

Phylogenetic trophic specialization: a robust comparison of herbivorous guilds

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Abstract Resource specialization is a key concept in ecology, but it is unexpectedly difficult to parameterize. Differences in resource availability, sampling effort and abundances preclude comparisons of incompletely sampled biotic interaction webs. Here, we extend the distance-based specialization index (DSI) that measures trophic specialization by taking resource phylogenetic relatedness and availability into account into a rescaled version, DSI*. It is a versatile metric of specialization that expands considerably the scope and applicability, hence the usefulness, of DSI. The new metric also accounts for differences in abundance and sampling effort of consumers, which enables robust comparisons among distinct guilds of consumers. It also provides an abundance threshold for the reliability of the metric for rare species, a very desirable property given the difficulty

of assessing any aspect of rare species accurately. We apply DSI* to an extensive dataset on interactions between insect herbivores from four folivorous guilds and their host plants in Papua New Guinean rainforests. We demonstrate that DSI*, contrary to the original DSI, is largely independent of sample size and weakly and non-linearly related with several host specificity measures that do not adjust for plant phylogeny. Thus, DSI* provides further insights into host specificity patterns; moreover, it is robust to the number and phylogenetic diversity of plant species selected to be sampled for herbivores. DSI* can be used for a broad range of comparisons of distinct feeding guilds, geographical locations and ecological conditions. This is a key advance in elucidating the interaction structure and evolution of highly diversified systems.

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Introduction

Trophic specialization is a key concept in ecology, but it is also surprisingly difficult to measure, with different methods often providing contradictory results. In its simplest form, it can be expressed as a list or number of diet items. Such lists can be refined into more informative specialization indexes by including other relevant information. For example, one can include aspects of resource diversity and selection that take frequency into account, or quantify use relative to availability (Colwell and Futuyma 1971; Manly et al. 1993). Furthermore, the amount of reciprocal specialization, in which species being the sole consumers of a given resource are considered more specialized (Blüthgen et al.

2006), and phylogenetic relationships among resource items can also be accounted for (Symons and Beccaloni 1999; Weiblen et al. 2006; Pellissier et al. 2012). The evolutionary relationship of resources is widely recognized as the most relevant trait mediating resource selection by herbivores and parasites (Ehrlich and Raven 1964; Poulin et al. 2011; Jorge et al. 2014), as it gives insights both related to resource trait similarity and coevolutionary processes. Thus, it is a more meaningful measure of resource breadth than counts of resource items.

The comparison of specialization between species within and among communities is also made difficult by the sensitivity of most metrics to sampling design and consumer abundance or frequency. This sensitivity is caused by the fact that many trophic interactions occur with extremely low frequency in food webs (Lewinsohn et al. 2005) and host specificity depends on the size of the host species pool (Jorge et al. 2014). These problems constrain host specificity comparisons between food webs of different dimensions and those sampled with different effort. This is especially true when considering how the host specificity of rare and common species differs. The range of potential (and actual) hosts used increases with the host species pool for generalist consumers, whereas strictly monophagous species are not affected. These problems often compromise the accurate measurement of specialization along ecological gradients, including latitudinal, altitudinal or successional gradients. For instance, Novotny et al. (2006) found no latitudinal trends in herbivore host specificity after they standardized plant abundance and phylogenetic diversity between tropical and temperate food webs, while Forister et al. (2015) documented higher specialization in the tropics without such standardization. These issues are especially important when comparing herbivores that belong to different guilds, which differ in feeding mode, overall abundance and mean specialization, and are often sampled using distinct methods.

A solution to some of these issues was advanced recently in the distance-based specialization index (DSI-Jorge et al. 2014), a host specialization measure that considers host phylogeny and is robust to differences in the abundance and sample size of host species. For any biotic resource, it is defined as a deviation of observed phylogenetic relatedness of resource species used by a given consumer species from a null expectation assuming random use of resources. This null expectation is generated from the resource species pool based on the availability of each resource species—which comprises its abundance, sampling intensity and local co-occurrence with each consumer species. More details and a formal definition of DSI are offered in the following section.

Here, we develop this approach to address another issue that makes the comparison of specialization difficult: its sensitivity to the abundance of herbivores sampled. To this end, we developed a standardization method for DSI

and test its performance using one of the most comprehensive plant–insect data sets available. We measure the diet specificity of four guilds of folivorous insects intensively collected or reared from a phylogenetically diverse set of rainforest woody plant species in Papua New Guinea. These guilds have previously been shown to have very different interaction structures with their host plants, comprising a wide range of species from rare to abundant and from specialists to broad generalists (Novotny et al. 2010), and thus they provide an outstanding testbed for our approach. We tested whether this scaled metric was indeed unaffected by herbivore abundance, and then compared it to other currently employed specialization metrics that do not incorporate plant phylogeny. We then addressed another common issue with host specificity studies, the inclusion of only a subset of the host community in the study. We used a rarefaction procedure to assess the sensitivity of DSI to the richness and phylogenetic scope of the pool of host plant species included in the samples. We show that rescaled DSI is independent of sampling intensity and plant abundance, making it suitable for specialization analyses that provide robust comparisons of a wide range of food webs.

