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## Quantifying diet breadth through ordination of host association

J. A. FORDYCE,<sup>1,5</sup> C. C. NICE,<sup>2</sup> C. A. HAMM,<sup>3</sup> AND MATTHEW L. FORISTER<sup>4</sup>

<sup>1</sup>*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA*

<sup>2</sup>*Department of Biology, Texas State University, San Marcos, Texas 78666, USA*

<sup>3</sup>*Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA*

<sup>4</sup>*Department of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Nevada 89509, USA*

**Abstract.** Many areas of research in ecology and evolutionary biology depend on the quantification of dietary niche width. For herbivorous insects, diet breadth has most often been measured as simply the number and type of host plant taxa attacked. We propose an index of host range (which we refer to as “ordinated diet breadth”) based on observed associations between plants and insects, and the calculation of multivariate distances among plants in ordination space. Similarities and distances are calculated based on host association and, in this context, potentially encompass multiple properties of plants, including phytochemistry, phenology, and other plant traits. This approach can distinguish between herbivores that utilize suites of hosts that are commonly used together and herbivores that attack unusual host combinations, and thus have a relatively broad diet breadth. For illustration, we use a data set of nymphalid butterfly host records, and compare taxonomic and ordinated host range. For a large number of butterfly taxa, we find that host use is clustered in multivariate space with respect to associations observed across all of the butterfly taxa. Applications are discussed, including a hypothesis test of nonrandom host association, and prediction of shifts and expansions of diet breadth.

**Key words:** *herbivory; host range; host switch; niche breadth; Nymphalidae; specialization.*

### INTRODUCTION

Variation in diet is common across biological scales of organization, from individuals to populations to evolutionary lineages (Futuyma and Moreno 1988, Bolnick et al. 2003, Devictor et al. 2010, Poisot et al. 2011), and understanding this variation is central to progress in numerous areas of research including population biology (Vázquez and Simberloff 2002), ecological speciation (Nosil 2012), and conservation (Boyles and Storm 2007). Herbivorous insects have long been used in studies of diet breadth, or dietary niche width, because they spend much of their life cycle in close association with discrete resources (host plants) that can be readily identified and experimentally manipulated (Jaenike 1990, Forister et al. 2012). The diet breadth of herbivores in the wild is traditionally quantified with a simple count of the number of plant taxa attacked, and this can be done at the level of plant species or higher taxonomic levels. Although convenient, taxonomic diet breadth is an incomplete

index of biological variation in diet. This is because, as Janzen famously wrote, “herbivores do not eat Latin binomials” (1979), which is to say that particular host plants differ in phytochemistry, physical defenses, mutualists, associated natural enemies, and numerous other traits that are not necessarily encompassed by a hierarchical taxonomy. Consequently, alternatives to taxonomic diet breadth have been suggested, with phylogenetic diet breadth possibly being the most widely used (Symons and Beccaloni 1999, Jorge et al. 2014).

Here we describe a novel index of diet breadth based on observed plant–insect associations that has conceptual and practical advantages. The essence of our approach is to use information on combinations of host plant taxa that are utilized by herbivores as a way to understand differences among plants from the insects’ perspective. Consider two hypothetical herbivores that each have a taxonomic diet breadth of four (i.e., they each attack a different suite of four host plants). In the case of the first herbivore, the four host plants are similar in relevant traits (secondary metabolites, protein, phenology, etc.), while in the case of the second herbivore, the four hosts are quite disparate, perhaps containing a

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<sup>5</sup>E-mail: jfordyce@utk.edu

variety of metabolite profiles or differing in available protein. Intuitively, the first herbivore has a more narrow diet breadth, while the second herbivore has a broader host range, even though they both attack four host plant species. Attempts to quantify such a distinction have previously relied on either phylogenetic distance as a proxy for relevant plant traits (Pearse and Hipp 2009), or experimental work that focuses on particular plant traits to the exclusion of others (e.g., phytochemistry [Honda 1995] or associated natural enemies [Ballabeni et al. 2001]). Here we suggest that observed host associations among herbivores provide a direct way to understand differences and similarities among host plants, and serve as a useful starting point for quantifying diet breadth and for discovering plant traits that are most important in determining plant–insect associations. Returning to the hypothetical example, if we could survey a large number of herbivores that potentially associate with the same eight plant species, then we might find that the four hosts of the first species are frequently utilized in combination, while the four hosts of the second species are only rarely utilized by a single herbivore.

