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RESEARCH ARTICLE

A new index to estimate ecological generalisation in consumer-resource interactions

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Abstract

1. Generalisation and specialisation in species-species interactions are key ecological concepts for interpreting the different interaction patterns observed in nature. Hence, finding the best way to operationalise them has been a major quest in Ecology. This quest has led to considerable conceptual development, and now the observed interaction pattern of a species is assumed to be a combination of three factors: its degree of generalisation, abundance-driven neutral effects, and sampling effects. Here, we aimed to assess the influence of these factors on the performance of previously proposed indices of generalisation.
2. To do so, we used simulated data that allowed us to separate and analyse independently the influence of each factor.
3. Our assessment shows that the estimates made by most traditional indices are affected by differences in resource abundance distribution, leading to over- or underestimation of how generalised a consumer is. To solve this problem, we propose a new index that remains unaffected by neutral effects and is robust to sampling effects.
4. Our new index may help to understand what interacting species require to keep viable populations and how they might respond to changes in resource availability.

KEYWORDS
generalisation, neutral effects, niche breadth, resource use, sampling effects, specialisation

1 | INTRODUCTION

Generalisation and specialisation are key ecological processes (Darwin, 1859, 1862). The former results in an organism interacting with (i.e. using) a broad range of potential resources, while the latter involves an organism becoming highly adapted to, and increasing the use of, a restricted subset of resources (Poisot et al., 2012). Despite food being the most common example of resources, they can also include breeding habitats and nesting sites (Devictor et al., 2010). Consequently, organisms exist within a generalisation-specialisation continuum for each resource dimension (Poisot et al., 2012). Over recent decades, ecologists have sought an optimal estimator for the degree of generalisation or an organism's position within this continuum (Pierotti et al., 2017).

Early indices for this purpose were adapted from indices developed for other applications (e.g. Shannon, 1948; Simpson, 1949). Hence, the degree of generalisation of a consumer species used to be quantified as the diversity or evenness of its interaction distribution (Levins, 1968). However, this operationalisation assumed an even resource abundance distribution, which is unlikely in nature (Schoener, 1974). Consequently, a consumer could be misclassified as a specialist when it was actually a generalist interacting with unevenly abundant resources. Therefore, such indices provided estimations that merged the consumer's “true” degree of generalisation and abundance-driven neutral effects (Devictor et al., 2010), since those effects are independent from actual specialisation (Feinsinger et al., 1981).

To disentangle degree of generalisation from neutral effects, indices were introduced to account for resource abundances (e.g. Hurlbert, 1978; Petraitis, 1979; Smith, 1982). These indices quantify the degree of generalisation by comparing a consumer's interaction distribution to the resource abundance distribution, a principle adopted by most contemporary indices (Pierotti et al., 2017). Further developments revealed that estimating the degree of generalisation was also significantly influenced by sampling effects (Fründ et al., 2016). For instance, insufficient sampling intensity could lead to inaccurate estimations, and different methods could yield asymmetrical sampling, heavily favouring some interactions over the others. Thus, an organism's observed interaction pattern is shaped by its degree of generalisation, neutral effects, and sampling effects.

The ecological literature abounds with generalisation indices (Devictor et al., 2010). Each index has its strengths and limitations (Fründ et al., 2016; Poisot et al., 2012), offering various strategies to address the aforementioned confounding factors (e.g. Pierotti et al., 2017; Vázquez & Simberloff, 2002). Here, we investigate how neutral and sampling effects (in particular sampling intensity) impact the performance of generalisation indices. We aimed to answer three key questions: (1) What do different generalisation indices measure? (2) How accurate are their estimations under the influence of neutral effects? And (3) how accurate are their estimations under variations in sampling intensity? This exploration led us to propose a novel index of generalisation that remains unaffected by neutral effects and is robust to sampling effects.

2 | MATERIALS AND METHODS

Henceforth “consumers” are the organisms or groups of organisms for which we measure their degree of generalisation, “resources” are the nutrients, habitats, organisms or groups of organisms used by the consumers, “to interact with” is the action of a consumer to use a resource, “interactions” is the number of recorded events of a consumer using a resource (equivalent to link weight in a network), and the sum of all interactions made by a consumer with all potential resources is its “sampling intensity”. Nevertheless, we understand that not all interactions between organisms represent consumer-resource relationships, but this generalisation helps unveil the main drivers of specialisation in a multitude of systems by focusing on what they have in common with one another (Pinheiro et al., 2019). We restrict ourselves to one-dimensional resources, as each consumer may be a generalist in one dimension (e.g. habitats), but a specialist in another (e.g. food). Here, we avoid using the word “niche” as it represents a more complex concept that encompasses resource use and other life-history traits (McInerny & Etienne, 2012).

2.1 | Indices of generalisation

In the quest for efficient ways to operationalise the concept of generalisation, several indices have been proposed under the name of “niche breadth”, “niche width”, “generalisation”, “specialisation”, “generalism”, “generality” or “specificity”. Despite other indices being available, we considered in our assessment only those that include in their formulae information about resource abundance distribution (Hurlbert, 1978). As a result, we compiled a list of eight published indices (Table 1).

For a given set of R resources, these indices estimate the degree of generalisation of a consumer by quantifying the similarity between the interaction distribution ($\mathbf{p}$), given by the proportion of interactions $\mathbf{p} = [p_1, p_2, \ldots, p_{R-1}, p_R]$ so that $\sum_{i=1}^{R} p_i = 1$, and the resource abundance distribution ($\mathbf{q}$), given by the relative abundance of resources $\mathbf{q} = [q_1, q_2, \ldots, q_{R-1}, q_R]$ so that $\sum_{i=1}^{R} q_i = 1$. The proportion of interactions can be estimated either from continuous (e.g. time on a flower, volume of consumed nectar, or occupied area) or discrete data (e.g. number of visits, consumption events, or parasites on a host). Furthermore, the relative abundance of resources can also be estimated either from continuous (e.g. plant cover, biomass, or nectar content) or discrete data (e.g. number of available flowers, fruits, prey, or nesting sites).

The values of these indices reach their maximum when the interaction distribution exactly follows the resource abundance distribution (i.e. $p_i = q_i$; for each resource i from 1 to R). With the exception of the compositional niche breadth index Wc (Pierotti et al., 2017), these indices reach their minimum values when the consumer interacts exclusively with the least abundant resource (i.e. $p_z = 1$; where z is the least abundant resource). Wc reaches its minimum when the

TABLE 1 Generalisation indices that account for resource abundances. These indices estimate how generalised a consumer is by comparing proportion of interactions of that consumer with each resource i, that is p_i (so that $\sum_{i=1}^{R} p_i = 1$), with the relative abundance of each resource i, that is q_i (so that $\sum_{i=1}^{R} q_i = 1$), for a set of R potential resources. $\mathbf{q}$ is the resource abundance distribution, containing the values of the relative abundance of resources: $\mathbf{q} = [q_1, q_2, \dots, q_{R-1}, q_R]$. $d_{\min}$ is the minimum theoretical value of d for the given number of recorded interactions and the resource abundance distribution, which is calculated using an algorithm that is available in the *bipartite* package for R (Dormann et al., 2008), and it is similar to the first algorithm introduced in Appendix S3. n is the sampling intensity. Normalised expressions (used to transform values into the range [0, 1]) were obtained from Blüthgen et al. (2006) and Pierotti et al. (2017), except for *Bs*, *FT* and *gen*, for which we provide details in Appendix S1.