Rescaling DSI

In its original formulation (Jorge et al. 2014), DSI is a Z-score. Hence, it measures specialization as a deviation from a random expectation (Eq. 1):

$$DSI_i = \left(\frac{MPD_i - \text{mean}(\text{Null}_i)}{\text{sd}(\text{Null}_i)} \right) (-1) \quad (1)$$

in which MPD_i (mean pairwise phylogenetic distance) is the observed average relatedness of all host plants used by herbivore species i weighted by their abundances. Null_i is the distribution of mean pairwise phylogenetic distances obtained by randomly drawing host sets from the host pool available to that herbivore species. For each herbivore species, the pool of hosts is defined as the set of host plants that co-occur with that herbivore, with the abundances observed in the sites in which the herbivore was recorded. From this pool, a set of hosts with the number of interactions observed for that herbivore is sampled. We note that any measure of interaction frequency can be used, but that the number of individuals representing a link is the most natural, because this is universally measured and best reflects the probability of that link occurring in additional sampling. This procedure is iterated many times sequentially (999 in our case) to obtain a null distribution of MPDs, whose mean and standard deviation are noted as $\text{mean}(\text{Null}_i)$ and $\text{sd}(\text{Null}_i)$ in Eq. 1. Therefore, DSI can be used either as a continuous metric of specialization, or to classify consumers according to their deviation from random expectation into specialists

(that use a set of resources clustered in phylogenetic space), generalists (over-dispersed) or non-selective (random), using significance thresholds in a manner analogous to established metrics of phylogenetic structure (Webb et al. 2002; Kembel 2009). Note that, similarly to these metrics, we multiply the Z-score by (-1) to invert values, so that positive DSI is obtained for phylogenetically clustered diets, more appropriate for a specialization index.

Similarly to any measure of effect size, DSI's power increases with the number of interactions observed, and thus a monophage, for example, will have different specialization values depending on the number of interactions recorded for that species. As the number of host plants sampled in a given iteration of the null model increases, a larger proportion of the variability in MPDs is contained within iterations, and the variability among iterations, $sd(\text{Null}_i)$, decreases as the number of interactions observed for each herbivore species increases. Thus, DSI is dependent on observed herbivore abundance, and the maximum possible absolute DSI values covary with the number of individuals (as well as interactions) recorded for each species. This dependency is strikingly apparent in our large and functionally heterogeneous data sets, which comprise a wide range of insect abundance values (shown for one guild in Fig. 1).

To overcome this problem and enable the comparison of consumers that differ in their recorded sample sizes, we propose to rescale the DSI index. DSI^* is calculated as DSI divided by its maximum or minimum possible values

determined for a given consumer species, based on its sample size and on the phylogeny of potential resource species (Eq. 2):

$$\text{DSI}_i^* = \frac{\text{DSI}_i}{|\text{DSI}_{\text{lim}}|}, \quad (2)$$

where DSI_i is as in Eq. 1 and $|\text{DSI}_{\text{lim}}|$ is the absolute value of the minimum (for negative DSI_i) or maximum (for positive DSI_i) limit for DSI_i of each herbivore species i , also calculated from Eq. 1. Minimum MPD = 0 corresponds to strict monophages, and as it is multiplied by (-1) in Eq. 1, it yields the maximum DSI value for the combination of plant phylogeny and number of interactions observed for that species. Given that MPD is measured among plant individuals, the maximum value cannot be estimated by simply assigning individuals to the two most distant host species in the plant phylogeny. Therefore, we estimate maximum MPD by an optimization algorithm of simulated annealing to find the distribution of individuals among resource species that maximizes the mean distance among individuals. This heuristic algorithm is adequate for combinatorial optimization problems, and was implemented for this specific problem in the R language using the simulated annealing functionality present in the function `optim` (Bélisle 1992). The rescaled DSI^* varies between -1 (maximum achievable generalization) and 1 (monophages or maximum achievable specialization).

These rescaled values allow the comparison of specialization between herbivore species and between different data sets, whereas the original DSI values, as a continuous metric, are less comparable between different data sets, thus limiting its use to the classification of species into specialists, generalists and non-selective feeders. The routine to calculate DSI^* is included in the `dizzy` R package to measure specialization in resource use, available at <http://github.com/leorjorge/dizzy>.