To quantify variation in diet breadth based on observed host associations, we draw on established methods from community ecology that are used to compare suites of co-occurring species found in different community samples or geographic locations (Anderson 2006). In our case, the co-occurring species are groups of herbivores that attack the same plant species. We extract multivariate distances among groups of host-associated herbivores, and use those distances to quantify what we refer to as ordinated diet breadth (ODB). Although a small number of previous studies have used ordination to study similarity of plant-associated insect faunas, to our knowledge, previous studies have focused primarily on the hosts, asking, for example, if insect associations can be used to predict the habitat (Holloway and Hebert 1979), systematic relationships (Futuyma and Gould 1979), or phytochemistry (Ricklefs 2008) of host plants. Building on these previous studies, the advance we offer is an index of herbivore diet breadth based on the ordination of host plants, and a quantitative framework in which novel host use might be predicted. The methods described herein can be employed using the package `ordiBreadth` in the R statistical computing environment (R Development Core Team 2011). We apply our method to both artificial data and a global database of host plant associations for butterflies in the family Nymphalidae as one example of a large plant–insect database (of which many have been reported recently, e.g., Baje et al. [2014], Morris et al. [2014], and Forister et al. [2015]). ODB is compared to taxonomic diet breadth, and for individual butterfly taxa we ask if the hosts utilized are more or less dispersed in ordination space than would be expected based on random host associations.

## METHODS

### *Ordinated diet breadth*

We begin with a matrix that describes host plant associations of the focal herbivores. Using this matrix, we calculate a pair-wise dissimilarity matrix (e.g., Jaccard) among plants. Note that this dissimilarity matrix is based upon plant dissimilarity in herbivore use, not herbivore dissimilarity in host plant use. Here, we choose the Jaccard distance because of its metric quality and its familiarity to ecologists. Other distance metrics (for example, a simple matching coefficient) can be used with this approach, though researchers should take into account how different resemblance metrics treat shared presence and absence information (see Legendre and Legendre 2012, Legendre and Lapoint (2004), Campbell et al. (2011)). We next apply this dissimilarity matrix to principal coordinates analysis (PCoA), thereby placing each possible host plant in multivariate space. As shown by Gower (1966), and further described by Anderson (2006), the result of such ordination is that the original distance between points based on the dissimilarity matrix is equal to the multivariate Euclidean distance. Once the ordination of the plants is completed, each herbivore species can be placed into this multivariate space at the multivariate centroid of its host plants.

We define raw ordinated diet breadth for species  $i$  as the sum of the Euclidean distances between each plant utilized by a species from the centroid for that species. Or  $ODB_{rawi} = \sum_{j=1}^p \sum_{k=1}^v \sqrt{(x_{ijk} - c_{ik})^2}$ , where  $p$  represents the total number of plants used by species  $i$ ,  $v$  represents the number of axes in the ordination,  $c_{ik}$  represents the centroid for the  $i$ th species on axis  $k$ , and  $x_{ijk}$  is the position for the  $j$ th plant used by the  $i$ th species, on the  $k$ th axis. Hereafter, we refer to this as  $ODB_{raw}$ , which can range between zero for an extreme specialist, to a maximum ordinated distance of an extreme generalist that feeds on all possible plants included in the matrix. The maximum possible value from these calculations will vary among data sets, and comparisons within and among data sets might be challenging to interpret. To ease the interpretation, we scale this raw ordinated diet breadth of each herbivore in relation to the maximum possible diet breadth of a hypothetical extreme generalist. This scaled ordinated diet breadth (hereafter, referred to simply as ODB) can be interpreted then as the proportion (or converted to a percentage) of possible diet breadth space occupied by a given herbivore. So as to not affect the ordination, the centroid and the sum of distances from the centroid that describes the diet of the hypothetical extreme generalist can be calculated after the ordination based on the observed herbivore data is completed. As would be expected, raw and scaled ordinated diet breadth are perfectly correlated, and both will be typically positively correlated with taxonomic diet breadth.

An additional characterization of ordinated diet breadth is to account for the effect of host plant richness

Table 1. Artificial data to illustrate ordination of diet breadth.

