

A comparative study of ecological specialization estimators

Timothée Poisot*†, Elsa Canard, Nicolas Mouquet and Michael E. Hochberg

Université Montpellier II, Institut des Sciences de l'Évolution, UMR CNRS-UM2, 5554, Place Eugène Bataillon, 34095 Montpellier CEDEX 05, France

Summary

1. Ecological specialization is a unifying concept in the biological sciences. While there are reliable ways to characterize specificity at individual and community levels, the evaluation of population and species-level measures is lacking. There is a need for such assessments given that populations and species are the relevant scales for most ecological and evolutionary processes.
2. Using examples of simulated and empirical data sets of bipartite networks representing a continuum of biological interactions, we evaluate six indices of specificity in terms of their robustness to incomplete sampling and information they extract from data.
3. Robustness differed between the measures and in their ability to differentiate specialists and generalists along a full continuum. On the empirical data sets, indices were less separated by their informativity than on the simulated data sets, which may be due to the heterogeneity of the former.
4. Based on these different evaluations for species-level (or population-level) specificity, we recommend the use of Resource range when no quantitative data are available and Paired Difference Index otherwise. These results will assist both applied and fundamental researchers in the characterization and interpretation of species specificity.

Key-words: bipartite networks, methodology, sampling, specialization, specificity

Introduction

Ecological specialization is the process by which an organism adapts to an increasingly narrow subset of its possible environments and persists in an increasingly narrow range of habitats (Futuyma & Moreno 1988; Devictor *et al.* 2010; Poisot *et al.* 2011a). The outcome of this process is that specialized organisms will have higher performances in a small subset of the range of their environmental conditions, both biotic (e.g. prey, hosts, mutualists) and abiotic (e.g. habitats, physical or chemical conditions). Specialization is influenced by numerous evolutionary and ecological processes (Kassen 2002; Poisot, Thrall & Hochberg 2012; Poisot *et al.* 2011b), and considerable research has shown how specificity is important in understanding species biology, behaviour, dynamics (Wilson & Hassell 1997), distributions and diversity (Levins 1968; Hudson, Dobson & Lafferty 2006; Lafferty *et al.* 2008). For example, specialists are more prone to extinction than generalists, and more negatively affected by environmental change (McKinney & Lockwood 1999; Colles, Liow & Prinzing 2009;

Clavel, Julliard & Devictor 2010; Barnagaud *et al.* 2011). Other research has suggested that generalist pathogens, because of their greater ecological, phenotypic and genetic variability (Kaci-Chaouch, Verneau & Desdevises 2008), are more likely to acquire new hosts, thus facilitating disease emergence (Woolhouse & Gowtage-Sequeria 2005). In the context of global change, the design of appropriate conservation strategies and disease control policies requires efficient ways of estimating specificity with the highest possible accuracy.

While there is considerable literature on specialization and its ecological and evolutionary consequences, practical information about how it is best measured at the species level is scarce and not integrated across fields [see Bolnick (2002), and Devictor *et al.* (2010) or Dormann (2011) for, respectively, individual and community level measurement issues]. One reason is that different fields have contrasted conceptual and lexical approaches to the same problem, resulting in a multiplicity of terms to describe specificity. Moreover, empirical studies have emphasized that specificity can be defined in different ways, including measures of potential specificity, such as preference for and performance on different resources (Van Nouhuys, Singer & Nieminen 2003; Singer *et al.* 2004), and measures of realized specificity such as observed resource use (Matich, Heithaus & Layman 2011).

Recently, considerable attention has been given to methods for estimating specificity, and in particular, the robustness of

*Correspondence author. E-mail: timothee.poisot@uqar.ca

†Present address: Département de Biologie, Université du Québec à Rimouski, 300 Allées des Ursulines, Rimouski, QC G5L 3A1, Canada.

Correspondence site: <http://www.respond2articles.com/MEE/>

measures to under-sampling, because exhaustive data sets are rarely obtained from the field (Blüthgen, Menzel & Blüthgen 2006). A number of other issues might affect the accuracy of specificity measurements. For instance, the interpretation of specificity will depend on whether it is a continuous or a discrete variable, and if the former, the resolution of its measurement (discrete or continuous data). In the simple case where two consumers both exploit the same two resources, if one performs equally on both, while the other performs better on one, then the latter exploiter is evidently more specific than the former. This information would be lost, however, if the ability to exploit a resource was measured as an ‘all or nothing’ binary variable, leading some authors to separate ‘specificity of associations’ (i.e. as measured using the adjacency matrix, corresponding to a binary view of specialization) and ‘specificity of impacts’ (i.e. as measured by various proxies for interaction strength; Bever 2003). Poulin, Krasnov & Moullot (2011) recently termed these same notions as ‘basic’ and ‘structural’ specificity (see Glossary). Most importantly, and although never tested, measures can differ in their ability to quantify specificity based on the strength of the interaction, which we will call ‘link strength’ (Berlow *et al.* 2004). As a consequence, different measures may not have the same ability to distinguish specialists from generalists: while some measures are able to differentiate specificity between species (i.e. in a rank-based approach e.g. Devictor, Julliard & Jiguet 2008), they are not necessarily able to accurately estimate their positions on the specialist–generalist continuum.

