quantitative measure of the IP of an indicator species for a target species or for any selected species assemblage. The IP is calculated from the observed occurrences of the indicator and target species in a matrix of survey sites. The method provides a list of indicator species, the presence of which will reliably indicate the occurrences of the target species assemblage in an area of interest without the need for complete species surveys. This method is useful for species that have a high conservation value and are difficult to detect or identify. The method is especially suitable for finding indicators for rare or threatened species, a task in which distribution models often fail, or for species for which knowledge on relevant habitat variables is lacking (Vaughan & Ormerod 2003). Initially species inventory data are required for the calculations, but the subsequent need for further species inventories is reduced.

Deriving the Method

Our goal was to attain a numerical value that would reveal the congruency of the distributional patterns of two species. We use the term *indicator species* (*I*) for species whose presence-absence data are used as an indicator of the presence and absence of another species, *target*

species (T). The index, which we call the IP of the indicator species, is calculated with information about the frequency with which the indicator and the target species occur in the matrix of sites and the frequency of their co-occurrence. We derived the following equation for the IP of an indicator species for the target species:

$$IP_I = \sqrt{\left\{ \left[\frac{S}{O_I} \right] \left[1 - \frac{(O_T - S)}{(N - O_I)} \right] \right\}}$$

where O_I is the frequency of occurrence of the indicator species I , O_T is the frequency of occurrence of the target species T , S is the frequency of shared occurrences of the species I and T , and N is the total number of sites surveyed.

The first part of the equation (S/O_I) is the proportion of shared occurrences (S) of the two species out of all the occurrences of the indicator species (O_I). This represents the strength of the positive prediction. Nevertheless, it does not take into account the frequency of target species occurrences that are outside the occurrences of the indicator species. When almost all the sites where the indicator species is present also include the target species, this term approaches 1, and the occurrence of the indicator species is a strong positive indicator of the occurrence of the target species.

The second part of the equation, $[1 - (O_T - S) / (N - O_I)]$, assesses how often the target species occurs without the indicator species. First, $(O_T - S)$ refers to the number of sites where the target species is present but the indicator species is absent. This is divided by $(N - O_I)$, which is the number of sites where the indicator species is absent. The ratio is the relative frequency of sites where the target occurs alone to the frequency of sites lacking the indicator. The larger the ratio, the more sites there are where the indicator is absent but the target is present. When subtracted from 1, the value reflects the ability of the absence of the indicator to correctly predict the absence of the target. If the target species only rarely occurs without the indicator species, this part of the equation approaches 1, and the absence of the indicator species is a strong indicator of the absence of the target species.

The values from these two parts of the equation provide four types of indication. The first part reveals the strength of the presence of the indicator species to indi-

cate the presence or absence of the target species. We call these types presence–presence and presence–absence indications (Table 1). The larger the value calculated from this part, the more powerfully the presence of the indicator species indicates presence of the target species. The smaller the value, the more powerfully the presence of the indicator species indicates the absence of the target species. The second part of the equation reveals the strength of the absence of the indicator species to indicate the presence or absence of the target species. We call these types absence–presence and absence–absence indications. The larger the value, the more powerfully the absence of the indicator species indicates the absence of the target species. The smaller the value, the more powerfully the absence of the indicator indicates the presence of the target species.

We wanted to find an indicator whose presence indicates the presence of the target species and whose absence indicates the absence of the target species. Thus, we needed to maximize the presence–presence and absence–absence indications. Multiplying the two parts of the equation combines these features of indication into one value. With multiplication we rescaled the product back to the original scale by taking a square root of the product. Values close to 1 imply a high IP of the indicator species and are attained when the target species tends to occur in sites where the indicator species is present and the target does not occur in the absence of the indicator. If neither condition is satisfied, then the equation yields a low IP value. The IP is 0 when the indicator and the target species share no occurrences ($S = 0$) and when the target species occurs in every site where the indicator species is missing ($O_T - S = N - O_I$), both refer to negative indication. If both parts of the equation equal 0, then there is a perfect negative indication in which the presence of the indicator indicates the absence of the target and the absence of the indicator indicates the presence of the target. Finally the result of the equation is undefined if the indicator occurs in all the studied sites ($O_I = N$), which reflects the inability of a ubiquitous species to provide any information on the distribution of the target species.