Materials and methods

We calculated rescaled DSI for the species in four guilds of folivorous insects in Papua New Guinea rainforests. Plant–herbivore interaction webs were sampled following protocols described in Novotny et al. (2002, 2010, 2012). Folivores were classified into guilds according to their feeding mode (chewing, sucking) and the intimacy of the association with their host plant (Novotny et al. 2012): mobile chewers are all externally feeding hemimetabolous larvae and all adults (Orthoptera, Phasmatodea, and Coleoptera); exposed chewers—all externally feeding and fully exposed holometabolous larvae (Lepidoptera, Coleoptera); semiconcealed chewers—all leaf rolling and leaf tying

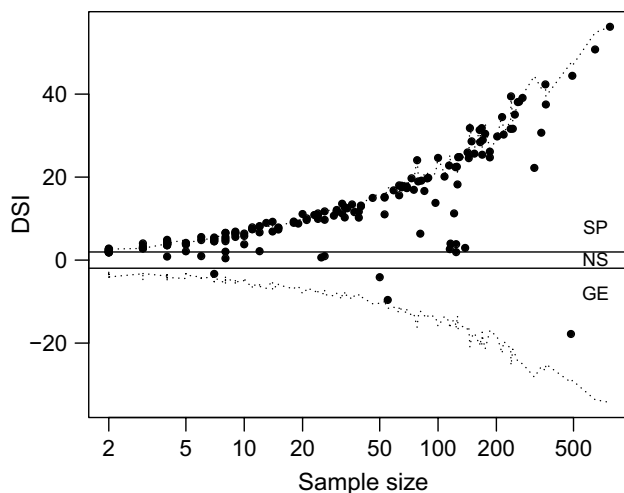


Fig. 1 Relationship between sample size (the number of individuals of herbivores) and the non-scaled distance-based specialisation index (DSI) for 170 species belonging to the guild of semi-concealed larval chewers in Papua New Guinea. Continuous lines mark the confidence interval thresholds to classify species as specialist (SP), non-selective (NS) or generalist (GE) feeders. The dashed lines indicate the maximum and minimum possible DSI for each sample size, used to rescale DSI

holometabolous larvae (Lepidoptera); miners—all leaf mining species (Lepidoptera, Coleoptera, Diptera).

Within each of these guilds, the full scope of herbivorous taxa was investigated. Folivorous guilds were sampled from 59 to 87 woody plant species per guild (125 plant species in total) at three study sites (Baitabag, Ohu, and Mis Villages) located within a 10 × 20-km area encompassing a mosaic of secondary and primary lowland hill forest in Madang Province (Papua New Guinea) for at least one year between 1995 and 2008. Plant selection included all major plant lineages as well as three clusters of closely related, congeneric species (*Ficus*, *Macaranga*, and *Psychotria* species; see Table S1 for plant list). A phylogeny of this set of plants was developed by Szefer et al. (2017), and further details are available as supplementary material S1.

Each plant species was sampled with equal effort (1500 m² of foliage area) for each guild, removing potential effects due to variations in host plant abundance. The insects, or leaves with semiconcealed or mining larvae, were hand collected from foliage. Mobile chewer adults were tested for feeding on the plant species from which they were collected; only insects that fed were included in the analyses. Larvae were reared to adults as far as possible; see Novotny et al. (2002, 2010, 2012) for further details. Host plant records supported by a single herbivore individual were excluded from the data set as poorly supported. This data filtering removed singleton species—which cannot be evaluated for host specificity—from the data set.

Larvae from all guilds and all adults were assigned to species. All adult insects were later identified by specialists as far as possible (Miller et al. 2003), and larval species were linked to corresponding adult species. Species identifications were often verified by dissection of genitalia and reference to type specimens. Comparisons of mitochondrial cytochrome oxidase I DNA sequence divergence with morphology were used for over 10,000 insect specimens (Lepidoptera in all guilds and Coleoptera and Diptera in miners) to verify our species boundaries, including polymorphic species and cases of sexual dimorphism (Hulcr et al. 2007; Craft et al. 2010). The complete interaction data are available online from (Novotny et al. 2012) at <http://dx.doi.org/10.5061/dryad.rg155q32>.

Analysis

We measured distance-based specialization (DSI) for all herbivore species, and applied rescaling as described above to obtain DSI*. Since only a single locality was studied, co-occurrence between plants and herbivores does not apply to this dataset, and the uniform sampling effort among host plants simplifies the measurement of availability, given that the observed abundance of herbivores on plants is a direct estimate of actual frequencies on plants. Thus, a null model

that samples plant individuals with equal frequency is adequate for this dataset. We compared the specialization values between guilds by means of a one-way permutation test, followed by pairwise comparisons among groups corrected by the method of Benjamini and Hochberg (1995).