The aim of the present study is to evaluate the performances of a range of different specificity indices in terms of their (i) ability to represent the absolute degree of specificity, (ii) robustness to incomplete sampling (as commonly encountered in field studies) and (iii) information content. We used both simulated and empirical data sets, the former enabling the assessment of possible scenarios not represented by the latter.

Methods

Hereafter, we refer to ‘species’ as the entities under consideration in measuring specificity, and ‘resources’ as the environments (habitats,

food, interaction partners, etc.) employed by the species (see Glossary). This terminology, although being a coarse simplification of a range of ecological scenarios (e.g. mutualistic networks do not involve *sensu stricto* consumers and resources), allows us to evaluate different specificity measures in bipartite species interactions. We focus on specificity indices calculated from observed link strength measurements (see Glossary). Our method, although applied to observational data, should apply more generally to other types of specificity, for example as inferred from the quantification of genotype-by-genotype interactions (Vale *et al.* 2008), gene frequency studies (Wehling & Thompson 1997) or any other proxy for link strength (Berlow *et al.* 1999). For clarity, we will briefly describe how such data should be organized so that the measures studied can be applied.

The measures studied use consumer performances on several resources to infer specificity (available in the ESM package for R (<https://r-forge.r-project.org/projects/esm/>). The vector of link strengths of the species under consideration is called **P** (with length *R*, and *r* non-zero elements). **T** is the sum of all elements of **P**. Because previous study emphasized the need for index normalization in cross-study comparisons (Poulin 2007), we standardized our measures so that they return values between 0 and 1, 0 corresponding to absolute generality and 1 to absolute specificity; thus, the formulas presented in Table 1 sometimes differ from their original derivations.

RESOURCE RANGE: RR

The RR index estimates specificity based on the fraction of resources exploited with a non-zero performance, regardless of the link strength with each resource (Schoener 1989):

$$RR = \frac{R - r}{R - 1} \quad \text{eqn 1}$$

Resource range is a normalization of the total number of links established from a given trophic level to the immediately lower one (or in the broader context of unipartite networks, how many links are established by a focal species, that is, its degree). Despite not using quantitative link strength information, we included this measure here because of its simplicity and frequent use (Novotny *et al.* 2002).

COEFFICIENT OF VARIATION (COV)

Julliard *et al.* (2006) described the ‘Species Specificity Index’, which is the coefficient of variation in the distribution of performances:

Table 1. Families of the different indices used in this study and their performances for different criteria. ‘Low robustness’ measures may include ranges that are robust, but not for connectance values observed in nature. A description of each index with its associated formula is given in the Methods. ‘Community context’ refers to the fact that some measures use the link strength distribution of surrounding species to evaluate the specificity of a focal species

	Index properties			Results		
	Data	Approach	Community context	Robustness	Informativity	Absolute values
RR	Binary	Richness	No	High	Low	+
CoV	Continuous	Variance	No	Low	Medium	–
HS	Continuous	Distance	No	Low	Low	–
PDI	Continuous	Variance	No	High	High	+
<i>d'</i>	Discrete	Distance	Yes	High	Low	–
SDI	Discrete	Richness	No	Low	Very low	–

CoV, coefficient of variation; PDI, Paired Difference Index; RR, Resource Range; SDI, species diversity index.

$$\text{CoV} = \frac{\sqrt{\sum_i (\mathbf{P}_i - \mu)^2}}{\mu R \sqrt{\frac{R-1}{R}}}, \quad \text{eqn 2}$$

where μ is the mean performance (the multiplier is a normalization of the index so that it yields values between 0 and 1).

SHANNON'S EVENNESS: HS

Schug *et al.* (2005) recommend the use of Shannon's H index to estimate tissue-promoter specificity, a type of interaction typically with few null interactions. Shannon's H can be applied to ecological specificity by assuming local population size as a proxy for the strength of each link, and total population as the sum of link strengths over all resources. We normalize H to yield values between 0 and 1:

$$\text{HS} = \frac{\sum_{i=1}^R \left[\frac{\mathbf{P}_i}{\mathbf{T}} \ln \left(\frac{\mathbf{P}_i}{\mathbf{T}} \right) \right]}{\ln(R)} + 1. \quad \text{eqn 3}$$

Since when $\mathbf{P}_i = 0$ this measure is not defined, we set all null interactions to very small values ε ($\varepsilon = 1 \cdot 10^{-12}$). This correction maintains the total number of resources (R) constant across all species in the network.

d'

Blüthgen, Menzel & Blüthgen (2006) proposed a species-level measure of specificity, d' , which is calculated first by finding d_i

$$d_i = \sum_{j=1}^c \left(p'_{ij} \ln \frac{p'_{ij}}{q_j} \right), \quad \text{eqn 4}$$

with c the number of resources, p'_{ij} the proportion of interactions divided by the sum of performances of species i , and q_j the sum of interactions of resource j divided by the total number of interactions in the matrix (Blüthgen, Menzel & Blüthgen 2006). The value of d' is then obtained by normalizing d_i , such that $d' = (d_i - d_{\min}) / (d_{\max} - d_{\min})$.

Note that because q integrates the sum of total interactions across the network, the value of d' returned for any given species is not independent from the performances of co-occurring species.

PAIRED DIFFERENCE INDEX: PDI

The 'Paired Difference Index' (PDI) takes into account that performances may have a variety of statistical distributions, and thus no single variability measure will apply equally to all data sets (Poisot *et al.* 2011b,c). PDI contrasts a species' strongest link on a resource with those over all remaining resources.

