LETTER

ECOLOGY LETTERS · cnrs · WILEY

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

Chanchanok Sudta[1] | Danielle M. Salcido[1] | Matthew L. Forister[1] |
Thomas R. Walla[2] | Santiago Villamarín-Cortez[1,3] | Lee A. Dyer[1,3]

[1]Department of Biology, Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, Nevada, USA

[2]Department of Biological Science, Colorado Mesa University, Grand Junction, Colorado, USA

[3]Instituto Nacional de Biodiversidad - INABIO, Quito, Ecuador

Correspondence
Lee A. Dyer, Department of Biology, University of Nevada, Reno 1664 N. Virginia Street, Mailstop 0314, Reno, NV 89557, USA.
Email: nolaclimber@gmail.com

Abstract

Insect herbivores are relatively specialized. Why this is so is not clear. We examine assumptions about associations between local abundance and dietary specialization using an 18-year data set of caterpillar–plant interactions in Ecuador. Our data consist of caterpillar–plant associations and include standardized plot-based samples and general collections of caterpillars, allowing for diet breadth and abundance estimates across spatial scales for 1917 morphospecies. We find that more specialized caterpillars are locally more abundant than generalists, consistent with a key component of the 'jack of all trades, master of none' hypothesis. As the diet breadth of species increased, generalists were not as abundant in any one location, but they had broader occupancy across the landscape, which is a pattern that could reflect high plant beta diversity and is consistent with an alternative neutral hypothesis. Our finding that more specialized species can be both rare and common highlights the ecological complexity of specialization.

KEYWORDS
abundance, diet breadth, diet specialization, generalists, long-term data, plant–herbivore interactions, scaling, specialists, tropics

INTRODUCTION

Insects are a remarkably diverse taxon, and herbivorous insects engage in some of the most consequential and common ecological interactions. The fields of ecology and evolutionary biology have benefited from studies of plant–herbivore interactions, especially studies on niche specialization, which have attracted decades of attention (Ehrlich & Raven, 1964; Forister et al., 2012; Mani, 1968), yet the ecological and evolutionary determinants of specialization are still a complex puzzle (Hardy et al., 2020). A common 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 while not being particularly well adapted to any one of them (Futuyma & Moreno, 1988; MacArthur, 1972). Two predictions are commonly associated with this idea. First, functional trade-offs have long been

hypothesized as a parsimonious explanation for the predominance of specialists (Poisot et al., 2011; Ravigné et al., 2009). If adaptation to one resource comes at the expense of lower performance on another resource, then specialists will be common, and generalists will be favoured only under certain circumstances (Wilson & Yoshimura, 1994). For example, a single-locus antagonistic pleiotropy for the ability to digest different food types favours specialization on a narrow diet (e.g. Zhong et al., 2004), whereas generalists might only be favoured under conditions of fluctuating resource availability (see Agrawal, 2020 for a discussion of trade-offs at this and other levels of ecological organization). Functional trade-offs in dietary specialization have received only minimal support (Gompert & Messina, 2016; Hardy et al., 2020; Joshi & Thompson, 1995) and are not our focus here.

We are interested in a second prediction involving ecological consequences of specialization, specifically the

idea that specialists should be more successful locally, whereas generalists are able to occupy more places across the landscape. This prediction follows from the idea that generalists are 'masters of none' and has often been tested in experimental contexts with a small number of taxa on a common diet (e.g. Tapia et al., 2015; Kelly & Bowers, 2016; also see discussion of the 'physiological efficiency' hypothesis in Scriber, 2010). That scale of experimental investigation highlights the lack of relevant ecological, field-based data sets in the literature (Dyer et al., 2015; Peterson et al., 2020). These expectations are related to but distinct from the positive association between abundance and distribution that has been observed across a wide range of taxa (Brown, 1984). The resource breadth hypothesis posits that the ability to use multiple resource types leads to both wider geographic distribution and greater abundance in any particular location where multiple resources can be accessed (Krasnov et al., 2004; Morris et al., 2021). The distinction between the resource breadth hypothesis and the master of none expectation involves scale: most herbivorous insects complete juvenile development on a single plant, and even herbivores that attack multiple species will often use a single host in any one location (Fox & Morrow, 1981); thus, we have the expectation (in the context of the jack-of-all-trades hypothesis) of a negative abundance–diet breadth relationship for herbivorous insects.