When a subset of the plant community in a given site is used to survey plant–herbivore interaction structure and diet specialization, there is potential for bias in the estimation. Especially for metrics that are counts of resource items, the higher the coverage, the higher the potential to detect generalization. To assess the bias in the calculation of specialization related to the size and phylogenetic scope of the host plants screened for herbivores, we calculated DSI* and host richness for sub-sets of the host plant species actually sampled for each guild. We used a technique similar to sample-based rarefaction of communities. In our case, increasingly large sets ranging from two to the total number of host-plant species are selected instead of communities, and specialization is measured for the herbivores feeding on those plants. Three different approaches were used to select these sets: (1) a random set of host plants, with 100 iterations for each sample size; (2) the set of host plants maximizing phylogenetic diversity (PD—Faith 1992), selected for each sample size; and (3) the set of host plants minimizing PD was selected for each sample size. For simulations (2) and (3) we used the algorithms implemented in the pda software (Chernomor et al. 2015) to select the sets maximizing and minimizing PD.

We measured specialization using other established metrics for the four guilds of herbivores: host species richness; host Simpson diversity (calculated from the distribution of herbivores among host plant species); *d'* (Blüthgen et al. 2006), a measure of reciprocal specialization widely employed in interaction network studies; and DSI* measured assuming no phylogenetic relationships between host plants (using a polytomic phylogeny instead of the actual phylogenetic relationships). Given that this metric assuming no phylogenetic relationships uses the same null models and standardization as DSI*, it still incorporates resource abundance and corrects for differences in consumer frequencies. We calculated the congruence between these metrics by means of linear models with one metric as response, and a second metric as well as the guilds as the predictor.

Results

Almost 60 thousand individual interactions were observed between 688 herbivore and 125 plant species (Table 1). Specialization varied widely among guilds, with a fivefold difference in richness of host species between more generalistic mobile chewers and specialized miners (Table 1).

Table 1 Summary statistics and specialization metrics for four guilds of folivorous insects in Papua New Guinea

Guild	Richness	Abundance	Host plants	Mean # of hosts	DSI	DSI*	d'
Mobile chewers	245	29331	59	6.96	5.93	0.71	0.28
Exposed larvae	149	6427	73	1.66	10.22	0.93	0.66
Semi-concealed chewers	170	12925	83	3.39	10.33	0.86	0.6
Miners	124	9740	63	1.24	8.85	1	0.72