Herbivores	Host plants										Taxonomic diet breadth	Ordinated diet breadth, ODB		
	A	B	C	D	E	F	G	H	I	J		Raw, ODB <sub>RAW</sub>	Scaled ODB (%)	Adjusted scaled, ODB <sub>adj</sub> (%)
1					x						1	0	0	0
2							x	x			2	0.86	17.6	8.80
3	x	x	x								3	0.56	11.4	3.80
4					x	x		x		x	4	1.22	25.1	6.28
5	x	x	x					x			4	1.37	28.2	7.05
6	x	x			x			x			4	1.50	30.9	7.73
7				x				x		x	4	1.78	36.7	9.18
8	x		x		x	x				x	5	1.81	37.2	7.44
9	x	x			x			x	x	x	6	2.32	47.8	7.97
10	x	x	x		x	x		x	x	x	8	3.33	68.5	8.56

Notes. Hypothetical herbivores are rows (1–10) and hypothetical host plants are columns (A–J). Cells with “x” indicate an interaction, such that a particular plant is attacked by a particular insect. Also shown are four indices of diet breadth: taxonomic (the number of hosts attacked), ordinated, scaled (ordinated diet breadth scaled to the maximum number of hosts that can be used), and adjusted (scaled diet breadth divided by the number of host species attacked).

by dividing the scaled ordinated diet breadth by the taxonomic diet breadth. This provides a value that is a measure of average dispersion from the multivariate centroid for each host plant used. This metric, adjusted scaled ordinated diet breadth (ODB<sub>adj</sub>), can be used to compare the average relative ordinated space occupied by herbivores, regardless of each herbivore’s taxonomic diet breadth. Table 1 shows a simple, hypothetical data set consisting of 10 herbivores and 10 host plants. We applied the ordinated diet breadth measures to these data to illustrate the approach and interpretation.

#### *Diet breadth of the Nymphalidae and hypothesis testing*

We applied the ordinated host breadth procedure to a data set of host plant family records for the butterfly family Nymphalidae (Hamm and Fordyce 2015a,b). In total, there were records for 379 genera of Nymphalidae and 131 host plant families. As with the example above, we used the Jaccard dissimilarity matrix for the PCoA. We asked whether the observed ordinated diet breadths of nymphalid genera occupy a random subset of multivariate space by comparing the observed ordinated diet breadth of each genus with a null expectation of a diet randomly assembled from the set of hosts present in the nymphalid data set. If the observed ordinated diet breadth is greater than the null expectation, it would indicate that the recorded diet breadth of a butterfly genus is overdispersed, suggesting that the diet breadth of the genus is more diverse than expected by chance. If the observed ordinated diet breadth is smaller than the null expectation, it would indicate that host breadth is underdispersed. Underdispersion suggests that overall host range is constrained and that diet breadth is less diverse than expected by chance.

The generation of the null distribution was done in two ways. First, we generated 10 000 random diets for each of the taxonomic host breadths in the data set (maximum = 22 plant families). Each of these random diets was then placed into the ordination based on the nymphalid data set, but did not contribute to the ordination, and the ODB was calculated. This generated a distribution of ODB values expected if the composition of host plants that comprise a diet was a random sample of host plants. We used this null distribution to assess if diets (for each of the different butterfly genera) were different from a random expectation ( $\alpha = 0.05$ ). Observed ODBs that fell below the 0.025 or above the 0.975 quantile of the null distribution were interpreted as genera that had under-, or overdispersed diet breadth, respectively. We choose here to examine the hypothesis as a two-tailed test, as we had no a priori expectation as to whether observed diets might be under-, or overdispersed.

Because the inclusion of any taxon’s diet will affect the ordination and will contribute to the distance between plants in ordination space, we generated a null distribution in a second way. Here, a unique ordination was done for each butterfly genus where the focal genus was not included in the ordination. Plant families were eliminated from the ordination if the focal genus had the only record of using that family. The genus was then placed in this ordination space and its ordinated host breadth was calculated. A null distribution was calculated as before. An R package, ordiBreadth, carries out the ODB analyses described above and includes functions for visualizing results and testing of diet breadth hypotheses (*available online*).<sup>6</sup>