We used an 18-year empirical data set from Ecuador, which included replicated elevational gradients (i.e. each elevational band had sites across the Ecuadorian Andes, and there were multiple collecting areas within the sites) to examine associations between diet breadth and caterpillar (larvae of Lepidoptera) abundance. The large geographic extent of this database (approximately 30,000 km^2) allowed for analyses to examine the potential effects of spatial scale on these relationships. There is no single measure of specialization that captures the complexities of insect diet breadth (Table S1). Thus, we have taken a multifaceted approach that includes taxonomic and phylogenetic diet breadth as well as an ordinated index based on the community of observed plant–herbivore associations (Table S1). We ask the simple question of whether there is an association between abundance and multiple measures of diet breadth and how that relationship might 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, unless it is an especially rare plant species. In contrast, there might be both adaptive and neutral explanations for a positive association between diet breadth and abundance (or occupancy), especially at the landscape scale (Forister & Jenkins, 2017; Peterson et al., 2020). From an adaptive perspective, having a broader geographic range could confer resilience

to environmental disturbance as a kind of bet hedging strategy for generalists. Neutral models typically assume that there are no trade-offs associated with expanding resource utilization and that a particular diet breadth is not associated with greater local abundance; at the same time, broader landscape occupancy in a neutral model can be an epiphenomenon of the ability to consume more host species (Forister & Jenkins, 2017). Thus, 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 (Scriber, 2010).

METHODS

Study location and collection protocol

We used 18 years of host plant–caterpillar interaction data collected within the Eastern Andes of Ecuador within the Napo Province between 2001 and 2018 (Figure 1a; 30,000 km^2 from 00.36°S and 77.53°W) along an elevational gradient (100–3800 m) 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 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 sampling of caterpillars along roads, trails, transects, or off-trail searching. The plot sampling was standardized by sampling all caterpillars within a 10-m diameter circular plot; within these plots, estimates of leaf area as a proxy for biomass for all plants were recorded, and each plot was located at least 10 m away from roads or trails. For both methods, caterpillars were collected and assigned a specific record number and their plant associations were experimentally verified by rearing all individuals to adult stages, in captivity, on the plants from which they were collected. If a caterpillar did not consume a host on which it was collected, it was either liberated or switched to a previously recorded host. Caterpillars and their host plants were identified to the lowest possible 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 morphological 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
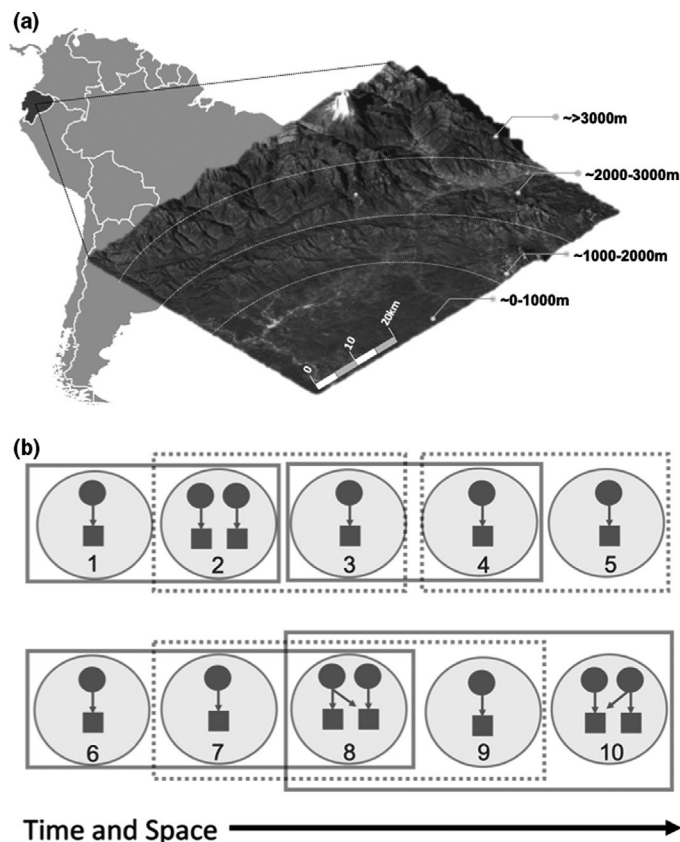
FIGURE 1 Study location and plot aggregation. (a) Samples were collected across different elevations. Plots were categorized into one of four distinct elevational bands (0–1000, 1001–2000, 2001–3000 and >3000 m a.s.l.); lines delineating the different elevations are not exact. (b) Effects of scale were evaluated at the plot level by sequentially aggregating plots (light grey circles) using an iterative moving window method (solid and dashed boxes) for which the size of the window (the number of plots aggregated) increased by an additional plot per step, then abundance was calculated. Mean density of a caterpillar species (circular nodes in the plot networks) was calculated based on the combined plot area or corrected for the leaf area of associated host plant genera (square nodes). In the sampling examples here, two plots (1–2, 2–3, 3–4, 4–5) and three plots (6–8, 2–9, 8–10) per window are combined for abundance estimates

