Title:

Jack-of-all-trades paradigm meets long-term data: generalist herbivores are more widespread and locally less abundant

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Abstract

Some of the most common ecological interactions are between plants and herbivorous insects, and these relationships are central to the study of ecological specialization. We address established assumptions about the positive association between local abundance and dietary specialization using a 17-year dataset on the caterpillars of Ecuador. Our long-term data include standardized plot-based samples as well as general, regional collections, allowing for investigations across spatial scales and using different indices of abundance for 1917 morphospecies of Lepidoptera from 33 families. We find that specialists are locally more abundant than generalists, consistent with a key component of the "jack of all trades, master of none" hypothesis, which has otherwise received poor to mixed support from previous studies that have mostly involved fewer species and shorter time series. Generalists achieve greater prevalence across the landscape, and we find some evidence for geographic variation in the abundance-diet breadth relationship, in particular among elevational bands. Interspecific variation in abundance also had a negative relationship with diet breadth, with specialists having more variable abundances across species. The fact that more specialized species can be both rare and common highlights the ecological complexity of specialization.

Keywords: Diet breadth, diet specialization, abundance, plant-herbivore, scale, tropics, long-term data, generalists, specialists

Introduction

Insects are a remarkably diverse taxon, and all ecological guilds of insects engage in some of the most consequential and common ecological interactions. Ecology and evolutionary biology have benefited from studies of plant-insect interactions, especially studies on ecology and evolution of specialization, which have attracted decades of attention (Ehrlich and Raven 1964; Mani 1968; Forister et al. 2012). A common explanation and expectation for specialization has been that "a jack of all trades is a master of none," which is, in the ecological context of dietary specialization, the idea that a generalist might be able to consume a wide range of resources but will not be particularly well adapted to any one of them (MacArthur 1972; Futuyma and Moreno 1988). Two predictions are associated with this idea. First, functional trade-offs have long been hypothesized as the most parsimonious explanation for the predominance of specialists. If adaptation to one resource comes at the expense of lower performance on another resource, then specialists will be common and generalists will be favored only under certain circumstances. For example, a single-locus antagonistic pleiotropy for the ability to digest different food types favors specialization on one food type, whereas generalists will only be favored under special conditions, such as high fluctuations in host plant availability. That prediction has received only minimal support (Hardy et al. 2020), and is not our focus here. We are interested in a second prediction involving ecological consequences of specialization, specifically the idea that specialists should be locally more abundant, while generalists might never be as abundant in any one location but might occupy more places across broader landscapes. This prediction has often been stated in experimental terms for a small number of taxa (e.g., specialists will outperform generalists when tested on a common resource), which highlights the lack of relevant ecological, field-based datasets in the literature (Dyer et al.

2015). However, testing the empirical pattern in the field is of central importance to our understanding of interaction networks and even ecosystem stability.

Studies that close the knowledge gap with respect to diet breadth and abundance at different scales are likely to contribute substantially to our understanding of specialization and the ecology and evolution of plant-insect interactions. Here, we use a 17-year empirical dataset from Ecuador, which included replicated elevational gradients, to examine associations between diet breadth and caterpillar (larvae of Lepidoptera) abundance, and to include potential effects of spatial scale on these relationships. The long-term data include intensive sampling across space and time, allowing for multiple measures of abundance. With these empirical data, we ask the simple question of whether there is an association between abundance and diet breadth for caterpillars in Ecuador and how the relationships between diet breadth and abundance vary across different scales of observation. We hypothesized that caterpillar abundance would decrease with increasing diet breadth, consistent with the "jack of all trades is a master of none" hypothesis, especially at smaller spatial scales where the local demographic advantage of being well-adapted to a host plant should be evident. At larger spatial scales, we expected to discover an advantage to dietary generalization: because generalists can be found on multiple host species, they should turn up in more surveys and plots, reflecting broader landscape-level occupancy.