Paired Difference Index is calculated as follows:

$$\text{PDI} = \frac{\sum_{i=2}^R (\mathbf{P}_1 - \mathbf{P}_i)}{R - 1}, \quad \text{eqn 5}$$

where \mathbf{P}_1 is the highest link strength, \mathbf{P}_i is link strength with the i th resource, and R is the number of resources in the data set. PDI can employ binary, categorical or continuous data. For example when data are 'all or nothing', the PDI is calculated measuring the number of interactions of strength 1 and comparing them to the total number of interactions (in which case $\text{PDI} = \text{RR}$).

SPECIES DIVERSITY INDEX (SIMPSON'S SDI)

Based on the property that specificity can be viewed as lack of evenness in the distribution of link strengths of a focal species, we included SDI (Simpson 1949) as a measure of specificity. Note that previous studies used HS for the same purpose (Tylianakis, Tscharntke & Lewis 2007).

$$\text{SDI} = \Sigma[P/(P-1)] / [\Sigma P \cdot (\Sigma P - 1)]. \quad \text{eqn 6}$$

Owing to the fact that this measure only accommodates discrete data, the same method of transformation as for d' was applied.

ABILITY TO DIFFERENTIATE SPECIALISTS AND GENERALISTS

One of the most important criteria for choosing a particular specificity measure is its ability to discriminate between specialists and generalists. Levins (1962) proposed that the shape of the performance trade-off reflects the potential for ecological specialization across multiple environments. Frank (1994) showed that by modifying a single parameter (ρ , that we call 'expected specialization', see legend of Fig. 1a), we can generate a continuum of trade-off shapes ranging from decelerating (indicating generalization, values of $\rho < 1$) to accelerating (indicating specialization, values of $\rho > 1$). We use this approach to simulate the distribution of link strengths within a vector \mathbf{P} (Fig. 1a). We consider one species exploiting 100 resources ranging from 'generalist' situations ($\rho < 1$) to 'specialist' situations ($\rho > 1$). We then examined the value returned by each specificity measure (with the exception of RR, which cannot accommodate quantitative data) to gauge their abilities to discriminate between specialists and generalists.

ROBUSTNESS AND INFORMATIVITY ANALYSES

We also evaluated the robustness of the different measures to missing data. Missing data in empirical networks reduce the number of resources and can bias the signal towards generalism, since all else being equal, we are more likely to omit specialists with each missing resource (in cases of consumer-resource interactions, missing consumers will not affect the estimation of species-level specificity). In addition, an index may be robust but not informative, introducing the need to analyse the quantity of information they yield (Bushberg *et al.* 2003). In both cases, we used both simulated and empirical bipartite networks to assess the behaviour of each specificity estimator. We describe data sources, and robustness and informativity analyses in detail below.

Empirical and simulated networks

We employed both empirical and simulated bipartite networks to evaluate specificity measures. We used all of the empirical bipartite networks listed in the NCEAS *InteractionWeb* data base (<http://www.nceas.ucsb.edu/interactionweb/>) as of January 2011. Unipartite data sets (i.e. food webs with multiple trophic levels) were transformed in a square matrix, with matrix rows being the organisms for which specificities are estimated. Because of differences in the types of systems, data quality and sampling methodology, the results obtained on empirical networks are comparatively less meaningful than those obtained from simulated data.

Simulated bipartite networks were also employed as empirical data are prone to two main types of bias. First, empirical webs may be incompletely sampled, and as such robustness to partial sampling

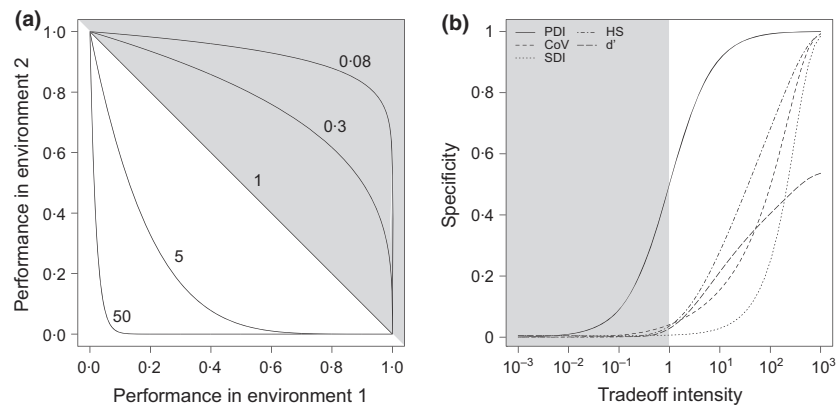


Fig. 1. (a) Illustration of different distributions of resource utilization for a particular species, ranging from complete generalism to complete specialism. The value next to each line is the dimensionless parameter ρ , giving the rate at which the link strength on resource 1 (y) decays with increases in link strength with resource 2 (x), based on $y = (1 - x)^\rho$. Specifically, when R resources are available (we used $R = 100$), the link strength of the species with the resource of rank r is $P_r = (1 - \frac{r}{R})^\rho$. Note that this formula is normalized, with values of 0 and 1 corresponding to the lowest and highest link strengths, respectively. Only the rate at which link strength decays on successive resources (i.e. specialization) varies with the value of the exponent. (b) Values returned by each specificity index as a function of ρ (expected specialization). In (a) and (b), the grey area indicates the separation between specialist and generalist strategies, with the white area indicating specialist strategies. While all evaluated indices function in a consistent way (i.e. higher values of ρ yield increased specificity), there are quantitative differences with respect to generalism (as discussed in the main text).

cannot be assessed. The actual degree of incomplete sampling cannot be known and is likely to differ between empirical webs. Second, the small set of empirical webs that could be assessed does not cover the full range of topologies found in nature, and consequently we increased the spectrum by employing numerically generated webs.