Our method is suitable for many types of species occurrence data, and the requirements for suitable data are

Table 1. Different kinds of species occurrence indications between the indicator (I) and the target (T) species.

Abbreviation	Type of indication*	Equation	Direction
Presence–presence	presence of I indicates presence of T	S/O_I	positive (larger value means stronger indication)
Presence–absence	presence of I indicates absence of T	S/O_I	negative (larger value means weaker indication)
Absence–presence	absence of I indicates presence of T	$1 - (O_T - S) / (N - O_I)$	negative (larger value means weaker indication)
Absence–absence	absence of I indicates absence of T	$1 - (O_T - S) / (N - O_I)$	positive (larger value means stronger indication)

*The scale is between 0 and 1 in each type of indication.

not stringent. The only feature of the data that prevents the orthodox use of the method is when there is a bias in the sampling effort or detection probability of a species. If, for example, sites in more natural conditions were surveyed more comprehensively than disturbed sites, a species might appear to be a good indicator even though it would also be detected in disturbed sites, provided the disturbed sites were surveyed as intensively as the natural sites. Random variation in the sampling effort does not prevent the use of the method, but increases the variation in species occurrence patterns and reduces the IP values because shared occurrences may be missed. Nevertheless, if two species do not have shared occurrences, random variation is not able to create them. Thus, IP is a conservative measure of indication when there is random variation in the sampling effort. To determine reliability of the method it is essential to know whether the attained IP values could be generated merely by chance. Significance testing can be performed by comparing IP values derived from actual data against data in which the occurrences of each species are randomized. The IP values derived from randomized data represent values that will occur merely by chance when species occurrences in the study sites are completely independent of each other. After replicating the randomization procedure a thousand times, 95% of the confidence limits for the IP values can be calculated to determine whether the observed IP values are more extreme than the expected ones on the basis of chance alone.

Application of the Method for Larger Target Groups

The method can also be applied in cases in which an indicator is needed for a larger group of target species. We call this IP for a group of species the *total indicator power* (TIP). The TIP can be calculated for a specific indicator species from all the pairwise IP values with the targets (IP_{T1-Tn}) by averaging over these pairwise values. The minimum of the pairwise values and its variance can be used. If the minimum IP value is high, then the indicator species is a reliable indicator of all of the target species, even though the mean TIP may be lower than that of some other indicator species. A high mean TIP value with a low variance indicates that the species is a good general indicator of the target species group, and a high mean value with a high variance indicates that the species is an extraordinarily good indicator of some species in the target group. A low TIP value with a low variance indicates that the species is a weak indicator of all the species in the target group.

The significance of the TIP value for a larger target species group can be tested with a basic meta-analytical approach. The p values are first calculated for each

species pair (IP) in the same way as for one target species. Then the standard normal deviates (Z) are derived for the p values, and the combined p value is calculated from the Z values according to the formula $(\sum Z_i)/\sqrt{n}$ (Rosenthal 1984). Determining the heterogeneity of the pairwise p values gives another estimate of the variation of the IP of the indicator species for the target species group. The heterogeneity value can be calculated according to the formula $\sum(Z_j - \text{mean } Z)^2$, and it is distributed as a chi-square value with $K - 1$ df (K is the number of species pair IP values to be compared) (Rosenthal 1984). When using the method for a larger species group we recommend that 5 statistics be reported: TIP, its significance and heterogeneity, the minimum IP value, and the variance of the IP values for the target species group.