<sup>6</sup> <https://cran.r-project.org/package=ordiBreadth>

While our primary interest was in the quantification of diet breadth, we also asked if the ODB approach could be used to predict host associations for which there is no record. Predicting such associations is relevant for identifying novel interactions with introduced species or for understanding sampling gaps. For each genus with at least two host family records, we systematically dropped each record individually and recorded how near to the centroid the missing plant family was in the new ordination. If the dropped plant family is nearer to the centroid compared to other plant families not used, we interpret this as indicating that the ODB has some ability to predict possible suitable hosts. We further compared the ODB approach to an approach where phylogenetic relatedness of plant families is used to predict missing host records. If inclusion of a missing plant family has a minimal effect on total phylogenetic distance, we interpret this as indicating that phylogeny has some predictive power to identify suitable hosts. We compared the ability of ODB and phylogenetic host breadth to predict host plant use by comparing the median rank distance to the centroid of the ODB analysis to the median rank effect on total phylogenetic distance of each of the plant families by each nymphalid genus. We used the phylogeny of angiosperm plant families from Davies et al. (2004), and thus we restrict this comparison to angiosperm host records.

Finally, we examined how host record quality (i.e., erroneous or incomplete) might affect the utility of the ODB approach to describe diet breadth. Here, we used our current Nymphalidae host records to examine the consequences of incomplete, or erroneous data. We randomly added or subtracted host records from the matrix, and examined how modifying the data affected correlation in host breadths among species between our observed (current host record matrix) and modified (by adding or subtracting records) host breadths. Our current matrix consists of 953 host records. We modified the matrix to have up to 500 fewer host records randomly removed and 500 additional, randomly applied host records. We replicated each value between 500 fewer and 500 additional records 50 times, resulting in 50 000 randomly modified host record matrices. We used the correlation of ODBs between the observed data and the modified data to examine how sensitive the ODB approach is to false positive records (modified matrices with randomly added records) and incomplete, or false negative records (modified matrices with randomly removed records; i.e., simulating a situation in which the original data was incomplete and asking how additional information would affect observed diet breadth).

## RESULTS

As illustrated with artificial data, ordinated diet breadth reveals distinctions among herbivores not captured by taxonomic diet breadth (Table 1, Fig. 1). Species 2 (Fig. 1A) utilizes two hosts and species 3 (Fig. 1B)

utilizes three, but the ordinated diet breadth of species 3 is smaller (concentrated in the lower right corner of the graph) because the three hosts that it utilizes comprise a small cluster of hosts (plants A, B, and C) that are close in ordination space. Note, in Fig. 1 we are only showing axes 1 and 2, but the multivariate distance to the centroid is calculated using all PCoA axes. Those three hosts are proximate in ordination space because they are used in some combination by more than half of the herbivores (Table 1). In contrast, the two hosts (plants G and H) used by species 2 are not used together by any of the other herbivores (Table 1), thus the ordinated diet breadth of species 2 is greater.  $ODB_{adj}$  standardizes diet breadth by taxonomic richness, so that comparisons of breadth can be made among species with different number of hosts. The  $ODB_{adj}$  of species 2 is 8.8%, which is to say that, on average, each host has a unique contribution of that percentage of host space, while the  $ODB_{adj}$  of species 3 is only 3.8%. The ordination of diet breadth can also distinguish between two herbivores that use the same number of host species. In panels C and D (Fig. 1), the herbivores both attack four hosts, but species 5 (panel C) has the more narrow ordinated host range because it attacks three hosts commonly used in combination (plants A, B, and C) plus the next-closest host (G) in ordination space. In contrast, the ODB of species 7 (panel D) encompasses a much greater region.

### *Diet breadth of the Nymphalidae*

Using a global database of nymphalid butterfly host associations, we calculated taxonomic and ordinated diet breadth for 379 butterfly genera associated with 131 host plant families (Hamm and Fordyce 2015a,b). The ordination of diet breadth revealed a high-dimensional space: the first three principal coordinates explain 4.4%, 4.1%, and 3.4% of the variation (see Appendix S1 for scree plot). The high dimensionality of the space makes visualization challenging, but clusters of host use can be identified from plotting the first two PCoA axes. In Fig. 2, ordination of diet breadth is shown for two taxa: one (*Pierella*) associated with seven host families (top panels), and another (*Adelpha*) with 21 host families (bottom panels); both butterfly genera are associated with nonrandom clusters of hosts at  $P < 0.05$ . That is, their ordinated host breadth was lower than the 0.025 quantile of the null distribution. Thus, the host range for both genera is narrower than expected if their host plant repertoire was a random sample of possible host plants. Profile plots organized by the rank distance from the centroid further illustrate that the host plant families for these genera are disproportionately closer to the centroid (Fig 2B,D)).