Reference	Name	Formula	Normalised expression
Schoener (1974)	Weighted reciprocal Simpson index	$Bs = \frac{1}{\sum_{i=1}^{R}\left(\frac{p_i}{q_i}\right)^2}$	$Bs' = \frac{Bs - \min(\mathbf{q})^2}{\frac{1}{R} - \min(\mathbf{q})^2}$
Hurlbert (1978)	Weighted reciprocal Simpson index	$B' = \frac{1}{\sum_{i=1}^{R}\frac{p_i^2}{q_i}}$	$B'' = \frac{B' - \min(\mathbf{q})}{1 - \min(\mathbf{q})}$
Petraitis (1979)	Likelihood measure of niche breadth	$\ln(W) = -\sum_{i=1}^{R} p_i \ln\left(\frac{p_i}{q_i}\right)$	$W' = \frac{W - \min(\mathbf{q})}{1 - \min(\mathbf{q})}$
Feinsinger et al. (1981)	Proportional similarity index	$PS = 1 - \frac{1}{2}\sum_{i=1}^{R} \lvert p_i - q_i \rvert$	$PS' = \frac{PS - \min(\mathbf{q})}{1 - \min(\mathbf{q})}$
Smith (1982)	Matusita measure	$FT = \sum_{i=1}^{R}\sqrt{p_i \times q_i}$	$FT' = \frac{FT - \sqrt{\min(\mathbf{q})}}{1 - \sqrt{\min(\mathbf{q})}}$
Blüthgen et al. (2006)	Normalised Kullback–Leibler divergence	$d = \sum_{i=1}^{R} p_i \ln\left(\frac{p_i}{q_i}\right)$	$d' = \frac{d - d_{\min}}{\ln(1/\min(\mathbf{q})) - d_{\min}}$
Fort et al. (2016)	Generalisation index	$gen = 1 - \frac{d}{\ln(n)}$	$gen' = \frac{(gen - 1)\ln(n) + \ln\left(\frac{1}{\min(\mathbf{q})}\right)}{\ln\left(\frac{1}{\min(\mathbf{q})}\right)}$
Pierotti et al. (2017)	Compositional niche breadth index	$Wc = \frac{1}{\sum_{i=1}^{R}\left(\ln\left(\frac{p_i}{q_i}\right) - \ln\left(\frac{\sqrt[R]{\prod_{i=1}^{R} p_i}}{\sqrt[R]{\prod_{i=1}^{R} q_i}}\right)\right)^2}$	$Wc' = e^{\frac{-1}{Wc}}$

consumer interacts exclusively with a single resource, regardless of its abundance.

We normalised the values of the indices, to [0, 1] (or to (0, 1] for *Wc*), to make them easier to compare within our assessment. Since the normalised Kullback–Leibler divergence (d') is intended to measure degree of specialisation (Blüthgen et al., 2006), results are presented as $1 - d'$. Additionally, the compositional niche breadth index (*Wc*) cannot handle 0s, requiring Bayesian-multiplicative replacement of count zeros (Martín-Fernández et al., 2015). To do so, it uses matrices with multiple consumers and resources, making its calculation impossible to be used for some data structures.

2.2 | A new index of generalisation: Alpha paired difference index (αPDI)

An additional index of generalisation is the paired difference index (PDI) (Poisot et al., 2012). It characterises the decay in preference as a consumer interacts with resources increasingly different to its most preferred resource (Poisot et al., 2011; Poisot et al., 2012). However, it was excluded from Table 1 as it does not account for resource abundances. Compared to similar indices, PDI stands out because it has some desirable properties (as assessed by Poisot et al., 2012): (1) it can use weighted interaction data, (2) it does not assume that the data follow a specific statistical distribution and (3) it estimates the position of consumers within the generalisation-specialisation continuum, with 0.5 as midpoint. The PDI of a consumer is calculated as follows:

$$\mathrm{PDI} = \frac{\sum_{i=2}^{R}\left(\frac{p_1}{p_1} - \frac{p_i}{p_1}\right)}{R-1} = \frac{\sum_{i=2}^{R}\left(1 - \frac{p_i}{p_1}\right)}{R-1} = \frac{\sum_{i=1}^{R}\left(1 - \frac{p_i}{\max(\mathbf{p})}\right)}{R-1}, \tag{1}$$

where, for a set of R potential resources, p_i is the proportion of interactions of the consumer with resource i (so that $\sum_{i=1}^{R} p_i = 1$), p_1 is the highest proportion of interactions among all resources, and $\mathbf{p}$ is the vector containing the proportion of interactions ($\mathbf{p} = [p_1, p_2, \dots, p_{R-1}, p_R]$). Note that Equation (1) slightly differs from the original equation for PDI proposed by Poisot et al. (2012). This happens because for PDI to produce values between 0.0 and 1.0 and to have 0.5 as a midpoint, the proportions of interactions (p_i) must be divided by their maximum (p_1) (Poisot et al., 2012). Thus, a value of $PDI = 1.0$ means that the organism is a consumer specialised in a single resource, while PDI = 0.0 indicates that it is interacting evenly with all resources.

Here, we propose a modification to control for neutral effects by using the selection ratio α (Manly, 1974). This selection ratio estimates the probability that a consumer would use resource i if the resource abundance distribution were even (Manly et al., 2002),

$$\alpha_i = \frac{p_i}{q_i \sum_{j=1}^{R}\frac{p_j}{q_j}}, \tag{2}$$

where p_i and p_j are respectively the proportion of interactions with resource i and j. q_i and q_j are respectively the relative abundance of resource i and j. This selection ratio, in a few words, provides new proportions of interactions (α_i), which are corrected by the relative abundance of resources (q_i). Thus, α_i can be incorporated into Equation (1) by replacing the uncorrected proportions of interactions

(p_i) to obtain a version of PDI that accounts for resource abundance distribution:

$$\text{wPDI} = \frac{\sum_{i=1}^{R}\left(1 - \frac{\alpha_i}{\max(\boldsymbol{\alpha})}\right)}{R-1} = \frac{\sum_{i=1}^{R}\left(1 - \frac{\frac{p_i}{q_i \sum_{j=1}^{R} \frac{p_j}{q_j}}}{\frac{\max\limits_{1 \le j \le R}\left(\frac{p_j}{q_j}\right)}{\sum_{j=1}^{R} \frac{p_j}{q_j}}}\right)}{R-1} = \frac{\sum_{i=1}^{R}\left(1 - \frac{p_i}{q_i \max\limits_{1 \le j \le R}\left(\frac{p_j}{q_j}\right)}\right)}{R-1}, \quad (3)$$

where $\boldsymbol{\alpha}$ is the vector containing the corrected proportions of interactions $\boldsymbol{\alpha} = \left[\alpha_1, \alpha_2, \ldots, \alpha_{R-1}, \alpha_R\right]$. If there is an even resource abundance distribution, then wPDI = PDI.