Numerical Examples

We used hypothetical species distributions to illustrate the function and outcomes of the method (Fig. 1). In these illustrations we showed the function of the method and changes in the IP values with different variables O_I , O_T , and S . In panels (a-c) of Fig. 1 we fixed O_I to represent rare, intermediate, or common indicator species, respectively, and in panels (d-f) of Fig. 1 we have fixed O_T to represent rare, intermediate, and common target species, respectively. In each case we created multiple cases with hypothetical species distributions and levels of shared occurrences. Any change in N will affect the IP, but this change is simply relative and does not affect the observed pattern. As a result we did not include variation in N in the examples.

One can see from Fig. 1(a-f) that the IP value always increases with increasing levels of shared occurrences, but an occurrence of an indicator species outside the range of a target species has a different effect on the slope than an occurrence of a target species outside the range of an indicator species. Thus, for example, an indicator species with 20 occurrences (Fig. 1a) may function as a relatively reliable indicator of a target species with about 70 occurrences if they share all the 20 occurrences of the indicator species. On the other hand, an indicator species with approximately 70 occurrences is not as powerful an indicator of a target species with 20 occurrences (Fig. 1d) even though they share 20 occurrences because, in this case, an occurrence of an indicator species does not provide strong evidence about the occurrence of a target species.

Next we present four hypothetical examples of the use of IP and TIP and the parameters describing them. In example 1 (Table 2) the indicator species shares a total of 870 occurrences with five target species. The proportion of shared occurrences with each of the target species varies only slightly, and the indicator species