A comparison of observed, ordinated diet breadth with ordinated diet breadth based on simulated, random associations between all nymphalid butterfly genera and their host plant families is shown in Fig. 3. At higher levels of generalism (more host families attacked), the deviation

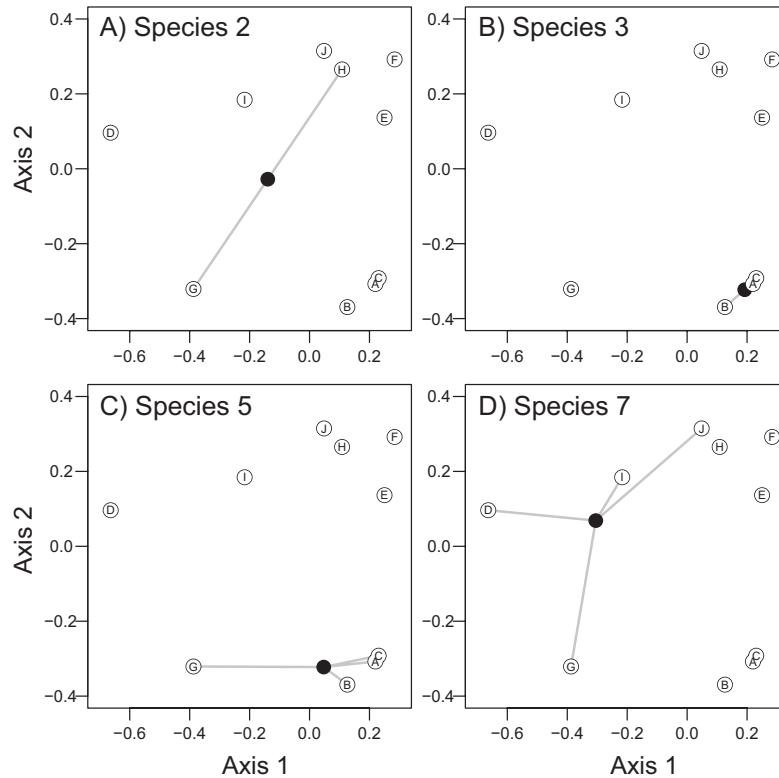


FIG. 1. Illustrations of ordinated diet breadth using artificial herbivore and plant species, with associations as shown in Table 1. Plant taxa are open circles labeled with upper case letters, and the host range of a single focal herbivore is illustrated in each panel, with the centroid as a black circle and the lines connecting to hosts of that herbivore. Comparing the herbivores shown in the first two panels, the herbivore in panel (B) has a wider taxonomic host range (three hosts) but a more narrow ordinated host range. The herbivores shown in panels (C) and (D) have the same taxonomic host ranges (four hosts) but the host range illustrated in panel (D) is wider.

from random becomes increasingly pronounced: observed, ordinated host ranges for the most generalist herbivores are less than would be expected based on random associations (they fall below the 95% highest density interval [HDI] predicted by the null distribution). This is likely due to increased power to detect deviations from random associations as diet breadth increases. However, deviations from random are not restricted to the more generalist taxa: the null hypothesis of random host use was rejected for 48% of the 168 butterfly taxa that utilize two or more host families. A similar pattern was evident using the method where the focal taxon was dropped from the data prior to ordination; there was a general pattern that diet breadth is more restricted than expected by chance alone, and genera with overdispersed diets were rare (Appendix S2). We also examined the utility of the ODB approach to predict known host associations (Appendix S3). Although imperfect, the ODB outperformed phylogenetic distance in the prediction of host associations. More than 60% of the time, the missing plant family was ranked lower when examining distance to the centroid compared to the rank when examining phylogenetic distance (binomial test,  $P = 0.002$ ) (Appendix S2). Overall, the ODB method is robust to

erroneous data (assuming errors are randomly distributed) and deviations from the observed data that exceeded as much as 50% of the data set retained high correlations between the results for the observed and manipulated data. The method is less sensitive to incomplete data (based on simulations where host records were randomly removed) compared to erroneous records (based on simulations where host records were randomly added; Appendix S4).