Finally, considering that PDI aims at measuring degree of specialisation, we can obtain an index of generalisation by subtracting wPDI from 1. Thus, we define the generalisation index αPDI as:

$$\alpha\text{PDI} = 1 - \text{wPDI} = 1 - \frac{\sum_{i=1}^{R}\left(1 - \frac{p_i}{q_i \max\limits_{1 \le j \le R}\left(\frac{p_j}{q_j}\right)}\right)}{R-1}. \quad (4)$$

The values of αPDI vary from 0.0 to 1.0. Unlike other indices, αPDI is symmetric with respect to its midpoint (Appendix S2), which means that values higher than 0.5 suggest generalisation, and values lower than 0.5 suggest specialisation. Therefore, a value of $\alpha\text{PDI} = 0.0$ means that the consumer is interacting exclusively with a single resource, while $\alpha\text{PDI} = 1.0$ means that the probability of that consumer to interact with all resources is fully explained by the resource abundance distribution. As for the previously mentioned indices, αPDI accepts the proportion of interactions and the relative abundance of resources to be calculated from either continuous or discrete data.

To control for sampling effects, the values of $\alpha\text{PDI}'$ can be corrected using a normalisation approach based on the total number of recorded interactions (Blüthgen et al., 2006; Dormann et al., 2008). Then, we define $\alpha\text{PDI}'$ as follows:

$$\alpha\text{PDI}' = \frac{\alpha\text{PDI} - \alpha\text{PDI}_{\text{min}}}{\alpha\text{PDI}_{\text{max}} - \alpha\text{PDI}_{\text{min}}}, \quad (5)$$

where $\alpha\text{PDI}_{\text{min}}$ and $\alpha\text{PDI}_{\text{max}}$ are the minimum and maximum possible theoretical values of αPDI for the given sampling intensity and the resource abundance distribution. Independently of the sampling intensity, the minimum possible value of $\alpha\text{PDI}'$ is the one obtained by a consumer interacting exclusively with a single resource, so that $\max(\mathbf{p}) = 1$. Therefore, in a hypothetical case of $R = 3$ potential resources the interaction distribution would be $\mathbf{p} = \left[1, 0, 0\right]$. Consequently, regardless of the resource abundance distribution, the minimum possible value of αPDI would be

$$\begin{aligned}\alpha\text{PDI}_{\text{min}} &= 1 - \frac{\sum_{i=1}^{3}\left(1 - \frac{p_i}{q_i \max\limits_{1 \le j \le 3}\left(\frac{p_j}{q_j}\right)}\right)}{R-1} \\ &= 1 - \frac{\left(1 - \frac{1}{q_1 \frac{1}{q_1}}\right) + \left(1 - \frac{0}{q_2 \frac{1}{q_1}}\right) + \left(1 - \frac{0}{q_3 \frac{1}{q_1}}\right)}{3-1} \\ &= 1 - \frac{2}{2} = 0.0.\end{aligned} \quad (6)$$

Since for any $R > 1$ the value of $\alpha\text{PDI}_{\text{min}}$ is always 0.0, $\alpha\text{PDI}'$ becomes

$$\alpha\text{PDI}' = \frac{\alpha\text{PDI}}{\alpha\text{PDI}_{\text{max}}}. \quad (7)$$

The value of $\alpha\text{PDI}_{\text{max}}$ is obtained using two algorithms that generate a theoretical interaction distribution (**px**) to find the maximum possible value of αPDI. For a given sampling intensity (n, where $n \in \mathbb{N}$), the first algorithm distributes the n interactions among potential resources by multiplying them by the elements of the vector representing the resource abundance distribution: $\mathbf{px} = \left[px_1, px_2, \ldots, px_{R-1}, px_R\right] = \left[(n)q_1, (n)q_2, \ldots, (n)q_{R-1}, (n)q_R\right]$. If any of the elements of **px** are not integers, the values are rounded down to the nearest integer. Rounding down these values will result in remaining interactions that come from the difference between the sampling intensity (n) and the sum of the elements of **px**. To reach the desired sampling intensity, that is $\sum_{i=1}^{R} px_i = n$, the algorithm performs a distribution process, where these remaining interactions are distributed one by one among the elements of **px**. Thus, a remaining interaction is first added to the first element of **px**, and αPDI is calculated. Then, this remaining interaction is added to the next element (instead of the previous element) to see if adding the interaction to that element increases the value of αPDI, compared to the previous. This process continues until the remaining interaction is added to px_R, and the algorithm chooses the distribution that maximises the value of αPDI. Next, it uses this chosen distribution as a new **px** to distribute one by one the remaining interactions, by repeating the process above. When all remaining interactions are distributed, the maximum calculated value of αPDI is selected as $\alpha\text{PDI}_{\text{max}}$ (Appendix S3).

The second algorithm is a modification of the first, which adds an initial step. In this step, all resources are assigned an interaction that is subtracted from n, so that all resources have at least one interaction: $\mathbf{px} = \left[1 + (n-R)q_1, 1 + (n-R)q_2, \ldots, 1 + (n-R)q_{R-1}, 1 + (n-R)q_R\right]$. Then, it follows the same procedure of the first algorithm (Appendix S3). Finally, the values obtained by both algorithms are compared and the highest value is chosen as $\alpha\text{PDI}_{\text{max}}$. This process of controlling for the total number of recorded interactions acknowledges sampling limitations and helps avoiding misinterpretations explained alone by the variation in sampling intensity (Blüthgen, 2010). Since the calculation of $\alpha\text{PDI}_{\text{max}}$ is based on integers, $\alpha\text{PDI}'$ only accepts discrete data to calculate the proportion of interactions. However, the relative abundance of resources can still be calculated from discrete or continuous data.