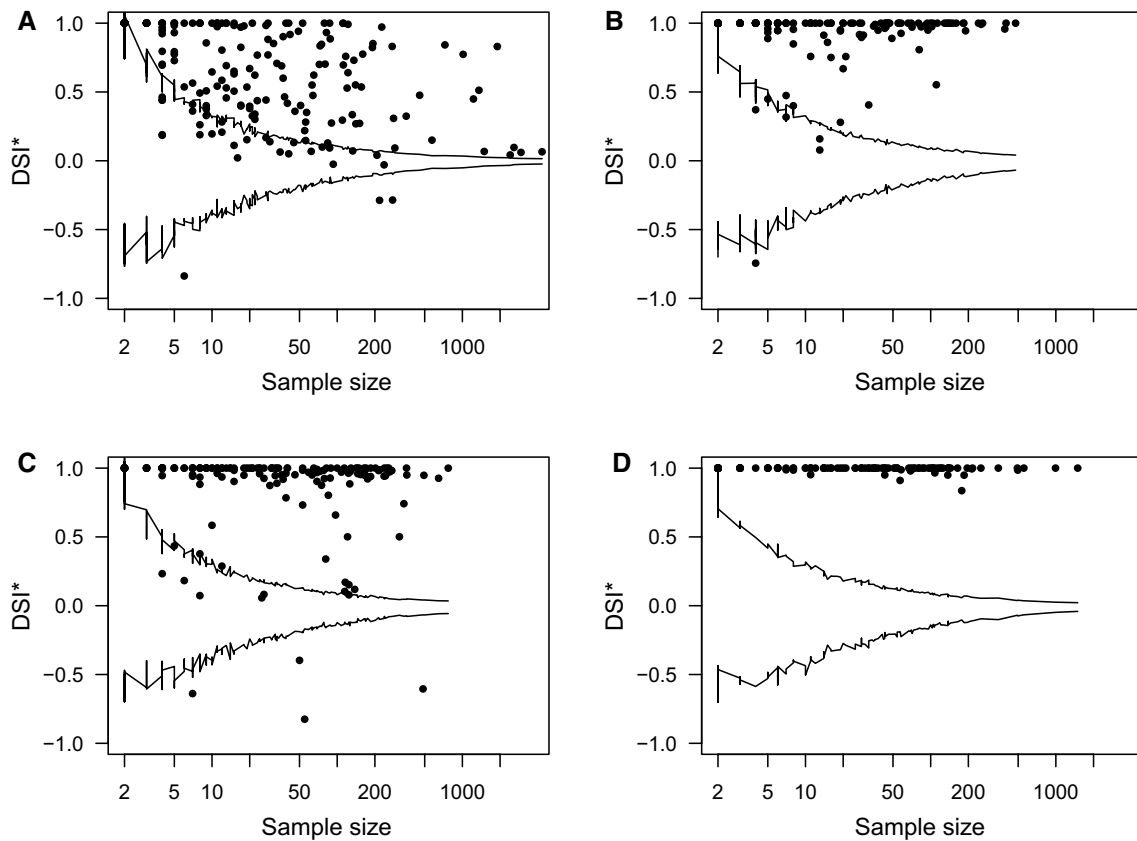


Fig. 2 Relationship between sample size and the distance-based specialisation index, rescaled by the maximum and minimum possible values for each sample size (DSI*), for species belonging to four guilds of folivorous insects in Papua New Guinea. **a** Mobile chewers,

b exposed larval chewers, **c** semi-concealed larval chewers, **d** miners. Lines indicate the confidence interval thresholds to classify species as specialist, non-selective or generalist feeders as in Fig. 1

Differences found with this simple measure of host breadth are also found, after adjusting for host-relatedness and availability in DSI and in DSI*, which is additionally adjusted for sample size. The differences between guilds were highly significant ($p < 0.0001$) for all guild pairs, except exposed vs. semiconcealed larval chewers, with a marginally significant difference ($p = 0.049$). DSI* was also unrelated to sampling intensity for all guilds (Fig. 2).

The plant rarefaction simulations showed that both measures of specialization, DSI* and number of host species, are affected by the number of plant species sampled (Fig. 3).

Moreover, positive or negative bias in phylogenetic diversity of plants selected did not affect this tendency (blue and red curves in Fig. 3). Importantly, the mean number of host plants recorded per herbivore increased monotonically and almost linearly as more plant species were sampled, whereas DSI* almost stabilized, in both cases beyond approximately 20 plant species analyzed.

DSI* was significantly correlated with currently used specialization metrics, with similar results for host-plant richness ($R^2 = 0.43$), Simpson diversity (0.56) and DSI* measured without phylogenetic weighting (0.57); richness and Simpson diversity were also correlated ($R^2 = 0.52$). In contrast, correlation of Blüthgen’s d' with DSI* was low