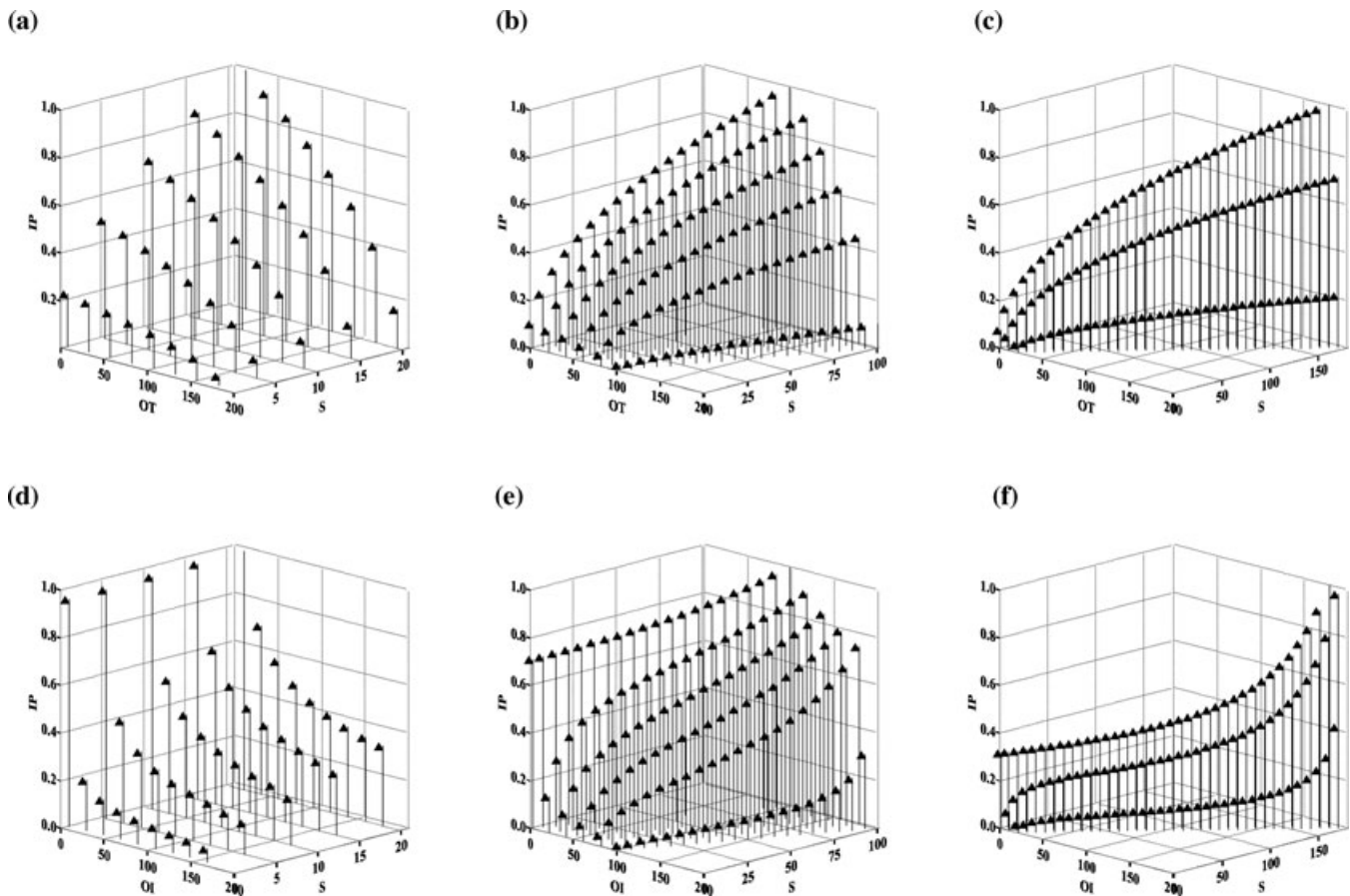


Figure 1. Illustrations of the variation of the indicator power (IP) value with different values of the variables O_1 (occurrences of indicator species), O_T (occurrences of target species), and S (shared occurrences of indicator and target species). In all the figures N is constant at 200. In panels (a-c), O_1 is constant at the (a) rare ($O_1 = 20$), (b) intermediate ($O_1 = 100$), and (c) common ($O_1 = 180$) levels. In panels (d-f), the level of O_T is constant. Scales for S vary among graphs.

indicates all the target species with a similar power. The IP values of all the target species are highly significant, as is the combined p value for TIP. Both the variance of the IP values and the heterogeneity of the p values are low. In example 2 the indicator species shares 890 occurrences with five target species. The TIP is the same, but the minimum IP value is very low, and the variance is much higher than in example 1. In this case the indicator species is not an equally powerful indicator for the whole species group, and further examination shows that it is not a powerful indicator for target species number 4. In example 3 the indicator species shares 310 occurrences with the target species group. The TIP and the variance of the IPs are both low. This indicator species is not a powerful indicator of any of the species in the target species group. In example 4 the indicator species shares 335 occurrences with the target species group. The TIP is the same as in example 3, but the variance is much higher. This, together with the significant heterogeneity, indicates that the target species group includes species with significantly different IP values. Analysis of the IP

values shows that the indicator species would be a very powerful indicator for target species number 3.

Empirical Example: Indicator Species for Red-Listed Polypores in White-Backed Woodpecker Territories

Background

The White-backed Woodpecker (*Dendrocopos leucotos*) is an endangered bird species in Fennoscandia (Rassi et al. 2001; Gärdenfors 2005). The species requires a habitat rich in dead and dying deciduous trees (Virkkala et al. 1993). Conservation efforts for this species have recently been combined with conservation efforts for some other endangered, mainly dead-wood-dependent species (Mild & Stighäll 2005).

We inventoried the polypores in protected White-backed Woodpecker nesting habitats and in habitats where the woodpecker has not been nesting but that have been protected as potential habitats of the bird

Table 2. Four example cases in which occurrences of multiple target species have been indicated with one potential indicator species (N is 1000 in all examples).*