calculate diet breadth of each caterpillar species. For our analyses, taxonomic diet breadth is the total number of unique host plant species consumed by a given caterpillar species or morphotype using all data from general collections and plots. We repeated all analyses using complementary methods for ordinated diet breadth and phylogenetic diet breadth (results are reported in detail in the supplementary materials). Ordinated diet breadth is based on all observed associations between plants and caterpillars and involves calculating multivariate distances among hosts in ordination space that is structured by the plant–caterpillar associations (Fordyce et al., 2016). For example, a caterpillar associated with three hosts that are rarely used by other herbivores will have a broader ordinated diet breadth (possibly consuming, for example, more unique combinations of phytochemical compounds) than a species that uses three hosts that are frequently used in combination by other caterpillar species (potentially because those three hosts are phytochemically relatively similar and interchangeable). Thus, this method potentially encompasses functional similarities (e.g. shared plant chemistry) among suites of hosts (Fordyce et al., 2016). We measured phylogenetic diet

breadth as the sum of the phylogenetic branch lengths spanning the diet breadth of a given herbivore using the pd() function (include.root = TRUE) from the R package picante (Kembel et al., 2010) and an angiosperm phylogeny from Davies et al. (2004). Both ordinated diet breadth and phylogenetic diet breadth were calculated at the host plant family level, as published angiosperm phylogenetic hypotheses did not include most of the host plants species and many of the genera in our data set. We are aware that other and often more complex phylogenetic indices of diet breadth exist (Jorge et al., 2017), but we have used the index most easily interpreted (involving branch lengths spanning hosts for a particular herbivore) for comparison with non-phylogenetic indices. We subtracted the phylogenetic distance of monophagous species from the phylogenetic distance of other species and calculated a z-score of phylogenetic diet breadth.

In contrast to diet breadth estimates, which included all available information, we only used data collected within plots to estimate caterpillar densities and landscape occupancy at plot and elevation scales. We calculated three indices of abundance or occupancy. First, the abundance of each caterpillar species was summed

within 10 m diameter plots (each plot had an area of 78.5 m^2) and standardized by the relevant host plant leaf area within the same plots. Leaf areas were estimated for each plant genus, and the same leaf area was assigned to all plant species belonging to that plant genus, despite some variation in size within a genus. Mean density for each species was calculated across plots. For example, if there are five individuals of a caterpillar species that consumes one host plant species, and this plot has 200 cm^2 leaf area of the caterpillar host plant, then the density is 0.025 in this plot. This measure represents local abundance standardized by plant availability. Second, we calculated an index of landscape occupancy as the frequency of observation for a particular caterpillar species across all plots. For this measure, regardless of the number of individuals for a given caterpillar species in a plot, frequencies are equal to one if the caterpillar species is present in the plot and zero if the caterpillar is absent. For these first two measures, calculations were made for plot and elevation scales for which adequate data were available. Third, we explored an alternative measure of density by calculating caterpillar density per unit plot area (instead of per available leaf area within a plot) 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) individual plots as well as those that were aggregated to form larger, contiguous sampling areas, (2) discrete elevational bands and (3) a regional scale encompassing our entire study area. For the plot scale, data were collected from a total of 455 plots across the study area. We examined the effect of scale on the relationship between diet breadth and density for different plot sizes by aggregating plots into groups that were temporally and spatially adjacent in the field, then 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 plots, a moving window method was applied (Figure 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 leaf area from plot 1 and plot 2 were summarized followed by all iterations of plot $n - 1$ and plot n (e.g. plots 2 and 3 were combined, then plots 3 and 4, etc. up to the final plot number). In the subsequent iteration, the window size increased to three plots and so on until the window size equalled the number of all plots. This approach minimized situations where aggregated plots

would include data from different years or from different sampling areas, providing data for addressing the influence of larger plot sizes on the association between abundance and diet breadth. Results presented in the main text are limited to groupings of 5 (~393 m^2 in total across aggregated plots), 25 (~1963 m^2), 50 (~3927 m^2) and 250 (~19,635 m^2) plots; additionally, results for all possible aggregates were calculated and are presented in the supplement (Figures S1, S3 and S5).