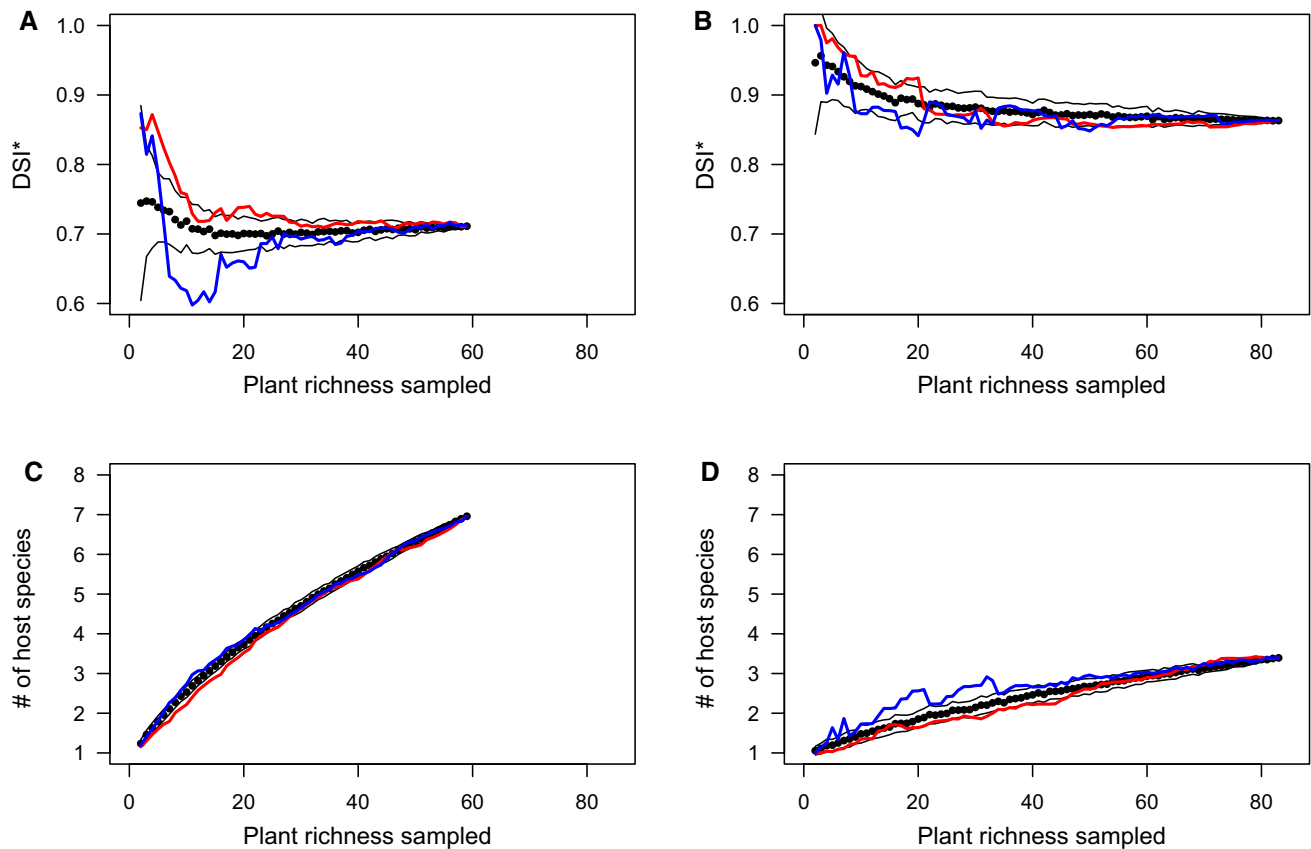


Fig. 3 The effect of the number of plant species selected for sampling and two measures of mean host specialization (**a, b** mean DSI*, **c, d** mean number of host species) for the herbivores belonging to two guilds (**a, c** mobile chewers, **b, d** semi-concealed larval chewers). In each graph, dots represent the mean specialization for all species

feeding on the selected set of plants, and the black lines its standard deviation. Blue and red lines represent, respectively, the specialization measured when selecting a set of plants with the minimum or maximum possible phylogenetic diversity

although significant ($R^2 = 0.17$; Fig. 4); and likewise, with richness ($R^2 = 0.12$) and Simpson diversity ($R^2 = 0.18$). It is important to highlight that the relationship of DSI* with these metrics was strongly non-linear and with high variability.

Discussion

In this study, we further developed a recently devised specialization metric, DSI, that measures specialization while accounting for the phylogenetic relatedness and ecological availability of resource species. By incorporating a rescaling procedure, the improved metric DSI* also adjusts the abundance of the consumer species, which allows the comparison of species with very different abundances, or of communities with different ranges of resource species richness.

With this new procedure, we show clear differences in the mean and variability of specialization among the four

guilds of folivorous insects on Papua New Guinea forest trees. DSI* had low sensitivity to the range of host plants sampled for herbivores, as its values stabilized at 20 plant species sampled in our data sets. Finally, we showed that DSI* is related to other simple measures of specialization, but has a very weak relationship with a currently widely employed metric, d' .

Rescaling DSI relative to the limits imposed by the sample size of herbivores and the phylogenetic tree topology ensures comparability of heterogeneous data sets or distinctive functional groups. DSI was designed (Jorge et al. 2014) as a broadly applicable resource specialization metric. It was first applied to compare species belonging to the same functional group, assessed with a common sampling protocol (Jorge et al. 2014), a special case with no differences in sampling method to influence comparisons. In the rescaled version that we present here, this approach is generalized and comparability among heterogeneous consumer sets enhanced in three ways. First, the metric has a straightforward interpretation—values are bounded by maximum and