Example number	O ₁	O _{T1}	O _{T2}	O _{T3}	O _{T4}	O _{T5}	S ₁	S ₂	S ₃	S ₄	S ₅	IP ₁ P ₁	IP ₂ P ₂	IP ₃ P ₃	IP ₄ P ₄	IP ₅ P ₅	TIP P _{TIP}	MinIP ₁₋₅	χ ² Het	VarIP ₁₋₅
1	400	300	200	200	160	250	200	200	140	140	190	0.65 <0.001	0.71 <0.001	0.56 <0.001	0.58 <0.001	0.65 <0.001	0.63 <0.001	0.56	0.416 0.981 4.673	0.003
2	400	300	200	200	160	250	300	200	195	65	130	0.87 <0.001	0.71 <0.001	0.70 <0.001	0.37 <0.001	0.51 <0.001	0.63 <0.001	0.37	0.323 3.717	0.037
3	400	300	200	200	160	250	90	80	50	40	50	0.38 1.000	0.40 1.000	0.31 1.000	0.28 1.000	0.29 1.000	0.33 0.734	0.28	0.446 11.178	0.003
4	400	300	200	200	160	250	30	40	200	35	30	0.20 1.000	0.27 1.000	0.71 <0.001	0.26 1.000	0.22 1.000	0.33 0.144	0.22	0.025	0.045

*Key: O_i, occurrences of indicator species; O_T, occurrences of target species; S, shared occurrences of the indicator species and the target species; IP, indicator power of the indicator species for the target species; TIP, total indicator power of the indicator species for all the target species in the target species group (i.e., mean of the IP values); p, 2-tailed significance of the IP value; MinIP, minimum indicator power of the indicator species for the species in the target species group; χ², χ² value derived from p values of IP₁₋₅; Het, significance of heterogeneity of p values of IP₁₋₅; VarIP, variance of the indicator power values of the indicator species for the target species group.

in southern Finland. Two red-listed polypore species, *Gloeoporus pannocinctus* and *Protomerulius caryae*, were relatively common in many of these areas. At present their occurrence in White-backed Woodpecker habitats is protected by chance; however, their protection could be combined with protection of the woodpecker if the occurrences were known. The most serious obstacles for combined protection are that both these polypore species are difficult to observe and identify and their occurrences vary from year to year because they are annuals (Halme et al. 2009). If, however, there were indicator polypore species that were easy to observe and identify, preferably perennial and, as such, with a constant seasonal occurrence, it would be easy to train the bird specialists conducting woodpecker inventories to recognize these species.

Methods

Our data were collected from 10 White-backed Woodpecker territories and five sites conserved as potential territories (each approximately 30–60 ha) in central Finland (61–62°N, 25–28°E). Within these territories we inventoried 122 forest stands (4–10 stands/territory, each typically 1–5 ha). In each stand we inspected coarse woody debris for the fruit bodies of polypores. We calculated the IP and TIP values for the target species *Protomerulius caryae* and *Gloeoporus pannocinctus*. As potential indicator species we selected species that form large-size fruit bodies on deciduous trees and are easy to observe and identify. We restricted the analysis to species with at least 10 occurrences to ensure that the indicator species would be common enough relative to the occurrences of the target species. Twenty-four species fulfilled these requirements.

Results

We identified 89 species. *Protomerulius caryae* occurred in 25 forest stands in 11 sites, and *Gloeoporus pannocinctus* occurred in 33 forest stands in 10 sites.

Six species had a significant IP value for *Gloeoporus pannocinctus*, and seven species for *Protomerulius caryae*. The target species have a relatively similar ecology: they can only inhabit deciduous trunks that have been decayed by two very common species, *Fomes fomentarius* or *Inonotus obliquus* (Niemelä 2005). As expected the species with the highest IP values for each of the target species also had, in most cases, the highest TIP (Table 3).