2.3 | Assessing the performance of the generalisation indices

2.3.1 | The quantitative niche model

To assess the performance of the nine generalisation indices considered in this study, we utilised the "quantitative niche model" proposed by Fründ et al. (2016) to generate theoretical consumer-resource

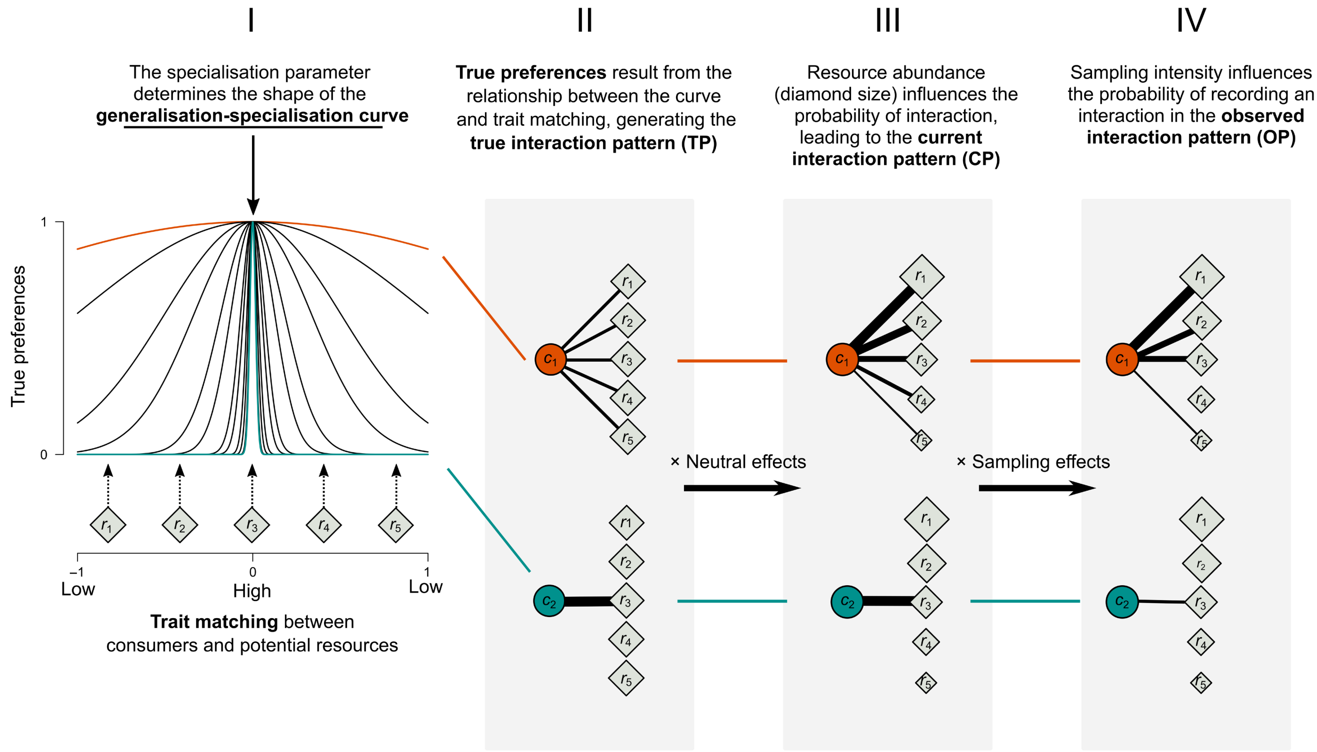

FIGURE 1 The quantitative niche model. For a given consumer (*c*) and a set of *R* potential resources (r_1 to r_R), the observed interaction pattern is a combination of three factors: true preferences, neutral effects, and sampling effects. (I) True preferences result from the relationship between the consumer's generalisation-specialisation curve and its trait matching with resources. (II) From these true preferences, the true interaction pattern is generated. (III) Neutral effects influence the probability of interaction between a consumer and resources, modifying the interaction pattern expected from their true preferences, and creating the current interaction pattern. (IV) Sampling effects (sampling intensity) influence what we observe from the current interaction pattern. Lines between consumers and resources represent interactions and line width is proportional to its weight (e.g. use frequency). Diamond size is proportional to resource abundance. This figure was inspired by Figure 1 from Fründ et al. (2016).

interactions. This model generates interaction patterns for consumers based on their "true preference" for a set of potential resources (Figure 1). The true preference of a consumer for a resource *i* (TP_i) is determined by its specialisation parameter (*s*) and the pairwise difference of trait values between the consumer and the resource, that is trait matching (t_i), representing a normal distribution:

$$TP_i = e^{\frac{-t_i^2(s^2)}{2}}. \tag{8}$$

The generalisation-specialisation curve (Figure 1I) is described by the true preferences, and its narrowness depends on the specialisation parameter (*s*). A consumer with a low specialisation parameter will interact with all resources evenly, regardless of trait matching. Conversely, a consumer with a high value of the specialisation parameter will preferentially interact with resources that match its traits. From these true preferences, the "true interaction pattern" is generated (Figure 1II): $\mathbf{TP} = \left[\frac{TP_1}{\sum_{i=1}^{R} TP_i}, \frac{TP_2}{\sum_{i=1}^{R} TP_i}, \ldots, \frac{TP_{R-1}}{\sum_{i=1}^{R} TP_i}, \frac{TP_R}{\sum_{i=1}^{R} TP_i}\right]$.

To include neutral effects, the model multiplies the elements of the true interaction pattern by the resource abundance distribution $\mathbf{q} = [q_1, q_2, \ldots, q_{R-1}, q_R]$, creating the "current interaction pattern" (Figure 1III): $\mathbf{CP} = \left[\frac{TP_1(q_1)}{\sum_{i=1}^{R} TP_i(q_i)}, \frac{TP_2(q_2)}{\sum_{i=1}^{R} TP_i(q_i)}, \ldots, \frac{TP_{R-1}(q_{R-1})}{\sum_{i=1}^{R} TP_i(q_i)}, \frac{TP_R(q_R)}{\sum_{i=1}^{R} TP_i(q_i)}\right]$. For any given set of *R* resources, the quantitative niche model generates its abundance distribution from the quantile function of a log-normal distribution. Hence, for a set of *R* resources the model uses the $\frac{r}{R+1}$ quantile as the abundance for each resource *r* in 1 to *R* (Appendix S4).

Finally, to simulate sampling effects, the model mimics the process of sampling discrete interactions (e.g. flower visits) to a given sampling intensity (*n*). This sampling process is done through a multinomial sampling where the probability of sampling an interaction with resource *i* depends on the current interaction pattern (**CP**). The result is a theoretical "observed interaction pattern" (Figure 1IV): $\mathbf{OP} = [OP_1, OP_2, \ldots, OP_{R-1}, OP_R]$, where $\sum_{i=1}^{R} OP_i = n$. The quantitative niche model does not contemplate other possible sampling effects besides sampling intensity, such as the influence of spatial aggregation of resources, how interaction detectability varies with sampling methods (Bartomeus, 2013), or resource availability through time (CaraDonna et al., 2021).

In summary, the stepwise simulation process generates true (**TP**), current (**CP**), and observed (**OP**) interaction patterns (Appendix S4), allowing us to isolate true preferences from neutral effects and sampling effects (Fründ et al., 2016).

2.3.2 | Generating theoretical consumer-resource interactions

Using the quantitative niche model, we generated datasets of theoretical consumer-resource interactions with $R = 5$, 15 and 55 potential resources, and 2000 hypothetical consumers per number of potential resources (i.e. 3), totalling 6000 consumers. For each value of R, consumers were assigned different specialisation parameters (s) from 0.1 to 60.0 in a logarithmic spaced sequence. For each combination of consumers and resources, trait matching values were assigned from an evenly spaced sequence of R elements from −1.0 to 1.0, where 0.0 represents a perfect match. With these parameters (Table 2), we generated the set of true interaction patterns (**TP**), where consumers varied from interacting exclusively with a single resource to interacting with all potential resources.