Methods

Study location & collection protocol

We used 17-years of host plant-lepidopteran herbivore interactions collected within the Eastern Andes of Ecuador between 2001–2018 (Fig. 1a; 420 km^2 from 00.36° S and 77.53° W) (Wagner 2020) along an elevational gradient (100-3800m) that included low montane forests and

paramo habitat to explore relationships between caterpillar diet breadth and density. Caterpillars were found by visual inspection of leaves using two distinct methods: general collecting and sampling within standardized circular plots (10 m diameter). Both collection protocols and rearing methods are fully described in previous publications (Dyer et al. 2007; Salcido et al. 2020). Briefly, general collection consisted of opportunistic collection of caterpillars along roads, trails, transects, or off trail searches while plots were designated at least 10 m from roads or trails and included estimates of plant diversity and genera-level leaf area. For both methods, caterpillars were collected and assigned a specific record number and reared to adulthood. Caterpillars and their host plant were identified to the lowest taxonomic level. In cases where the resolution of taxonomic identifications was limited to family or genus, caterpillar or host plant morphotypes were assigned based on family or genus designations in combination with character descriptors. We removed data for which either host plant or caterpillar family and descriptors were unavailable.

Diet breadth and density estimates

We used host plant and caterpillar taxonomic identifications from both general collections and plots to calculate diet breadth of each caterpillar species. For our analyses, diet breadth is the total number of unique host plants consumed by a given caterpillar species or morphotype using all data from general collections and plots. We used only data collected within plots to estimate caterpillar densities at plot and elevation scales. The abundance of each caterpillar species was summed for each 10-m diameter plot (78.5 m^2). We also calculated an index of landscape occupancy as the frequency of observation for a particular caterpillar species across plots. Density per available host plant area and occupancy were summarized for plot and

elevation scales for which adequate data were available. Additionally, we explored an alternative measure of density by calculating density per unit plot area and reported associated results in the supplement.

Spatial scales

To evaluate the effect of spatial scale on associations between diet breadth and abundance we examined patterns at various scales (in order of increasing area): 1) plot scale (including plots that were aggregated to form larger subsets), 2) discrete elevational bands, and 3) a regional scale. For plots, data were collected from a total of 455 plots. We examined the effect of scale on the relationship between diet breadth and density at the plot-level, by aggregating plots into groups and calculating the average density and occupancy for each caterpillar species across all plot groups. This process was iterated for plot groupings of increasing size. To group them, a moving window method was applied (Fig. 1b). The window size was equivalent to the number of plots grouped together (n=2-455 plots) and moved sequentially (in order of time that the plots were completed) along the plot data in order to maximize spatial and temporal similarities among plots. For each iteration, the window size increased by one plot. For example, for a window size of two, caterpillar abundance and area from plot 1 and plot 2 was summarized followed by all iterations of plot n-1 and plot n. In the subsequent iteration, the window size increased to three plots and so on until the window size equaled the number of all plots. Results presented in the main text are limited to groupings of 5 (~393 m^2), 25 (~1963 m^2), 50 (~3927 m^2), and 250 (~19535 $m^{2)}$) plots, however, results for all possible aggregates were calculated and are presented in the supplementary text.

Plots within four distinct elevational bands: 1) 0 m - 1000 m, 2) 1000 m - 2000 m, 3) 2000 m - 3000 m, and 4) above 3000 m were aggregated (Fig. 1a), and these elevational bands are ecologically very distinct (Pyrcz et al. 2009). Density was calculated based on the total caterpillar abundance within each elevational band per available host plant area. While turnover is substantive at a finer elevational scale (e.g., Sklenár and Ramsay 2001), elevational bands were defined based on data availability and to allow for sufficient data at distinct elevations.

To examine caterpillar abundance at the regional level, total abundance for each caterpillar species was summarized across the entire dataset. This included caterpillars collected from both plot-based and opportunistic collection methods. With the data summarized at this level, we needed another method to account for the fact that generalists could be observed more often simply because they occur on a wider range of host plants. Thus, we calculated the number of times that a caterpillar has been collected, divided by the number of hosts on which it occurs (in other words, average abundance per host). For example, if a caterpillar A has a total abundance of 10 and a diet breadth of 2 (it uses 2 host plant species), the density per host species is 5. Prior to the analyses described here, we identified extreme outliers and singletons (species for which there was only one record in the dataset) and removed them from statistical analyses. Due to its unusually high abundance from sampling bias for related research projects, we also removed *Eois olivacea* (Geometridae: Larentiinae).