We used the procedure described by Blüthgen *et al.* (2008) to simulate bipartite networks, each containing 50 species and 40 resources. Preliminary studies showed our results to be insensitive to this choice; the 40×50 size of the networks is a compromise between sufficient resolution and computation time.

We employed connectance (i.e. the number of established links expressed as a proportion of the size of the network) to classify simulated and empirical networks on a continuum (see Discussion). Our simulated data set had 260 networks covering a larger range of connectance values than what is observed in nature. Note that the simulated networks we used have the same relationships between nestedness and connectance as the available empirical data.

Analysis

We conducted two analyses to evaluate the relative merits of the different specificity measures. First, we evaluated index robustness to missing data, using a method originally applied to extinctions in networks (Mommott, Waser & Price 2004). We randomly removed columns (resources) from the data set (100 replicates for each level of removal), with a minimum of five resources remaining after the removals. This procedure simulates a randomly sampled community, thus approximating unbiased field sampling. The specificity of each species in the resulting community is compared to its values in the original community, and the absolute error is calculated (averaged by the number of species). Higher absolute errors indicate that the measure is not robust to sampling errors.

Second, we investigated the informativity (ζ) of each measure, using the 'signal-to-noise' ratio. Let \mathbf{S} be a vector containing the specificities of all species in a network i , as measured using a given index (e.g. RR, PDI, or d'). This ratio is measured by dividing the mean of the specificity values for all the species in the network by their stan-

dard deviation ($\zeta_i = \mu_S / \sigma_S$). A high value indicates that the index is highly informative (i.e. will quantitatively contrast different interaction strength distributions). A low value indicates that even though the link strengths distributions of two species are different, specificity estimates are similar, which would make the index less useful as a measure of specificity. Note that ζ is defined for each measure and for each network. To allow a meaningful comparison of the informativities of the different indices over the whole range of networks, we employ a summary statistic ('total informativity', TI), defined as the sum of informativity levels multiplied by their densities. The latter was estimated using a Gaussian cluster on 500 points (Silverman 1986).

Results

ABILITY TO DIFFERENTIATE SPECIALISTS AND GENERALISTS

Figure 1 presents the values of the six specificity indices based on simulated distributions of link strengths. Qualitatively, as expected, all indices yield higher specificity as the trade-off in the distribution of link strengths becomes more accelerating. Quantitatively, the indices show two different behaviours. With the exception of PDI, all indices increase beyond 0 with increasing expected specialization, but only do so once the critical threshold of $\rho = 1$ (linear trade-off, i.e., neither specialist nor generalist) is reached. In contrast, PDI increases below this threshold and reaches a value of 0.5 at $\rho = 1$ (Fig. 1), meaning that the absolute value of PDI is the position on a specialist–generalist continuum.

ROBUSTNESS TO SAMPLING ERROR

Figure 2 presents the robustness of each of the indices to situations where resources are not completely sampled (on