## DISCUSSION

Ordinated diet breadth uses observed associations among hosts and herbivores to calculate diet breadth based on multivariate distances among plants. Different indices can be calculated from the ordination of plant–insect associations (Table 1). We have focused on the scaled ordinated diet breadth (ODB) and the adjusted ordinated diet breadth ( $ODB_{adj}$ ) because the interpretation of each is useful and straightforward: the former is the percent of ordination space occupied relative to an extreme generalist that uses all possible hosts, and the latter compensates for the effect of taxonomic richness and, thus, is an average unique contribution to ODB of each host. Herbivores with identical

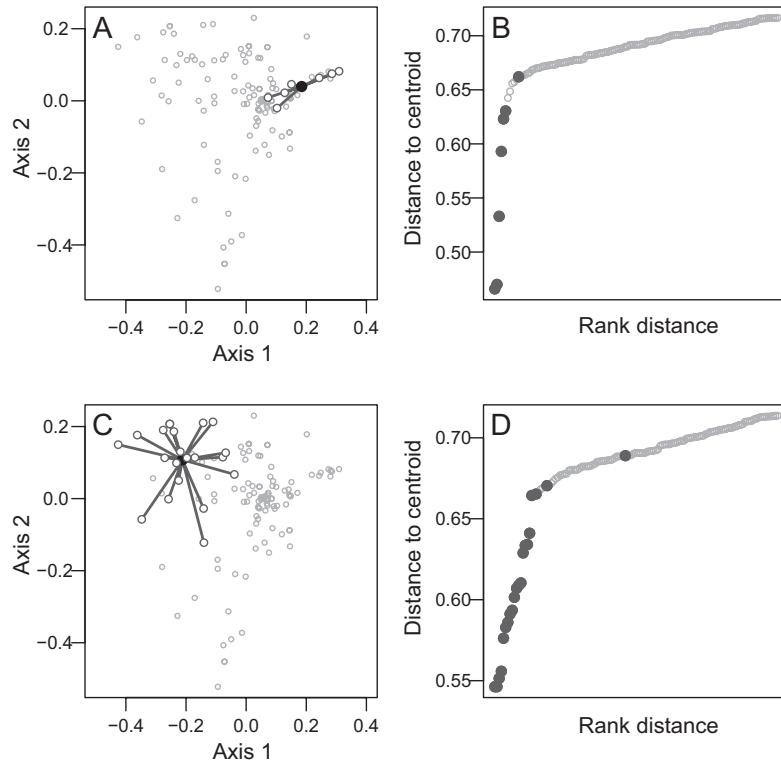


FIG. 2. Ordinated host range and plant profile plots for two of the butterfly taxa studied. In panels (A) and (C), the open circles are host plant families ordinated based on associations observed across all 379 butterfly taxa; the solid points are the centroids of diet breadth for the two butterfly genera (*Pierella* and *Adelpha*); and lines connect centroids to the hosts utilized by those genera. In panels (B) and (D), all hosts are organized relative to their distance from the diet breadth centroid for the two butterfly genera, with rank distance on the x-axis and metric distance (unitless) on the y-axis. Solid points are hosts that are utilized and light gray points are un-utilized plant families.