Statistical inference

We used Bayesian linear models to estimate beta coefficients for the association between abundance or occupancy and diet breadth for plot, elevational and regional scales. Models were fit in JAGS (version 3.2.0) utilizing the rjags package in R (R version 3.6.3 and RStudio version

153 1.2.5042) using (for each analysis) two Markov chains and 1,000,000 steps each; performance
154 was assessed through examination of chain histories (burnin was not required), effective sample
155 sizes and the Gelman and Rubin convergence diagnostic. Response variables (abundance and
156 occupancy) were modeled with assumptions of normally distributed residuals with means
157 dependent on an intercept plus diet breadth as a predictor variable. We used weakly informative
158 priors: priors on beta coefficients were normal distributions with mean of zero and precision of
159 0.001 (variance = 1000); priors on precisions were modeled as gamma distributions with
160 rate = 0.1 and shape = 0.1. We report point estimates for beta coefficients and corresponding 95%
161 credible intervals (CI). Values for density, occupancy, and diet breadth were log transformed
162 ($\log_{10}$) prior to analyses.
163

164 **Results**

165 Caterpillar density per available host area showed a negative relationship with diet
166 breadth for plot and elevational scales, except for the highest elevation band (Fig. 2a-b, Table 1,
167 Fig. S1). This relationship reflects a tendency for more specialized caterpillar species to be more
168 abundant wherever they are found. In contrast, occupancy (frequency of occurrence across the
169 landscape) showed a positive relationship with diet breadth for all plot cluster sizes (Fig. 2c,
170 Table 1, Fig. S2); however, the relationship varied across different elevation bands (Fig. 2d,
171 Table 1). A positive relationship was observed at the middle elevation bands (1000-2000 m and
172 2000-3000 m) while weak positive and negative relationships between occupancy and diet
173 breadth were observed at the low (< 1000 m) and high (>3000 m) elevation bands respectively
174 (Fig. 2d, Table 1). At our largest spatial scale, using all data, including plots and general
175 collections, we did not detect a relationship between density per available host plant species (β=

-0.076, 95% CI [-0.15, -0.0061] and diet breadth (Fig. 3). When density was calculated per plot area, patterns at both plot and elevation scales were similar to trends observed for occupancy (Fig. S3-4).

Discussion

As a theoretical expectation, the idea that a "jack of all trades is a master of none" has withstood decades of examination with limited consensus, depending on the organisms and the traits being examined (Futuyma and Moreno 1988; Forister et al. 2012). For many morphological traits, biophysical constraints in vertebrates have produced clear examples where an ecological generalist underperforms specialists (Oufiero et al. 2012). The story has been more complicated for herbivorous insects, where the focal trait is typically developmental performance in juvenile life history stages, and specialists have often not outperformed generalists when experimentally evaluated on a common resource (García-Robledo and Horvitz 2012; Agrawal 2020). Instead of an experimental framework, we have taken a different approach by examining the relationship between abundance and diet breadth measured across large spatial and temporal scales in the field, and consistent with expectations we find that specialists tend to be locally more abundant while generalists occupy more places on the landscape. This result raises the possibility that specialists are indeed better adapted to their host plants, while generalists benefit from being able to colonize more hosts. That general pattern is largely robust to observations taken at different elevational and spatial scales (Fig. 2), although we did not detect a signal at the very largest scale that included general collecting (Fig. 3), possibly because our measure of "abundance" at that level is not as sensitive as the plot-level counts of individuals used at the smaller spatial scales.