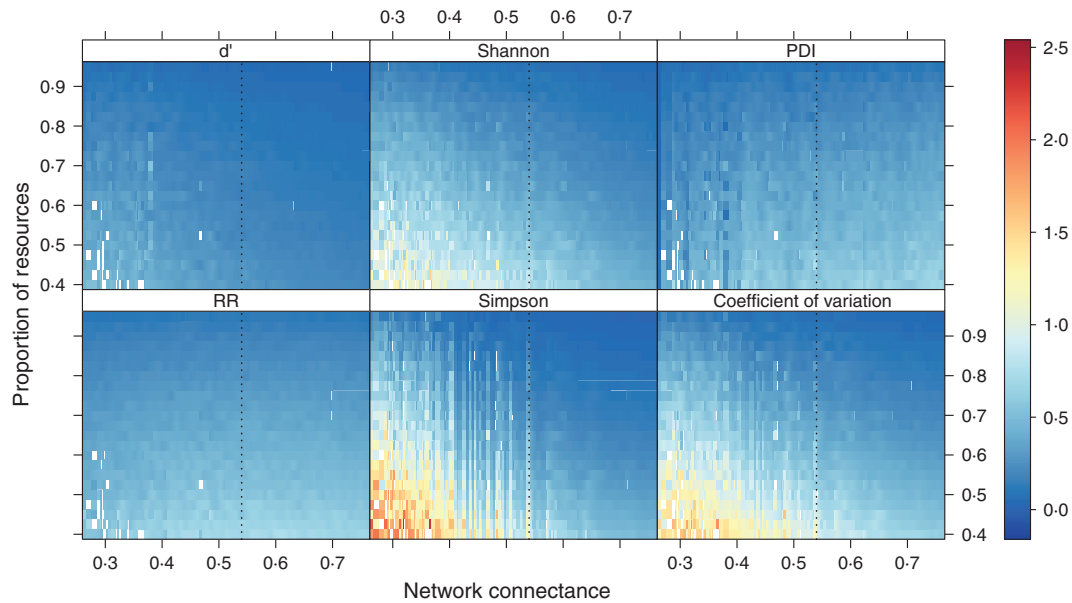


Fig. 2. Robustness to resource removal as a function of connectance. The y-axis is the proportion of resources sampled (closer to 1 means the network is complete). Intensity of the fill is the standard error of specificity, estimated for 100 replicates. White areas correspond to null interactions (i.e. removing too many interactions in a weakly connected network led to an empty matrix). Areas where blue is the prominent colour indicate that the index is robust to sampling limitations. The dashed line represents the higher connectance in the empirical data set.

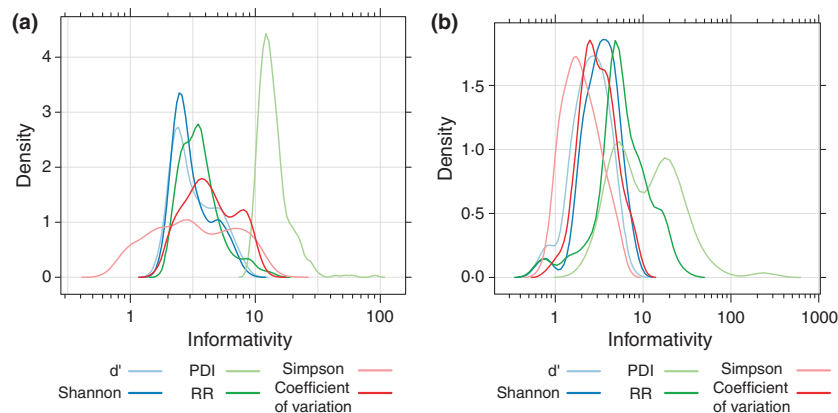


Fig. 3. Distribution of informativities (the signal-to-noise ratio – on a log scale) for simulated (caption a) and empirical (caption b) networks. Networks were considered together regardless of their connectances, as we found that connectance introduced only small quantitative differences. More informative indices have distributions shifted to the right. See Table 2 for a summary statistic of informativity.

Table 2. Total informativity (TI) of the six indices evaluated in this study. Higher values indicate higher TI. See main text for details

	Simulated webs	Empirical webs
RR	252.07	254.50
CoV	277.45	225.27
HS	255.30	268.22
PDI	501.95	253.96
d'	253.05	175.01
SDI	142.74	131.32

CoV, coefficient of variation; PDI, Paired Difference Index; RR, Resource range; SDI, species diversity index.

simulated webs). Robustness to missing resources differed particularly at low connectance values (Fig. 2). Two broad patterns emerged. SDI, CoV and HS are robust on highly

connected networks, but less robust to the range of connectance values observed in natural systems (left of the vertical line in Fig. 1). Conversely, d' , PDI and RR are robust over the whole range of connectance values examined, and maintain this property even though sampling is incomplete.

INFORMATIVITY

Figure 3 shows informativity levels of the six indices on the simulated (Fig. 3a) and empirical (Fig. 3b) data. TI calculations are presented in Table 2. High TI indicates the accurate tracking of small differences in species-interaction strength distributions. For the simulated networks (Fig. 3a), PDI is the most informative measure (TI = 502), and SDI is the least informative (TI = 142). All other indices are of similar total

informativity (TI = 255). A similar pattern is observed for the empirical networks (Fig. 3b), although differences in TI are reduced. Four of the six indices have similar total informativities (TI = 250–270) with HS having the highest value, and two indices being distinctively lower, with SDI (TI = 131) being the lowest.

Discussion

Characterizing specificity is challenging, because there are many possible quantitative descriptions, and a given index may not perform equally well based on different criteria. Yet, given the relevance of this concept to ecological and evolutionary processes (Devictor *et al.* 2010; Poisot *et al.* 2011a), it is important to evaluate a range of alternatives. In particular, the question of how specificity indices perform to incomplete sampling and observational error is essential if we are to integrate experimental or field data (which is often incomplete) with theoretical work and simulations (where all data are available). In addition, given the importance of specialization in evolutionary biology (Futuyma & Moreno 1988; Futuyma 2010), there is a need to assess how indices relate to classical estimators of the tendency for specialization, such as can be inferred from fitness sets and adaptive functions (Levins 1968; Frank 1993; Egas, Dieckmann & Sabelis 2004; Débarre & Gandon 2010).

We suggest that a general index of specificity should satisfy each of the following three criteria: (i) meaningful numerical values associated with the full range of possibilities, going from pronounced skew (i.e. specificity) to even distributions of link strengths (i.e. generality), (ii) robustness to under-sampling and (iii) informativity (i.e. strong signal-to-noise ratio). Whereas several studies have investigated robustness to sampling (Blüthgen, Menzel & Blüthgen 2006; Vázquez *et al.* 2007; Dormann *et al.* 2009), the other properties considered in the present study have been generally overlooked. Our results show that no single index performs best on all data sets and for all criteria considered. The different indices investigated yield contrasting values of specificity on an identical data set, because most of them are unable to differentiate true generalists (equal link strength on most of the resources) from marginally specialized organisms (a small fraction of relatively stronger links). Although our study focuses on bipartite species-interaction networks, our results are relevant to other types of ecological network, and more broadly to all domains in which the notion of specificity is relevant. This illustrates the need for careful application and interpretation of specificity indices, given that as discussed below, only a few of the indices emerged as choices for different scenarios.