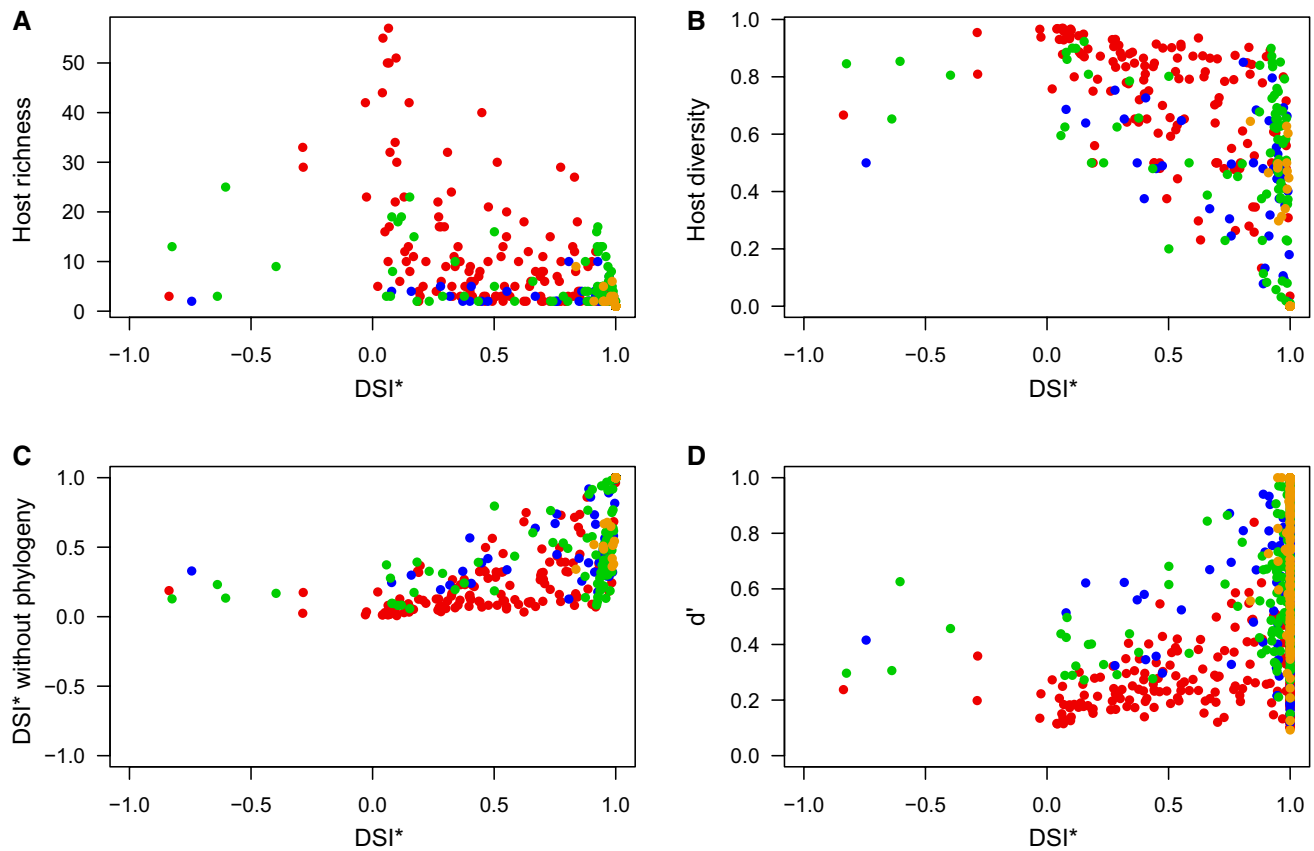


Fig. 4 Relationship between the rescaled distance-based specialization index (DSI*) proposed in this study and four other measures of specialization or diet breadth. **a** Host richness, **b** host Simpson diversity, **c** DSI* assuming no relationship among hosts (a polytomic phy-

logeny), **d** d' (proposed by Blüthgen et al. 2006). Blue dots represent exposed larval chewers, green dots semi-concealed larval chewers, red dots adult chewers and orange dots are leaf-miners

minimum values that represent extremes of achievable diet. Secondly, DSI* values are directly comparable among any given set of herbivores, regardless of their abundance, occurrence and the set of host plants in which they were sampled. Finally, the option to test for significance of specialization is retained, as in the unscaled version of DSI, by reference to an explicit null model of non-selective consumption.

Additionally, as the thresholds for classification between specialization categories can also be rescaled, it is possible to appraise whether the sampling effort of herbivores and phylogenetic diversity of the plants is sufficient to detect specialization or generalization. If the minimum or maximum possible DSI do not deviate from the non-selective thresholds for a given phylogeny, the sample size must be considered too small to measure specialization. Our analysis shows that the range of DSI* values consistent with random host selection narrows down considerably with increasing sample size, as the statistical power of the test increases (Fig. 2). The ensuing classification of species into host specificity categories, particularly the random plant selection, should be treated with caution for poorly sampled species.