Next, we introduced neutral effects by generating current interaction patterns (**CP**) by using resource abundance distributions generated from a log-normal distribution of mean ln(10) and standard deviation of 1.5. Then, each current interaction pattern was sampled to four levels of sampling intensity (n): 10, 50, 100, 500 interactions. Thus, an observed interaction pattern (**OP**) was generated per number of potential resources (3), per consumer (2000), and per level of sampling intensity (4), for a total of 24,000 vectors. In summary, we generated 6000 true, 6000 current, and 24,000 observed interaction patterns (Table 2).

To analyse the performance of Wc', given its logistical limitation, the different interaction patterns we generated were embedded into matrices of four new consumers. These matrices were also generated using the quantitative niche model, maintaining all the parameters from the original simulation, except for the specialisation parameter, which, for each new consumer, was a random number from 2000 possible values of a logarithmic spaced sequence from 0.1 to 60.0. The results were, for each of the generated interaction pattern, a 5-by-R matrix. These matrices were used exclusively for calculations regarding the Wc' index.

2.3.3 | What do different generalisation indices measure?

All indices considered in our study intend to quantify the degree of generalisation of a consumer. On the one hand, as the generalisation-specialisation curve becomes broader (Figure 1l), we expect the values of these indices to increase. On the other hand, as the curve becomes narrower, the values should decrease. Therefore, our first assessment consisted in analysing how the degree of generalisation calculated with every index varied along with variations in the specialisation parameter. To do so, we used Spearman correlations between each value of specialisation parameter and the degree of generalisation calculated from the true interaction pattern (**TP**) corresponding to that parameter (s). We used Spearman correlations because we anticipated that indices would vary monotonically with the specialisation parameter, but not necessarily linearly. A good index of generalisation is expected to exhibit a negative correlation with the specialisation parameter.

2.3.4 | How accurate are their estimations under the influence of neutral effects?

Indices of generalisation should provide accurate estimations regardless of how uneven the resource abundance distribution is. To assess

TABLE 2 Summary of the parameters used to generate the different interaction patterns with the quantitative niche model.

Parameters	What it controls for	Values used for generating data
Specialisation parameter (s)	How narrow the generalisation-specialisation curve is. Therefore, the higher the specialisation parameter, the narrower the curve	2000 values from 0.1 to 60.0 in a logarithmic spaced sequence
Number of potential resources (R)	How many resources are available in the area for the consumer to interact with	For each value of the specialisation parameter (2000), we used 5, 15 and 55 potential resources (a total of 6000 combinations)
Trait matching (t)	How well a consumer can interact with resources based on its traits and the traits of resources. In other words, how different other resources are to the most preferred resource (e.g. r_3 in Figure 1)	An evenly spaced sequence of R values from −1.0 to 1.0. Having an odd number of potential resources allowed us to have a most preferred resource ($t = 0.0$) in all simulations
Resource abundance distribution (**q**)	How abundant a resource is related to the others, that is, the vector of relative abundance of resources	A vector of R values generated from a log-normal distribution of mean ln(10) and standard deviation of 1.5. For a set of R resources we used the $\frac{r}{R+1}$ quantile as the abundance for each resource r in 1 to R
Sampling intensity (n)	How many interactions are sampled to generate the observed interaction pattern	For each current interaction pattern, we used four levels of sampling intensity: 10, 50, 100 and 500 interactions. This generated 6000 vectors of observed interaction patterns per level of sampling intensity

the influence of neutral effects on index performance, we compared the degree of generalisation calculated from each of the 6000 true interaction patterns (**TP**) to the degree calculated from their corresponding current interaction patterns (**CP**). For each index and number of potential resources (*R*), we calculated the mean squared error (MSE) as a measurement of accuracy of the estimation. A good index of generalisation is expected to exhibit values of MSE close to 0.0, indicating it is unaffected by neutral effects.

2.3.5 | How accurate are their estimations under variations in sampling intensity?

Sampling effects, specifically sampling intensity, influence the accuracy of estimations provided by any index. Nevertheless, it is important to know whether an index requires a smaller or larger number of recorded interactions to provide accurate estimations. To assess the influence of sampling effects on the estimation of degree of generalisation, we analysed how the accuracy of the estimation provided by each index changed as sampling intensity increased. To do so, we compared the degree of generalisation calculated from each of the observed interaction patterns (**OP**) to the expected degree calculated from their corresponding true interaction pattern (**TP**). We calculated the MSE as a measurement of accuracy of the estimation for each index and number of potential resources (*R*).

2.4 | A test with empirical consumer-resource networks

We tested the performance of $\alpha PDI'$ when estimating the degree of generalisation in empirical consumer-resource interactions. To do so, we used a data set of 74 host–parasite networks of interactions between fleas and mammals across the globe. This extensive database has been analysed in several studies on ecological interactions (Felix et al., 2022; Fortuna et al., 2010; Krasnov et al., 2004; Vázquez et al., 2007). Additional information on the species involved in these interactions and references is available in the Appendix S5.

For each consumer (flea), we calculated its degree of generalisation using $\alpha PDI'$, and used a Spearman correlation to determine whether the estimated value of $\alpha PDI'$ was correlated to sampling intensity and the number of potential resources. In our analysis, for each host species, we used its total number of captures as a proxy for resource abundance (including individuals without fleas), and the number of individual parasites collected per host species as a proxy for the number of interactions. However, we must recognise that, in many cases, the estimation of resource abundance is difficult and can be biased. In host–parasite networks, the estimation of host abundance may be distorted because different host species have different trappability or require different trapping methods (e.g. snap- or live-traps for mice and voles, pitfall traps for shrews, special traps for moles, and hunting for squirrels).

All analyses were made in the R language (R Core Team, 2022), using the packages *bipartite* (Dormann et al., 2008), and user-defined functions developed by Fründ et al. (2016), Pierotti et al. (2017), and us. Code and processed data used in all analyses are available in the supplement.

3 | RESULTS

Our analysis revealed a negative correlation between all indices and the specialisation parameter (all indices $rho = -1$, $p < 0.001$), which indicates that they behave as good indices of generalisation when there are no neutral or sampling effects. However, independently of the number of potential resources, most indices were influenced by neutral effects, yielding inaccurate estimates (Figure 2). Notably, inaccuracies were predominantly associated with high values of the specialisation parameter, meaning that most indices tend to overestimate the degree of generalisation of specialists (Figure 2). Only Wc' and αPDI presented minimum bias and error.

Regarding sampling effects, increasing sampling intensity led to decreased bias and MSE, indicating improved accuracy for all indices (Figure 3; Appendix S5). However, for most indices, particularly for αPDI′, αPDI and Wc', estimates were more inaccurate at lower values of the specialisation parameter. This means that generalists require higher sampling intensity for accurate estimation than specialists (Figure 3). Furthermore, higher sampling intensity was also required for accurate estimation as the number of potential resources increased. In all cases, αPDI′ outperformed αPDI and Wc' (Figure 3). Four indices (B'', W', PS' and FT') were more robust to sampling effects than others, however it seems to be related to index symmetry (Appendix S2). Bs' was the worst performing index in all cases. For many simulated consumers it was impossible to calculate Wc' (Figure 3); other indices did not show this problem.