We found that the six indices yielded different specificity distributions for the same reference network. This can be explained by the fact that these indices exhibit different behaviours on a continuum ranging from extreme generalism to extreme specialism (Fig. 1). With the notable exception of PDI, none of the indices were able to correctly distinguish generalism from very low degrees of specialism, which would be necessary for example to assess underlying cost structures

(Egas, Dieckmann & Sabelis 2004). As an illustration, using an expected specialization value of 50 (the leftmost line in Fig. 1a), for which we expect the index to indicate high specificity, most of the indices yielded relatively low values, while PDI yielded a value > 0.9 (i.e. high specificity, Fig. 1b). The fact that other measures only return information for very high values expected specialization ($p > 10$) could be an advantage, in that they can be employed to detect fine-scale variations in specificity among extremely specialized organisms. Accurate characterization of specificity is important because some authors work on ranks to circumvent the problem of interpreting absolute values (Devictor, Julliard & Jiguet 2008), and as such there is the risk of misinterpreting low specificity values as reflecting some level of generalism. An additional limitation of the rank-based approach is that it lumps specialists and generalists together and thus cannot inform on the underlying ecological and evolutionary processes that may favour the emergence of maintenance of specialists or generalists (Greenman & Hoyle 2008; Johnson, Malenke & Clayton 2009; Wiklund & Friberg 2009). Absolute values of PDI are straightforward to interpret, since any value below 0.5 indicates generalism, and any value above 0.5 indicates specialism. While all of the indices are able to quantify the degree of specialism (i.e. they return higher values with increased specialization), based on our analysis PDI yields more information on the degree of absolute generalism, and as such will be informative across a wider range of ecological scenarios.

We found that network structure (measured here as connectance) influenced the robustness of several specificity indices. Although it is unknown how the ecological effect of specialists and generalists may change in different network topologies, we believe that to assess this, it is important that we estimate specificity using indices consistent in their behaviour across a range of network structures. In this respect, we suggest that the use of RR and PDI allows the reliable estimation of specificity for different kinds of networks, because they display higher robustness over the range of connectances found in nature and are highly informative. Given that RR does not account for differences in link strength, it will best employed as a measure of interaction (basic) specificity, whereas PDI can be used as a measure of structural specificity (Poulin, Krasnov & Mouillot 2011). Note also that RR and PDI yield the same specificity estimates for binary data, meaning that these two measures could be used indiscriminately on this kind of information (and can easily be compared in meta-analyses).

As a final note, we stress that the indices presented here focus solely on the association matrix (and as such were evaluated in a ‘common garden’ situation in which all resources are at equal frequencies), and neglect any systematic bias in the interaction matrices. The two most common biases are phylogenetic relationships involving consumer species or resources, and variation in resource availability. Several studies have integrated phylogenetic information in specificity analyses (Poulin & Mouillot 2003, 2005), and recent theoretical developments suggest the importance of including phylogenetic information in explaining community structure (Cavender-Bares *et al.*

2009; Nieberding, Jousset & Desdevises 2010). In most cases, this is performed by correcting specificity values for non-independence because of evolutionary relatedness (Simková *et al.* 2006). Sufficiently species-rich data sets could be corrected for phylogenetic effects by partitioning variance (Desdevises *et al.* 2003), and methods exist to remove the impact of the relative frequencies of resources on the interaction data (Vázquez *et al.* 2007). For example, Julliard *et al.* (2006) proposed evaluating specificity at finer spatial resolutions, and to weigh specificity distributions using habitat frequencies. More recent advances suggest that information about both phylogenetic relatedness and relative resource abundance can be used to correct the observed interaction matrix (Nieberding, Jousset & Desdevises 2010). We cautiously suggest that our conclusions may hold even when data are corrected for the aforementioned biases, although we did not apply these corrections, we tested the indices over a wide range of link strength distributions. Correcting data for non-independence would affect the distribution of link strength, but not change the behaviour of the measure.

In conclusion, based on our evaluations, we encourage researchers to make use of RR to estimate the specificity of associations (i.e. Schoener's generality) and PDI to estimate the specificity of impacts (i.e. the skewness of the link strength distribution), with the possibility to use other measures to detect fine-scale variation in specificity among highly specialized species. Previous literature has established that quantitative information on link strength is not necessary for some problems (Briand 1983; Briand & Cohen 1987), and in these cases, PDI and RR are equivalent. We believe that these results will be of use beyond ecological and evolutionary scenarios involving populations and species. In recent years, quantifying specificity has proven to be important for the analysis of social networks (Onnela *et al.* 2007; Palla, Barabási & Vicsek 2007), gene expression in tissues (Liu *et al.* 2008), and residual interactions in proteins or protein/protein interactions (Csermely 2008; Palotai & Csermely 2009). We argue that our results will be broadly applicable to estimating specificity in these and other fields.