199 The other classic expectation from the jack-of-all-trades hypothesis is that the local
200 advantage of specialists derives from genetic trade-offs that prevent the maximization of fitness
201 across resources (Levins 1968; Agosta and Klemens 2009). That explanation has been
202 repeatedly questioned, with very few exceptions (e.g., Gompert and Messina 2016), and it is
203 important to note that the results reported here do not support or address the idea of genetic
204 trade-offs. Instead, it should be remembered that other explanations for a local specialist
205 advantage have been proposed (Fry 1996), including more efficient natural selection for
206 populations exposed to a single resource (Whitlock 1996). Regardless of the mechanism
207 explaining the tendency towards higher densities of more specialized species, an important
208 finding here is not only the sign and magnitude of that relationship, but also the shape of the
209 variance. In particular, the range of densities observed for specialists is orders of magnitude
210 greater than the range for densities of generalists (Fig. 2A). This broad distribution of densities
211 for specialists counterintuitively raises the possibility that being a host specialist is a more
212 multifaceted condition than host generalization. Specialists, for example, likely contend with a
213 different suite of natural enemies that affect local abundance in ways that are heterogenous and
214 deserve further study (Singer and Stireman 2005). Future investigations could, for example,
215 target dramatic differences that we report in the ratio of specialists to generalists that we report
216 among host genera (Fig. S5).

217 In conclusion, the results reported here are a reminder that many decades are often
218 needed for the evaluation of basic assumptions that underlie ecological theory, especially when
219 that theory is applied to complex traits such as digestion, development, and host use. A similar
220 study was recently conducted with armored scale insects, with the conclusion that diet breadth
221 and abundance are not linked (Peterson et al. 2020). Although Peterson et al. (2020) did not

222 detect an overall abundance-diet breadth relationship, it is the case that the most abundant
223 species tended to be extreme specialists. There is clearly much yet to be learned about ecological
224 and dietary specialization, and the observations reported here are made more relevant in the
225 midst of ongoing reports of declining insect abundances from around the world (Salcido et al.
226 2020; Wagner 2020). We hope that coming decades see long term datasets, such as the one used
227 here, being used simultaneously to motivate conservation and to test long-standing and
228 unresolved ideas about how the natural world works.
229

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239
240

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Table 1. Summary statistics of density per available host plant area and occupancy at plot and elevation level.

Level of observation	Density per available host plant area		Occupancy	
	β coefficient	95% CI	β coefficient	95% CI
Plot level (cluster size)				
5	-0.35	[-0.47, -0.22]	0.64	[0.56, 0.72]
25	-0.36	[-0.49, -0.23]	0.54	[0.46, 0.61]
50	-0.36	[-0.48, -0.23]	0.47	[0.39, 0.54]
250	-0.35	[-0.47, -0.24]	0.24	[0.15, 0.32]
Elevation level				
Low (<1000 m)	0.097	[-1.72, 1.63]	0.12	[-0.33, 0.50]
Mid 1 (1000-2000 m)	-0.31	[-0.49, -0.12]	0.43	[0.34, 0.53]
Mid 2 (2000-3000 m)	-0.35	[-0.48, -0.21]	0.62	[0.52, 0.71]
High (>3000 m)	-0.73	[-1.48, 0.068]	-0.049	[-0.30, 0.20]