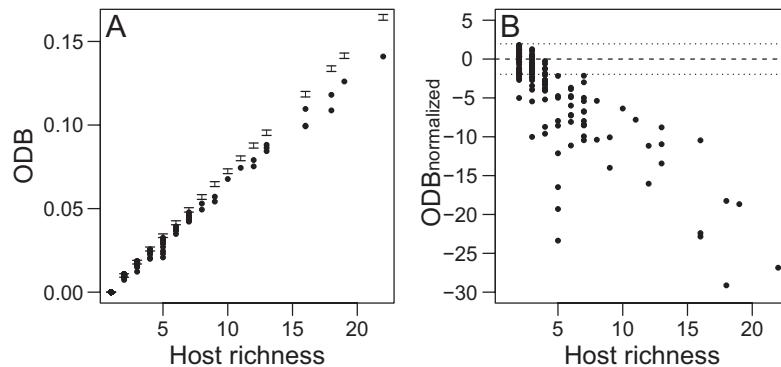


FIG. 3. (A) Comparison of taxonomic diet breadth (host richness) (x-axis) with scaled ordinated diet breadth (ODB; y-axis). Pairs of horizontal lines represent 0.025 and 0.975 quantiles from simulations of random host associations for different numbers of host taxa attacked, and points correspond to the observed diet breadths of butterfly taxa. For butterfly taxa that attack larger numbers of hosts, deviations from simulations become more pronounced (more generalized butterflies attack increasingly nonrandom subsets of hosts). (B) Comparison of taxonomic diet breadth (x-axis) with normalized ordinated diet breadth. The data are the same as in panel (A), but shown as normalized standard deviations to visualize effect size. Dotted lines indicate 95% confidence intervals of the normalized null distribution.

taxonomic diet breadth can have different ODB and  $ODB_{adj}$  if they use plants that are used more or less frequently in combination by all of the herbivores (e.g., species 5 vs. species 7 in Fig. 1). Because ordinated diet breadth is

based on patterns of observed associations between plants and herbivores, it potentially captures many aspects by which plants differ (such as phytochemistry, phenology, associated natural enemies, and others), and thus reveals

differences among herbivores that could be important for the study of any evolutionary or ecological process involving the quantification of diet breadth.

Applying the ODB approach to global nymphalid host associations, we find that many of the butterfly genera use nonrandom assemblages of host plant families. Note that our example data set was resolved at the level of butterfly genera, but of course the method is applicable to any taxonomic level, including lower taxonomic or demic levels such as populations and species (as in our hypothetical data in Table 1). More generalized nymphalid taxa show increasingly more clustered host use than would be expected based on random associations (Fig. 3). Superficially, it is perhaps surprising that generalists are not attacking hosts more (rather than less) indiscriminately. However, it is likely the case that hosts are never added at random to the diet of an insect herbivore (i.e., there are ecological or phytochemical reasons that host plant species are colonized), and nonrandom patterns of association are more readily detected in generalists with connections to a greater number of plants.

It is important to note that one of our tests for clustered host use (nonrandom association) was based on an analysis in which the focal butterfly taxon is first removed from the diet matrix to generate the ordination of hosts to which its patterns of host association are then compared. Thus a signal of nonrandom host use for a given herbivore taxon implies that it uses a suite of hosts that are predictably associated based on the host records for the whole suite of herbivores being studied.

One of the benefits of the ordination method that we propose is that it has immediate implications for predicting records of novel host use, including expansions and shifts in diet. The preference profile plots that we generate can be used to rank currently unused or unknown hosts based on their distance from the centroid of host associations for a given herbivore, and thus generate predictions that could be directly tested with experimental work. Plants that are near the centroid but currently not utilized by the herbivore could be considered as suitable candidate hosts. See for example Fig. 2, where we can suggest that families Amaranthaceae and Fabaceae (among others) might be acceptable to *Adelpha*. This prediction is based on the observation that these two potential host families are the two nearest the centroid of *Adelpha* that are not known to be used by the genus (Appendix S5). Their proximity in ordination space is a consequence of host associations recorded for all nymphalids, and thus those other genera act like bioassays that pose hypotheses of novel host use for a focal taxon.

Empirically, ordinated diet breadth should be of interest to researchers because it captures differences and similarities among herbivore diets that might be intuitively apparent, such as common associations among subsets of host plants that comprise a diet, but not previously quantified. However, there is still work to be done to determine the utility of different diet breadth indices

for different purposes. For example, there are other distance measures to be explored, which might be well suited to particular data structures or experimental designs. If shared absence of host plant use is considered to be informative, using a simple matching coefficient to construct a distance matrix might be illuminating. Other areas in which advances could be made include the development of tools to deal with the scale of sampling, as different null expectations should arise from local vs. global data sets because herbivores have complete access to hosts at the former but not the latter scale. This issue has recently been well treated for phylogenetic diet breadth by Jorge et al. (2014) and similar approaches could be applied to ODB. Finally, a rigorous comparison of ODB with phylogenetic diet breadth will be important, potentially at multiple taxonomic scales (e.g., diet breadth measured at the scale of host plant families as well as diet breadth measured at the scale of host plant species). Although there is much yet to be done, we hope that the ordination approach described here will serve as a useful hypothesis testing tool, and adds to the conversation about measuring ecological specialization that has always been central to ecology and seems to be gaining momentum in recent years.

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