Acknowledgements

We thank J.D. Bever, S. Gandon, S. Kéfi and P.H. Thrall for discussions, C. Dormann, V. Devictor, S. Morand, D. Mouillot, and E. Thébaud for commenting on early versions of the manuscript, and two anonymous referees for helpful comments. Thanks are due to the contributors and curators of the NCEAS *InteractionWeb* data base. M.E.H. is funded by a grant from ANR 'EvolStress' (ANR-09-BLAN-099-01). N.M. is funded by a grant ANR-BACH-09-JCJC-0110-01. T.P. is funded by a CNRS – Région Languedoc-Roussillon doctoral grant. M.E.H., N.M. & T.P. are funded by ANR 'EvolRange' (ANR-09-PEXT-011). E.C. was supported by a MENRT grant from the French Ministry of Higher Education and Research.

References

Barnagaud, J.Y., Devictor, V., Jiguet, F. & Archaux, F. (2011) When species become generalists: on-going large-scale changes in bird habitat specialization. *Global Ecology and Biogeography*, **20**, 630–640.

Berlow, E.L., Navarrete, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, **80**, 2206–2224.

Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585–598.

Bever, J.D. (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist*, **157**, 465–473.

Blüthgen, N., Menzel, F. & Blüthgen, N. (2006) Measuring specialization in species interaction networks. *BMC Ecology*, **6**, 9–15.

Blüthgen, N., Fründ, J., Vázquez, D.P. & Menzel, F. (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology*, **89**, 3387–3399.

Bolnick, D.I. (2002) Measuring individual-level resource specialization. *Ecology*, **83**, 2936–2941.

Briand, F. (1983) Environmental control of food web structure. *Ecology*, **64**, 253–263.

Briand, F. & Cohen, J.E. (1987) Environmental correlates of food chain length. *Science*, **238**, 956–960.

Bushberg, J.T., Seibert, J.A., Leidholdt Jr, E.M. & Boone, J.M. (2003) *The Essential Physics of Medical Imaging*. Lippincott Williams & Wilkins, Philadelphia.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Clavel, J., Julliard, R. & Devictor, V. (2010) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*, **eView**, 100603064122016.

Colles, A., Liow, L.H. & Prinzing, A. (2009) Are specialists at risk under environmental change? Neoeological, paleoecological and phylogenetic approaches. *Ecology Letters*, **12**, 849–863.

Csermely, P. (2008) Creative elements: network-based predictions of active centres in proteins and cellular and social networks. *Trends in Biochemical Sciences*, **33**, 569–576.

Débarre, F. & Gandon, S. (2010) Evolution of specialization in a spatially continuous environment. *Journal of Evolutionary Biology*, **23**, 1090–1099.

Desdevises, Y., Legendre, P., Azouzi, L. & Morand, S. (2003) Quantifying phylogenetically structured environmental variation. *Evolution*, **57**, 2647–2652.

Devictor, V., Julliard, R. & Jiguet, F. (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117**, 507–514.

Devictor, V., Clavel, J., Julliard, R., Laverne, S., Mouillot, D., Thuiller, W., Vénail, P., Villéger, S. & Mouquet, N. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology*, **47**, 15–25.

Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, **1**, 1–20.

Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, **2**, 7–24.

Egas, M., Dieckmann, U. & Sabelis, M.W. (2004) Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. *The American Naturalist*, **163**, 518–531.

Frank, S.A. (1993) Evolution of host-parasite diversity. *Evolution*, **47**, 1721–1732.

Frank, S.A. (1994) Coevolutionary genetics of hosts and parasites with quantitative inheritance. *Evolutionary Ecology*, **8**, 74–94.

Futuyma, D.J. (2010) Evolutionary constraint and ecological consequences. *Evolution*, **64**, 1865–1884.

Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.

Greenman, J.V. & Hoyle, A.S. (2008) Exclusion of generalist pathogens in multi-host communities. *The American Naturalist*, **172**, 576–584.

Hudson, P.J., Dobson, A.P. & Lafferty, K.D. (2006) Is a healthy ecosystem one that is rich in parasites? *Trends in Ecology & Evolution*, **21**, 381–385.

Johnson, K.P., Malenke, J.R. & Clayton, D.H. (2009) Competition promotes the evolution of host generalists in obligate parasites. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3921–3926.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D. (2006) Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, **9**, 1237–1244.

Kaci-Chaouch, T., Verneau, O. & Desdevises, Y. (2008) Host specificity is linked to intraspecific variability in the genus *Lamellodiscus* (Monogenea). *Parasitology*, **135**, 607–616.

Kassen, R. (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology*, **15**, 173–190.

- Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R. & Thielges, D.W. (2008) Parasites in food webs: the ultimate missing links. *Ecology Letters*, **11**, 533–546.
- Levins, R. (1962) Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *The American Naturalist*, **96**, 361–373.
- Levins, R. (1968) *Evolution in Changing Environments. Some Theoretical Explorations*. Princeton University, New Jersey.
- Liu, X., Yu, X., Zack, D.J., Zhu, H. & Qian, J. (2008) TiGER: a database for tissue-specific gene expression and regulation. *BMC Bioinformatics*, **9**, 271.
- Matich, P., Heithaus, M.R. & Layman, C.A. (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal of Animal Ecology*, **80**, 294–305.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.
- Memmott, J., Waser, N.M. & Price, M.V. (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 2605–2611.
- Nieberding, C., Jouselin, E. & Desdevises, Y. (2010) The use of co-phylogeographic patterns to predict the nature of host-parasite interactions, and vice versa. *Biogeography of Host-Parasite Interactions* (eds S. Morand & B. Krasnov), pp. 59–69. Oxford University Press, Oxford.
- Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841–844.
- Onnela, J.-P., Saramäki, J., Hyvönen, J., Szabó, G., Lazer, D., Kaski, K., Kertész, J. & Barabási, A.-L. (2007) Structure and tie strengths in mobile communication networks. *Proceedings of the National Academy of Sciences*, **104**, 7332–7336.
- Palla, G., Barabási, A.-L. & Vicsek, T. (2007) Quantifying social group evolution. *Nature*, **446**, 664–667.
- Palotai, R. & Csérmely, P. (2009) Network modules help the identification of key transport routes, signaling pathways in cellular and other networks. *Annalen der Physik*, **18**, 822–829.
- Poisot, T., Thrall, P.H. & Hochberg, M.E. (2012) Trophic network structure emerges through antagonistic coevolution in temporally varying environments. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 299–308.
- Poisot, T., Bever, J.D., Nemri, A., Thrall, P.H. & Hochberg, M.E. (2011a) A conceptual framework for the evolution of ecological specialisation. *Ecology Letters*, **14**, 841–851.
- Poisot, T., Lepennetier, G., Martinez, E., Ramsayer, J. & Hochberg, M.E. (2011b) Resource availability affects the structure of a natural bacteria-bacteriophage community. *Biology Letters*, **7**, 201–204.
- Poulin, R. (2007) Are there general laws in parasite ecology? *Parasitology*, **134**, 763–776.
- Poulin, R., Krasnov, B.R. & Mouillot, D. (2011) Host specificity in phylogenetic and geographic space. *Trends in Parasitology*, **27**, 355–361.
- Poulin, R. & Mouillot, D. (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology*, **126**, 473–480.
- Poulin, R. & Mouillot, D. (2005) Combining phylogenetic and ecological information into a new index of host specificity. *The Journal of Parasitology*, **91**, 511–514.
- Schoener, T.W. (1989) Food webs from the small to the large. *Ecology*, **70**, 1559–1589.
- Schug, J., Schuller, W.P., Kappen, C., Salbaum, J.M., Bucan, M. & Stoeckert, C. (2005) Promoter features related to tissue specificity as measured by Shannon entropy. *Genome Biology*, **6**, R33.
- Silverman, B.W. (1986) *Density Estimation*. Chapman and Hall, London.
- Simková, A., Verneau, O., Gelnar, M. & Morand, S. (2006) Specificity and specialization of congeneric monogeneans parasitizing cyprinid fish. *Evolution*, **60**, 1023–1037.
- Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.
- Singer, M.C., Carriere, Y., Theuring, C. & Hartmann, T. (2004) Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. *The American Naturalist*, **164**, 423–429.
- Tylianakis, J.M., Tschamntke, T. & Lewis, O.T. (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*, **445**, 202–205.
- Vale, P.F., Salvaudon, L., Kaltz, O. & Fellous, S. (2008) The role of the environment in the evolutionary ecology of host parasite interactions. *Infection, Genetics & Evolution*, **8**, 302–305.
- Van Nouhuys, S., Singer, M.C. & Nieminen, M. (2003) Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. *Ecological Entomology*, **28**, 193–202.
- Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, **116**, 1120–1127.
- Wehling, W.F. & Thompson, J.N. (1997) Evolutionary conservatism of oviposition preference in a widespread polyphagous insect herbivore, *Papilio zelicaon*. *Oecologia*, **111**, 209–215.
- Wiklund, C. & Friberg, M. (2009) The evolutionary ecology of generalization: among-year variation in host plant use and offspring survival in a butterfly. *Ecology*, **90**, 3406–3417.
- Wilson, H.B. & Hassell, M.P. (1997) Host-parasitoid spatial models: the interplay of demographic stochasticity and dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 1189–1195.
- Woolhouse, M.E. & Gowtage-Sequeria, S. (2005) Host range and emerging and reemerging pathogens. *Emerging Infectious Diseases*, **11**, 1842–1847.

Received 24 August 2011; accepted 30 October 2011

Handling Editor: Robert Freckleton

Glossary

Link strength	Interaction intensity established between two species. Link strength can be, for example, a measure of performance, frequency of encounter or impact or fitness consequences of the interaction, depending on which methodology applies to the system under consideration
Consumer & resource	Denote, respectively, the focal organism for which the interaction range is being assessed (e.g. a predator species) and the set of organisms with which the focal organism interacts (e.g. prey species)
Specialization	Adaptive and ecological process leading an organism to become more markedly adapted to a subset of its possible resources, leading to an increase in the link strengths with these resources
Specificity	The state of an organism defining a restricted number of interactions, or the skew in link strengths or performances over a subset of interactions
Specificity of associations vs. of impacts	Specificity of association is inferred by counting the number of links established by a consumer with different resources (corresponding to the ‘generality’ <i>sensu</i> Schoener 1989), and specificity of impacts accounts for the link strength of each of the established interactions
Generalist	Consumer having similar link strengths over most of its possible resources
Specialist	Consumer having stronger link strengths in association with a limited subset of its possible resources. The strengths of a specialist’s links decrease as it moves away from its optimal resource