Because the ecological requirements of the target species were similar, it was not surprising that the most powerful indicator species for both of them were in most cases the same. Neither was it surprising that the TIP values were not heterogeneous, and that the variances of the IP values for the species were small. In this example

Table 3. The five potential indicator species with the highest total indicator power for the target species (N is 122 in all cases).*

Indicator species	O_1	O_{Glopan}	S_{Glopan}	$Pres_{Glopan}$	Abs_{Glopan}	IP_{Glopan}	p_{Glopan}	TIP	MinIP	χ^2 Het	VarIP
		O_{Procar}	S_{Procar}	$Pres_{Procar}$	Abs_{Procar}	IP_{Procar}	p_{Procar}	p_{TIP}			
<i>Gloeoporus dichrous</i>		33	19	0.46	0.83	0.62	<0.001	0.65		0.000	
	41	25	20	0.49	0.94	0.68	<0.001	<0.001	0.62	1	0.002
<i>Pbellinus lundellii</i>		33	6	0.55	0.76	0.64	0.007	0.63		0.008	
	11	25	5	0.45	0.82	0.61	0.010	<0.001	0.61	0.927	<0.001
<i>Pbellinus laevigatus</i>		33	17	0.43	0.80	0.58	0.018	0.59		0.414	
	40	25	16	0.40	0.89	0.60	<0.001	<0.001	0.58	0.520	<0.001
<i>Cerrena unicolor</i>		33	13	0.45	0.78	0.59	0.008	0.58		0.000	
	29	25	11	0.38	0.85	0.57	0.008	<0.001	0.57	1	<0.001
<i>Antrodiella pallescens</i>		33	18	0.39	0.80	0.56	0.049	0.58		0.627	
	46	25	18	0.39	0.91	0.60	0.002	0.004	0.56	0.428	0.001

*Key: O_1 , occurrences of indicator species; O_{Glopan} and O_{Procar} , occurrences of target species; S_{Glopan} and S_{Procar} , shared occurrences of the indicator species and the target species; $Pres_{Glopan}$ and $Pres_{Procar}$, value of presence-presence prediction for the target species; Abs_{Glopan} and Abs_{Procar} , value of absence-absence prediction for the target species; IP_{Glopan} and IP_{Procar} , indicator power of the indicator species for the target species; p_{Glopan} and p_{Procar} , two-tailed significance of the IP value; TIP , total indicator power of the indicator species for all the target species in the target species group (i.e., mean of the IP values); p_{TIP} , significance of the TIP value; MinIP, minimum indicator power of the indicator species for the species in the target species group; χ^2 , χ^2 value derived from p values of IP_{Glopan} and IP_{Procar} ; Het, significance of heterogeneity of p values of IP_{Glopan} and IP_{Procar} ; VarIP, variance of the indicator power values of the indicator species for the target species group.

we recommend the use of the species with the highest TIP values in Table 3 as the indicator species for red-listed polypores occurring in White-backed Woodpecker habitats in central Finland.

Discussion

We recommend that our method be employed as follows. First, calculate the IP for each pair of potential indicator and target species of interest. Second, use either indicator species with the highest IP for different target species or calculate the TIP and try to determine an indicator species that would function as a powerful indicator of the whole target species group simultaneously. The optimal approach depends on the case in question.

There is an analogy between the IP and the measures derived from the confusion matrix in species distribution modeling, in which the observed presences and absences are compared with the predicted presences and absences of a single species (e.g., Fielding & Bell 1997; Allouche et al. 2006). Nevertheless, most of the measures based on the confusion matrix do not use all the available information and are thus inferior to IP. More comprehensive measures, such as odds ratio, kappa, and normalized mutual information (NMI), fail because they are vulnerable to situations in which, for example, a proposed indicator species is far more common than the target species. We do not recommend using these methods in the evaluation of indicator species. In contrast, our measure may turn out to be useful in assessing the classification accuracy of predictive distribution models.