322 **Figure legends**

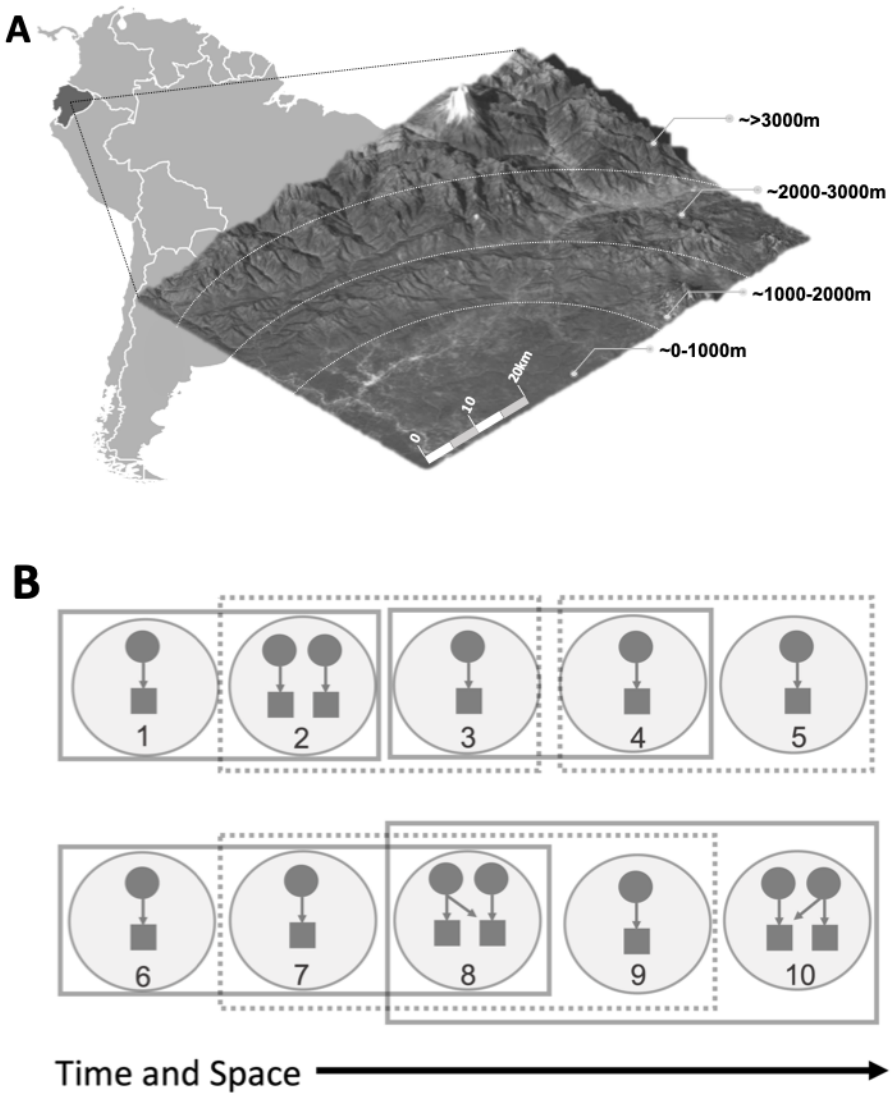
323 **Figure 1**. This study took place in the Northeastern Andes in Ecuador, and plot-level data were
324 aggregated to examine the effect of increased scale on the relationship between density and diet
325 breadth. A) Samples were collected within the Napo Province across different elevations. Plots
326 were categorized into one of four distinct elevational bands (0-1000m, >1000-2000m, >2000-
327 3000m, >3000m from sea level); although substantial species turnover occurs at finer scales, we
328 only had sufficient data for these groups. Lines delineating the different elevations are not exact
329 and are intended to be used as a heuristic tool. B) Effects of scale were evaluated at the plot level
330 by sequentially aggregating plots (circles) using a moving window method (solid and dashed
331 boxes). The moving window method was applied to the plot data iteratively: each time the size
332 of the window (the number of plots aggregated) increased by one more plot. For a window size
333 of five (e.g., plots 1-5), every two plots were sequentially aggregated. In the next iteration, every
334 six plots were sequentially aggregated (e.g., plots 1-6). For each aggregate and caterpillar species
335 (circular nodes), abundance was summarized. Density was calculated based on the combined
336 area or corrected for the leaf area of associated host plant genera (square nodes). Density across
337 all plot aggregates for a given species were averaged.

338 **Figure 2.** Relationship among diet breadth and caterpillar density corrected for available host
339 area (cm^2) and occupancy (landscape presence) at different scales of observation: a) and c) are
340 plot scales, and b) and d) are elevation scales. Plot-level data were combined for each caterpillar
341 species (points) for various plot aggregates (blue: 5 plots, red: 25, green:50 and purple:250) to
342 evaluate the effect of scale. For the elevation analysis, discrete elevation bands included: 0 -
343 1000 m (red), 1000-2000 m (green), 2000-3000 m (purple), and above 3000 m (blue). Points

were set to a transparency value given the quantity of points, such that darker hues indicate a high density of points.

Figure 3. Relationship between caterpillar density per host plant species and diet breadth at a regional scale. Points were set to a transparency value given the quantity of points, such that darker hues indicate a high density of points.