Finally, we observed a slight yet positive correlation between degree of generalisation and sampling intensity when using αPDI′ on empirical consumer-resource interactions ($rho = 0.36$, $p < 0.001$). Thus, the values of αPDI′ increased with sampling intensity (Figure 4a). Conversely, we observed a marginal correlation between degree of generalisation and the number of potential resources ($rho = -0.05$, $p = 0.052$; Figure 4b). Notably, generalists (i.e. αPDI′ > 0.50) were infrequent in the analysed networks, which predominantly comprised specialists (Figures S4C and S9–S12).

4 | DISCUSSION

In general, all indices displayed the desirable correlation with the shape of the generalisation-specialisation curve, yielding higher values as the curve becomes wider. At first glance, they all seem promising as indices of generalisation, as they measure the span of resources used by consumers (Roughgarden, 1972). However, regarding neutral effects, most indices exhibited unsatisfactory performance. Despite their aim to mitigate the influence of different

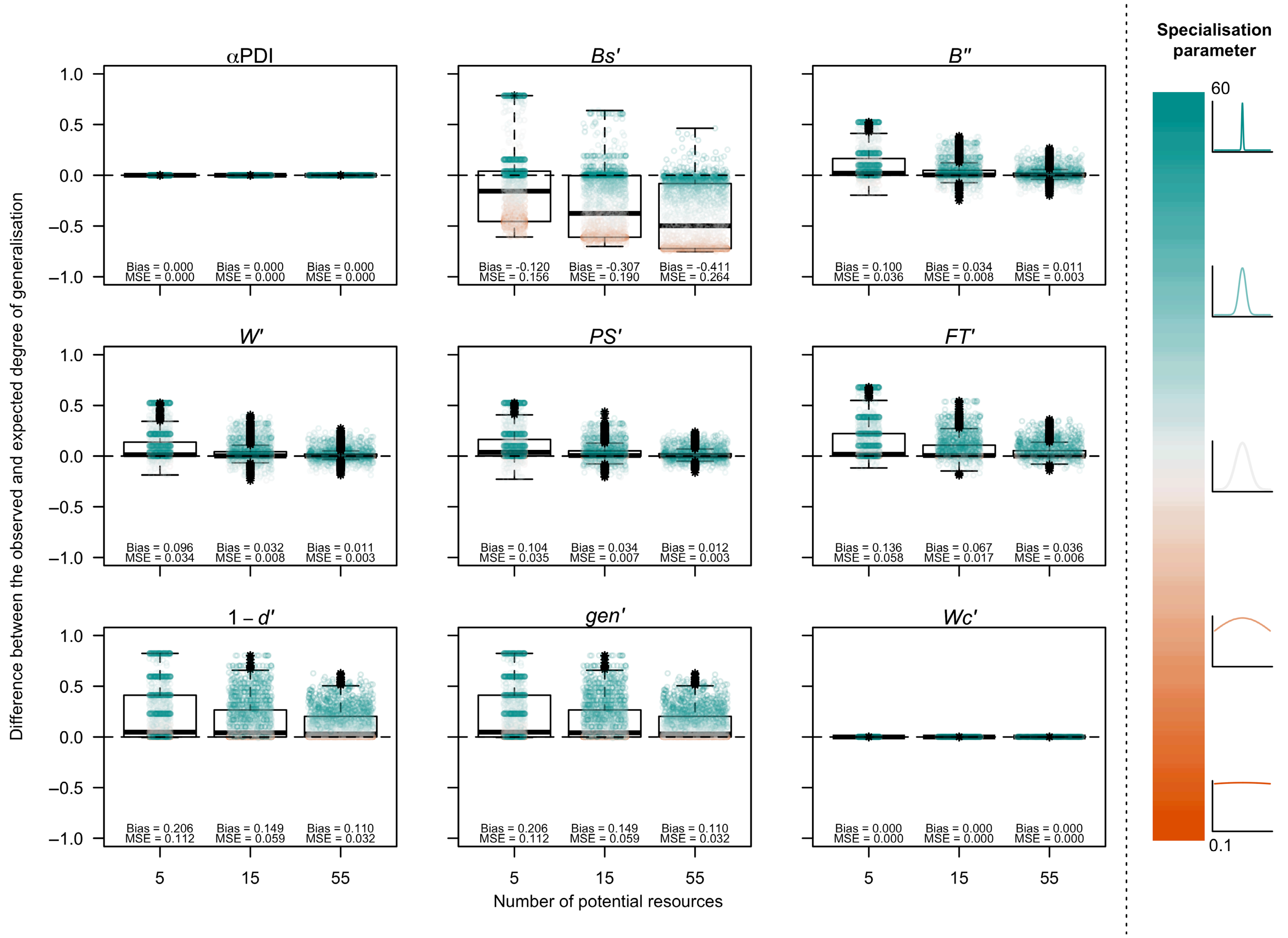

FIGURE 2 Unlike most indices of generalisation, αPDI and *Wc*′ are not influenced by neutral effects. Plots show how different indices perform under neutral effects. Each point represents a consumer using a set of potential resources (5, 15 and 55) based on its specialisation parameter (0.1 in orange to 60.0 in blue). For an index with ideal performance, all points should fall on the dashed horizontal line where the difference between the observed (calculated on the current interaction pattern) and expected (calculated on the true interaction pattern) degree of generalisation is 0.0. Points above the line indicate overestimation of generalisation, while points below the line indicate underestimation. The dominant blue points in the plots suggest that most indices tend to overestimate the degree of generalisation of specialised consumers. In addition, plots show the bias and the MSE for each number of potential resources. Curves on the right side of the coloured grid of the specialisation parameter depict how the shape of the generalisation-specialisation curve changes as the specialisation parameter increases.

resource abundances, only *Wc*′ and αPDI remained unaffected. Such contrasting outcomes stem from how indices operationalise extreme specialisation and how their values behave towards this extreme.

An extreme specialist is theoretically adapted to interact exclusively with a single resource, reflecting a narrow generalisation-specialisation curve (Poisot et al., 2012). Irrespective of resource abundance, indices should consistently reflect minimal generalisation for such a consumer. Yet, most indices operationalise an extreme specialist as a consumer interacting exclusively with the least abundant resource, omitting those interacting solely with any other more abundant resource. Conversely, the operationalisation of an extreme specialist given by *Wc*′ and αPDI aligns more closely with conceptual intuition and definitions such as monophagy or monolecty: a consumer interacting with a single resource, regardless of its abundance (Pierotti et al., 2017). This explains why *Wc*′ and αPDI perform optimally under neutral effects, and why inaccuracies from other indices are usually related to high values of the specialisation parameter.