The choice of subsets of the local plant community to assess herbivore specialization is a recurring controversy in insect–plant interaction studies (Novotny et al. 2006; Dyer et al. 2007). The detection of herbivores feeding on multiple hosts increases with the number of sampled plant species. However, it is not clear how much bias is introduced by not sampling the entire plant community. Moreover, given the prevalence of phylogenetic clustering of herbivore diets (Ehrlich and Raven 1964; Weiblen et al. 2006; Jorge et al. 2014), if the set of host plants included in a study is phylogenetically clustered or overdispersed, specialization measures are likely to be biased, even when measured by indices that adjust for plant phylogeny. To further probe this problem, we compared DSI* with the simpler metric, the number of host-plant species, by rarefaction of sampled plant species. This showed that DSI* is less sensitive to sampling extent than the number of host species. In the present study DSI* stabilized for plant samples greater than 20–30 species, or about one-third of the total set of resource species (Fig. 3). Sampling phylogenetically biased sets of host plants did affect DSI* values; as expected, minimizing phylogenetic

diversity of host plants returns both lower DSI* values and higher numbers of host plant species than random or maximized phylogenetic diversity.

By a commonly employed criterion, stabilization of the rarefaction curve, we ascertain a minimum number of host plants necessary for a reliable estimation of specialisation in this community. This approach can be widely employed to test for sufficient coverage of resource diversity to measure consumer specialization in communities, regardless of the specialization metric employed. Furthermore, if a phylogeny of the plants is available, the sensitivity to the phylogenetic bias in plant sampling can also be assessed.

The gain in comparability and flexibility of DSI* detailed above allowed us to increase the number of host-plant species for each guild, since we were not restricted to a fixed set of plants across all guilds. In this study, the new specialization values do not deviate significantly from previous analyses of a standardized subset of plant species (Novotny et al. 2010, 2012). This result shows that the differences between guilds is large enough to be robust to different metrics, and reinforces that this combination of information from different sets of plants for each herbivore guild, with different richness and sample sizes, does not change the overall conclusions.

Although DSI* is correlated with other specialization metrics, this correlation was variable and the relationship is strongly non-linear, which indicates that these metrics capture different aspects of specialization (Fig. 4). The more meaningful and rigorous DSI* gives a very different specialization pattern, both within and among guilds. Thus, even though it is generally correlated with established metrics, the addition of phylogenetic relatedness, resource availability and consumer abundance yields unique results, not available in studies employing other measures of specialization. This distinction is even more evident when comparing the congruence between metrics for the guilds separately. For the correlation with richness of host plants (Fig. 4a), the largest deviations are found in the mobile chewers, which have a high proportion of non-selective feeders and feed on widely varying numbers of hosts regardless of phylogenetic relationship, while miners are classified as highly specialized by both indices. For Simpson host diversity, the divergence between metrics is higher in miners, which feed on very few and closely related host species, but may have different abundance distributions on these plants (Fig. 4b). Additionally, both of these metrics and also DSI* without the phylogeny (Fig. 4c) do not allow for overdispersion of diets, and thus perform very poorly for generalist species. We deem this recognition of generalists as herbivores with overdispersed diets a conceptual advance, since it introduces a mechanism for generalization.

The differences with Blüthgen's d' are even more striking. Monophagous species always have DSI* = 1,

whereas they may have a wide range of d' values because d' stipulates reciprocal specialization (specialists feed on plants not used by other species), which corresponds to linkage symmetry (Bascompte et al. 2006). In contrast, DSI* requires no such symmetry between consumers and resources. These metrics express different concepts, whose ecological and evolutionary implications are equally distinct, for example d' relates to the ecological resilience of interactive webs (Bascompte et al. 2006). In plant–herbivore interaction webs, evolutionary relationships among plants are important and herbivores sharing the same plant species may not be in direct competition. For these, as well as other biotic interaction webs, we propose that DSI* is more meaningful as a general metric for comparisons among consumers than other specialization metrics.

Comparative studies among insect herbivore species in a broad range of feeding guilds, geographical locations and ecological conditions are key to comprehending interaction structure and the evolution of these extremely diverse species (Lewinsohn et al. 2005; Lewinsohn and Roslin 2008). Even though here we focus on an intensive study within a single local community, the framework developed enables robust comparisons among quite distinct communities, and a community-level specialization metric based on DSI* has been recently developed (Jorge et al., submitted). The importance of phylogenetic information for the host specificity assessment in food webs has been long recognized (Ehrlich and Raven 1964; Strong et al. 1984; Lewinsohn et al. 2005), but only recently are species-level phylogenies becoming widely available for phylogenetic approaches on the community level. DSI* provides an analytical tool to use this information in host specificity analyses.

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Author contribution statement LRJ co-developed the idea of the paper, led the analysis and writing; VN contributed to idea of the paper, insect data set, and manuscript writing; STS and GDW developed plant phylogeny data and analysis, commented on the manuscript; SEM led taxonomic analysis of insects, commented on the manuscript; YB contributed to the insect data, commented on the manuscript; TML co-developed the idea of the paper, contributed to writing.

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