Some other methods, developed for determining the level of co-occurrence of two species, could also function

as tools for determining suitable indicator species (e.g., Stone & Roberts 1990; Gotelli & McCabe 2002; Mackenzie et al. 2005). Unlike these methods our method makes a distinction between false-negative and false-positive predictions. False-positive prediction about species occurrence is, in some conservation situations, less dangerous (from the perspective of conservation, ignoring the economic costs) than false-negative prediction. This is because, in the case of a false-positive prediction, sites may become protected despite being uninhabited by any populations of the target species. Nevertheless, our method functions in the opposite way because one occurrence of the indicator species without the target species (false positive) has a stronger negative effect on the IP than the absence of the indicator when the target is present (false negative). This feature makes our method especially suitable for practical conservation, in which the goal is often to correctly determine the sites that are occupied in order to allow accurate planning of the future conservation actions. In the real world the conservation planner is always constrained by the conservation budget and must be able to find the most likely inhabited sites among the potential target sites. By observing the strength of the presence and absence predictions provided by our method (Table 1), the conservation planner will be more informed about the risk of false-positive and false-negative predictions.

As useful as it is to know which species are positive indicators of the target species, it may in some cases also be beneficial to know which species only rarely occur together. Our method enables the identification of such species. This may be of high value, especially when there is a need to identify areas with low conservation values or sites where exotic species are absent. With our method it is possible to estimate both the strength of the positive

prediction (i.e., the proportion of shared occurrences of indicator and target species) and the strength of negative prediction (i.e., the probability of target species occurring outside the range of indicator species). These different indications can be estimated by focusing on the different types of indications given by the method (Table 1).

One could argue that a rare species may only be indicated by another rare species because a more common species must also always occur outside the occurrences of a rare species and thus could not work as a proper indicator. One could then ask, what is the potential use of an indicator species if it is as rare as the target? Nevertheless, we do not see this as an obstacle to using the method. First, our method enables calculation of the TIP for a larger target species group. A relatively common species may share rather many occurrences with many rare target species, even though it does not share all of its occurrences with any of them (Table 2, example 1). Second, two equally abundant species may differ in their detectability or in their identifiability. Thus it may be useful to know whether one of them might work as an indicator of the other, even though they occur in nature at similarly low frequencies.

There are some complications to our method. First, the IP provided by our method is sensitive to the quality of the data. In any field inventory the probability to detect a species when it is present at the studied site is <1 . The lower the detectability, the lower the IP of the indicator species. Nevertheless, this variation does not restrain the use of our method if the detectability is evenly low for all the proposed indicator species and target species. Problems arise, however, if some species are much more likely to be detected than others. Nevertheless, such problems are not easily accounted for by any existing method (Mackenzie et al. 2005).

Like the methods developed earlier, our method also provides empirical knowledge of the congruency of the occurrences of two species. The most important advancement our method offers is that, in addition to the shared occurrences, the proportion of unshared occurrences is also taken into account. This feature introduces another complication. By extending the study area without achieving any more occurrences of either indicator or target species, it is possible to increase the IP value between the species simply because the proportion of unshared occurrences decreases in relation to the number of sites where neither of the species is present. Nevertheless, the proportion of occurrences of both species that are unshared is included in the method, which allows determination of whether the potential indicator species truly is a strong indicator of the absence of the target species. This complication should be borne in mind when using the method, and the data should only include sites that are relevant to the question being studied.

The third complication of our method is related to the extrapolation of the results to other biotopes and geographical areas. The relationships between the distributions of species depend on the extent and grain size of the study (Hess et al. 2006). The problem manifests itself once one starts extrapolating the results outside the region in which the data were collected, and uncertainty increases with increasing geographical distance. This is the case because our method is based on the congruency of the indicator and target species, instead of on a causal relationship. Therefore we do not recommend extrapolating the results obtained with our method outside the geographical region in which the data for indicator estimation were collected. Instead, interpolation inside the same geographical area in which the data were collected is possible, and the indicator species can be used in sites where there is no earlier knowledge of species occurrences.

Our method gives a numerical value for the power of the proposed species to indicate the target species. This enables evaluations of the indicator species and species lists in a new, objective way. We suggest that both researchers and land-use managers use the method to develop reasonable strategies for collecting information on the occurrence of species valued as important and, following this, assess the conservation value of different areas.

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