Figure 1


A
~>3000m
~2000-3000m
~1000-2000m
~0-1000m
0
10
20km
B
1
2
3
4
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Time and Space

Figure 2

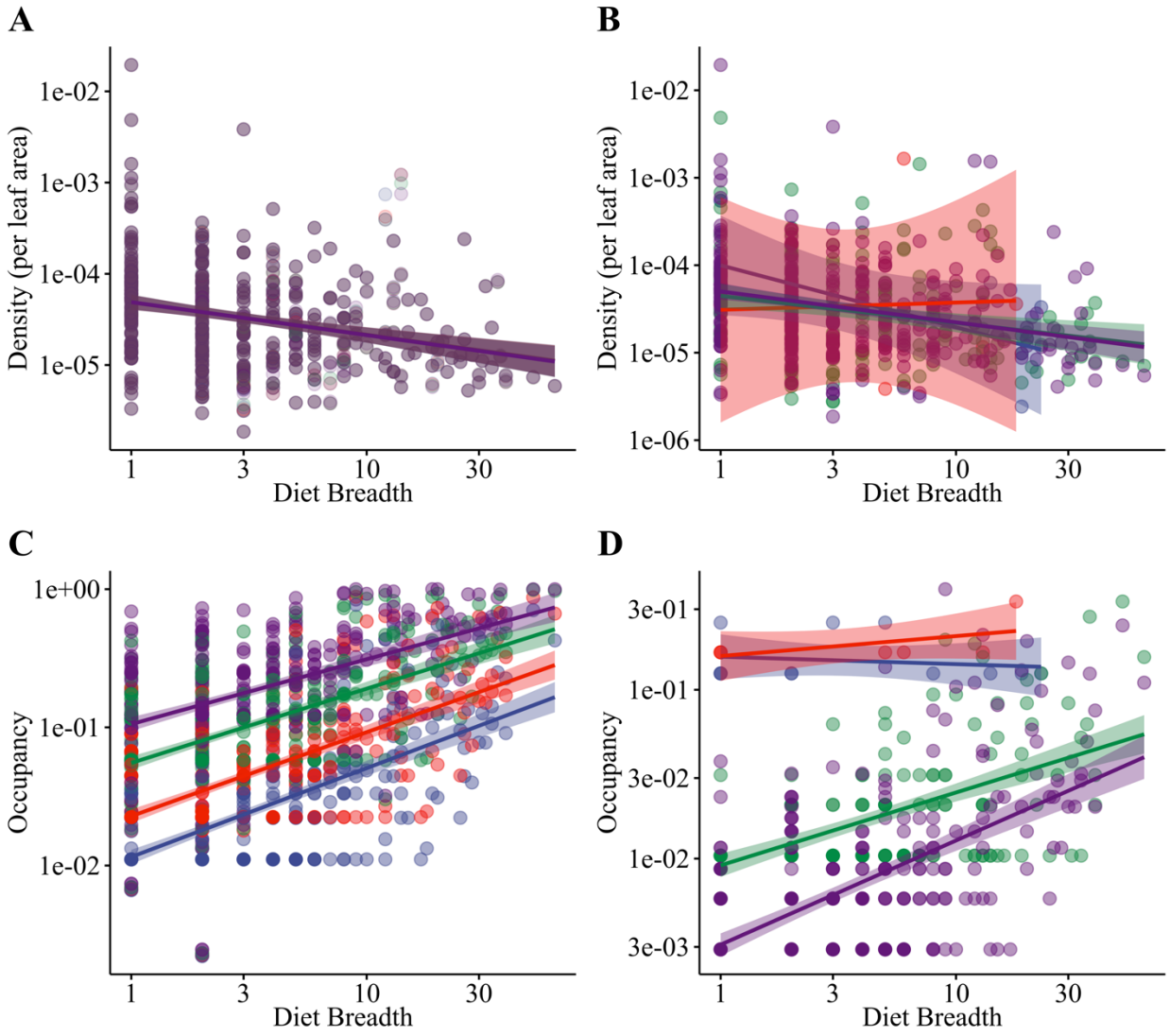
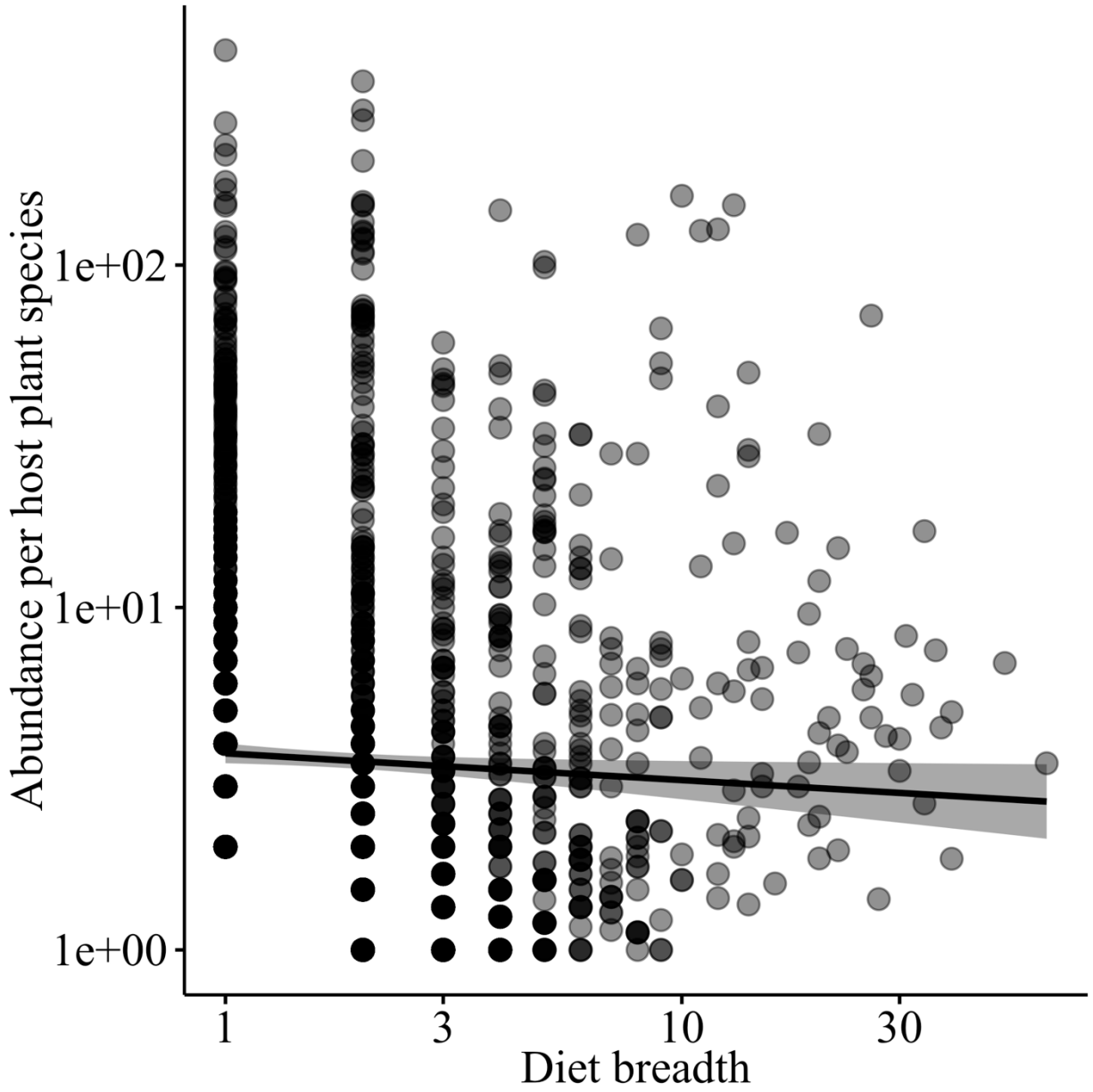

A
B
C
D
Density (per leaf area)
Occupancy
Diet Breadth
1e-02
1e-03
1e-04
1e-05
1e-06
1e+00
1e-01
3e-01
3e-02
3e-03
1
3
10
30

Figure 3


Abundance per host plant species
1e+02
1e+01
1e+00
1
3
10
30
Diet breadth