Regarding sampling effects, all indices yielded more accurate estimations with increased sampling intensity. Unlike specialists, accurately estimating the degree of generalisation of a generalist requires higher sampling intensity, especially with a larger number of potential resources. Thus, most inaccurate estimations correspond to low values of the specialisation parameter. Additionally, asymmetric indices whose values exhibit larger changes towards extreme specialisation (all indices but *Wc*′ and αPDI) are apparently more accurate (Appendix S2), because they are more sensitive to changes in underused resources (Smith, 1982). Since these asymmetrical

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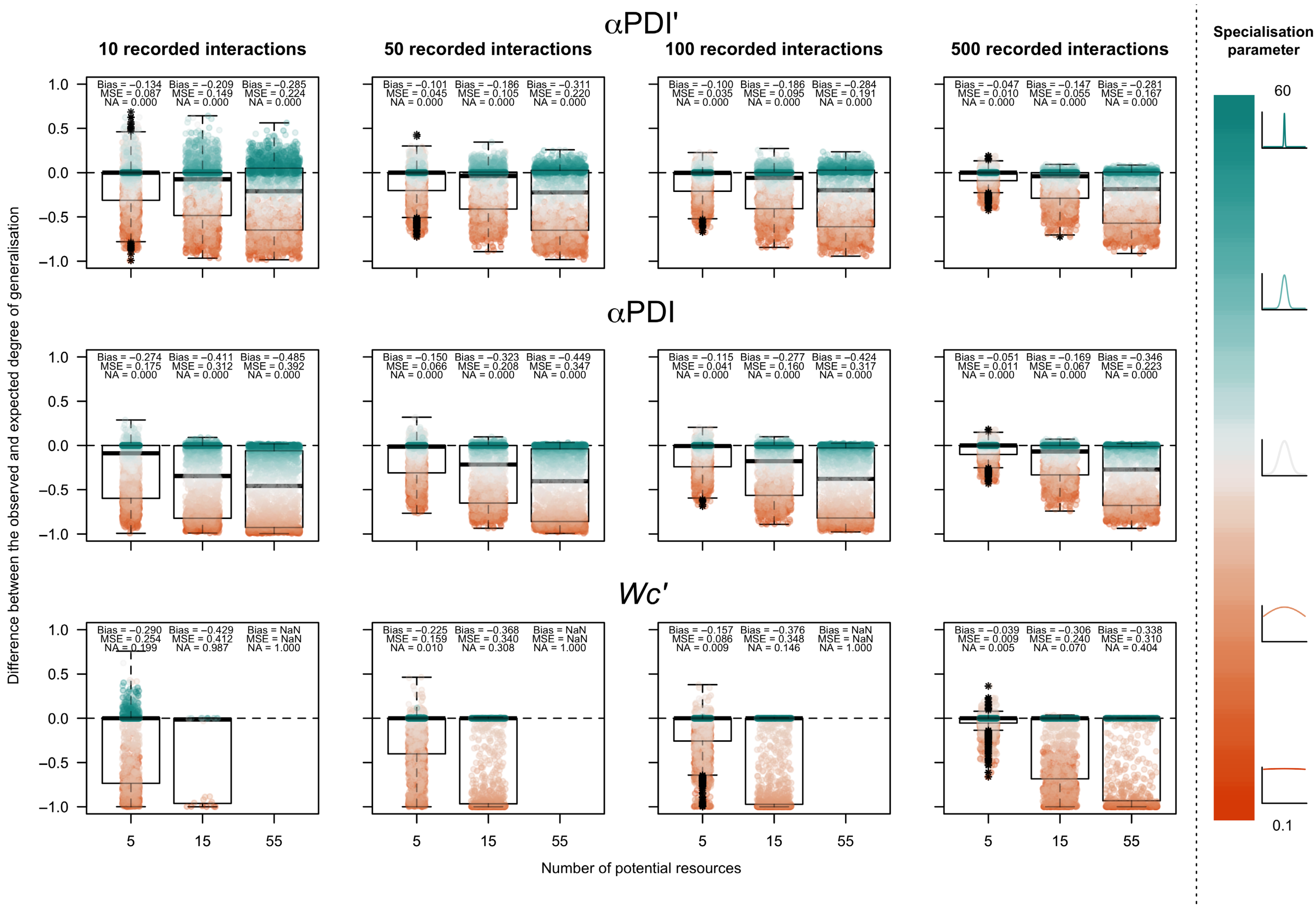

FIGURE 3 Under sampling effects, αPDI′ and αPDI perform better than *Wc*′. Each point represents a consumer using a set of potential resources (5, 15 and 55) based on its specialisation parameter (0.1 in orange to 60.0 in blue). For an index with ideal performance, all points should fall on the dashed horizontal line where the difference between the observed (calculated on the observed interaction pattern) and expected (calculated on the true interaction pattern) degree of generalisation is 0.0. Points above the line indicate overestimation of generalisation, while points below the line indicate underestimation. The dominant orange points in the plots suggest that indices tend to underestimate the degree of generalisation of generalists. In addition, plots show the bias and the MSE for each number of potential resources. For many consumers, *Wc*′ was unable to estimate their degree of generalisation, for which the proportion of not available information is presented (NA). In contrast the values of αPDI′ and αPDI were available for all consumers (all NA = 0.0). Curves on the right side of the coloured grid of the specialisation parameter depict how the shape of the generalisation-specialisation curve changes as the specialisation parameter increases.

indices exhibit smaller changes towards generalisation, the difference between the observed and expected degree of generalisation of generalists will also be smaller, making indices to be seemingly more accurate, and clarifying why most indices seem more robust to sampling effects than *Wc*′, αPDI and αPDI′.

When selecting an index of generalisation, we should prioritise how well it operationalises the concept of generalisation, including what it means to be a generalist and a specialist. Our analysis of neutral effects highlights that most indices, except for *Wc*′ and αPDI, fail in this respect. Therefore, the choice narrows down to *Wc*′, αPDI, and its corrected version αPDI′. However, the logistical limitation of *Wc*′ (i.e. requiring Bayesian-multiplicative replacement) hinders its application in various data structures. Although αPDI′ is more robust to sampling effects than αPDI, it is not immune to them. Therefore, statistical techniques, such as confidence intervals through accelerated bias-corrected bootstrapping, could help obtaining more reliable estimates (Efron, 1987). However, index performance under other sources of sampling effects remains to be investigated. Using, αPDI or αPDI′ to classify consumers as generalists or specialists improves previous approaches (see Fort et al., 2016; Simmons et al., 2019).

Our test on empirical consumer-resource interactions showed that the studied flea-mammal networks are mainly dominated by specialists. This finding is consistent with the ubiquity of the power law and truncated power law degree distributions in ecological networks (Jordano et al., 2003; Vázquez, 2005). Yet, considering that our simulations showed that generalists require increased sampling intensity for accurate estimation, and noting the weak but positive relationship between the values of αPDI′ and sampling intensity, the interpretation of these long-tailed degree distributions as specialisation warrants further investigation.

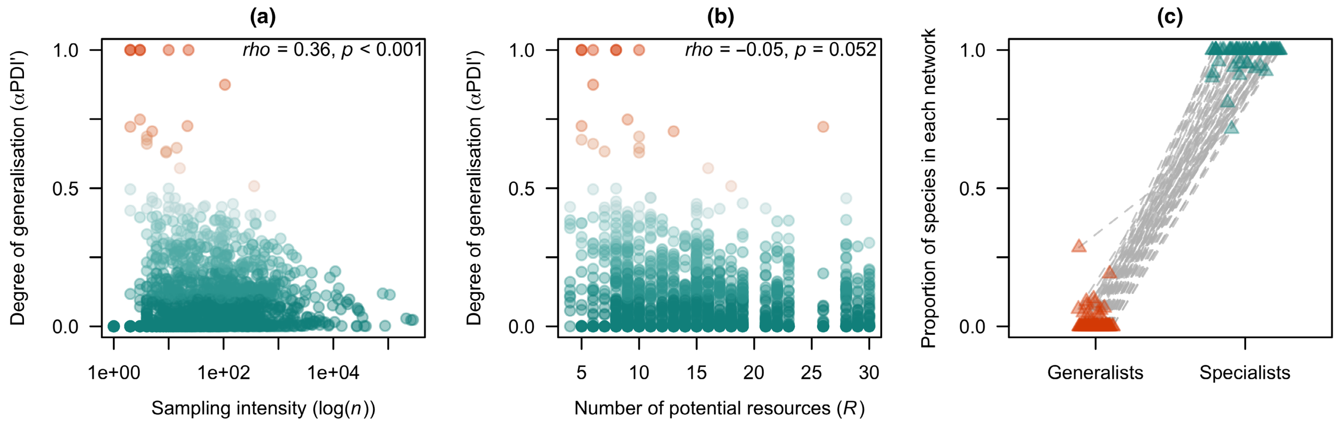

FIGURE 4 Testing αPDI′ on empirical consumer-resource interactions. (a) Degree of generalisation correlates positively with sampling intensity, (b) but has no significant correlation with the number of potential resources. Each point represents a consumer (fleas) interacting with a set of potential resources (mammals). Colours are associated with the value of αPDI′, with points becoming more orange or blue as the consumer is more generalist or specialist, respectively. (c) The networks analysed are composed mainly of specialists. Each pair of triangles (joined by the dashed line) depicts one of the 74 empirical networks.

Despite having tested αPDI′ with flea-mammal networks, all assessed indices estimate a consumer's degree of generalisation in relation to a resource set, independently of coexisting consumers. Not being network indices per se (with the exception of a modified version of *d*′; Blüthgen et al., 2006), they do not quantify how coexisting consumers share resources, or the resulting network patterns. Still, in a natural context (e.g. an ecological community), these indices assume that competition has shaped the generalisation-specialisation curve akin to a realised niche (Hutchinson, 1957). Thus, a consumer's degree of generalisation varies across different consumer communities.

Moreover, when using αPDI or αPDI′, defining the set of potential resources is crucial, especially unused ones. Including abundant, unused resources may lead to misleading outcomes (Feinsinger et al., 1981). However, depending on the ecological question, retaining such resources might be necessary. For example, when studying a consumer assemblage, the full resource set used by the assemblage might define potential resources (Jorge et al., 2014). Nevertheless, the fact that the classification of a consumer either as a generalist or specialist using αPDI′ depends on the set of potential resources should not be seen as a methodological weakness but as a good approximation to reality. For instance, a koala, a generalised consumer of *Eucalyptus* leaves (Colwell & Futuyma, 1971), will be classified as such, if all *Eucalyptus* species are considered as potential resources. Alternatively, it could be deemed a specialist if leaves from various plant genera constitute the potential resource set.

Notably, an individual's degree of generalisation might differ from its population's degree (Araújo et al., 2011). However, using αPDI and αPDI′ on individuals will not contrast their interactions against the population's. While these indices classify individuals on the generalisation-specialisation continuum, they do not quantify individual specialisation (but see Bolnick et al., 2002; Pierotti et al., 2017; Roughgarden, 1974), or any other type of specialisation in consumer-resource interactions (Blüthgen et al., 2008; Dormann, 2011).

Furthermore, αPDI and αPDI′, as many other indices, disregard phylogenetic relationships or ecological similarity between resources (Colwell & Futuyma, 1971), which considerably influence consumer-resource interactions (Pinheiro et al., 2019). In cases where resources are species, strategies like stepwise reduction of potential resources by aggregating species into higher taxonomic units can be used (Blüthgen et al., 2006). Newer approaches employ phylogenetic information to quantify generalization (e.g. Jorge et al., 2014; Pardo-De la Hoz et al., 2022), though their performance under neutral and sampling effects remains unclear.

Lastly, interpreting specialization hinges on interaction type, given that many consumers engage in multiple interactions (Mello et al., 2015). In trophic interactions like frugivory and flower visitation, consumers can feed on various resources, yielding omnivore diets (Brosi, 2016; Muchhala & Tschapka, 2020). Besides, most frugivores, nectarivores, polinivores and pollinators do not see the plants as their whole world, except for a few cases of extreme specialization, such as fig wasps (Janzen, 1979). Therefore, many "specialists" in mutualistic interactions might be "tourists", not relying solely on these interactions for survival (Mello et al., 2015). However, ectoparasitic interactions, such as those studied here, entail parasites being fully dependent on their hosts for food and habitat (Krasnov, 2008). Thus, specialization does not always mean dependency. Due to these interaction-type disparities, consumer classification as generalist or specialist must consider natural history, with indices serving as proxies for ecological generalization concepts, and not the other way round.

In conclusion, our assessment suggests that αPDI and αPDI′ are good candidates for estimating generalization in consumer-resource interactions. These indices can help obtain fresh insight into long-standing ecological questions like the abundance-generalization dilemma (Fort et al., 2016), the link between specialization and disturbance susceptibility (Vázquez & Simberloff, 2002), and keystone species in mutualistic networks (Mello et al., 2015). Therefore, they may become important tools for many fields, from theoretical ecology to conservation biology, aiding in accurate consumer generalization measurement.

AUTHOR CONTRIBUTIONS

Sebastián Montoya-Bustamante, Carsten F. Dormann, and Marco A. R. Mello conceived the ideas and methods. Boris R. Krasnov collected the data and compiled the datasets. Sebastián Montoya-Bustamante analysed the data. Sebastián Montoya-Bustamante and Marco A. R. Mello wrote the first version of the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14284.

DATA AVAILABILITY STATEMENT

All processed data and code used in this study, as well as a tutorial for the calculation of the new indices, are available on GitHub via Zenodo (Montoya-Bustamante & Mello, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. On the normalisation of indices.
Appendix S2. On the midpoint of indices and index symmetry.
Appendix S3. On the algorithms to estimate αPDI_{max}.
Appendix S4. On the quantitative niche model.
Appendix S5. On the host–parasite networks.

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