Plots within four distinct elevational bands: (1) 0–1000 m, (2) 1001–2000 m, (3) 2001–3000 m and (4) above 3000 m were aggregated (Figure 1a); these elevational bands are ecologically distinct (Pyrcz et al., 2009). Density was calculated based on the total caterpillar abundance per available host plant leaf area within each elevational band. While turnover is substantial at a finer elevational scale (e.g. Sklenár & Ramsay, 2001), elevational bands were defined based on data availability and to allow for sufficient data at distinct elevations.

Finally, to examine caterpillar abundance at the regional level, total abundance for each caterpillar species was summarized across the entire data set and standardized by the number of host plant species that a caterpillar consumed. This included caterpillars collected from both plot-based and opportunistic collection methods. For regional data, species with more generalized host ranges can be observed more often simply because they occur on a wider range of host plant species (and are, thus, encountered more frequently); thus, we calculated the number of times that a caterpillar has been collected, divided by the number of host species on which it occurs (in other words, this is the average abundance per host species). For example, if a particular caterpillar species has a total abundance of 10 and a diet breadth of 2 host species, the density per host species is 5 at this regional scale. Prior to the analyses described here, we identified and removed an extreme outlier and singletons (species for which there was only one record in the 18-year database). We removed one species (an outlier), *Eois olivacea* (Geometridae: Larentiinae), because it had unusually high abundance from sampling bias associated with related research projects, and we removed 2972 singletons. Final analyses included 1917 morphospecies of larval Lepidoptera (caterpillars) from 33 families feeding on 398 plants morphospecies from 90 families.

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) using the 'rjags' package in R (R version 3.6.3) using (for each analysis) two Markov chains and 1,000,000 steps each; performance was assessed through examination of chain histories (burn-in was not required because of rapid

convergence), effective sample sizes and the Gelman-Rubin convergence diagnostic. Response variables (abundance and occupancy) were modelled with assumptions of normally distributed residuals with means dependent on an intercept plus diet breadth as a predictor variable. We used weakly informative priors: priors on beta coefficients were normal distributions with mean of zero and precision of 0.001 (variance = 1000); priors on precisions were modelled as gamma distributions with rate = 0.1 and shape = 0.1. We report medians from posterior distributions for beta coefficients and corresponding 95% credible intervals (CI). Values for density, occupancy, and taxonomic diet breadth were log transformed (log_{10}) prior to analyses.

RESULTS

Caterpillar density based on available host area declined with increasing diet breadth at the level of individual plots (Figure 2a, Table 1, Figure S1A). The overall relationship between diet breadth and caterpillar abundance per available host area was also negative: the beta coefficient estimated from linear models was −0.36 (95% credible intervals: −0.48 to −0.23) for all plot clusters (Table 1, Figure S1A), and this negative relationship is not dependent on the number of plots being aggregated. The raw effect size associated with this relationship (predicted from a simple linear regression of untransformed density on diet breadth) can be interpreted as an increase in diet breadth from 1 to 10 host plants yielding a 36% (95% confidence interval: 34.8% to 37.2%) decrease in abundance per leaf area, and this effect size is similar for the other negative beta coefficients reported in Table 1. Similarly, three out of four elevational bands showed a negative relationship between caterpillar abundance per available host plant area and diet breadth (Figure 2b, Table 1) with the same magnitude of effect sizes. Overall, this negative relationship between abundance and diet breadth reflects a tendency for more specialized caterpillar species to be more locally abundant relative to species that consume a greater number of hosts.

In contrast, occupancy (frequency of occurrence across the landscape) increased with increases in diet breadth for all plot cluster sizes, and the estimate for the slope was dependent on plot cluster size: decreasing with increasing cluster size (Figure 2c, Table 1, Figure S1B). The raw effect size associated with the overall positive relationship (for all plot cluster sizes) can be interpreted as an increase in diet breadth from 1 to 10 host plants yielding a 18% (95% confidence interval: 17.5% to 18.5%) increase in the percentage of plots occupied. However, the relationship between occupancy and diet breadth varied across different elevation bands (Figure 2d, Table 1). A positive relationship was observed at the middle elevation bands (1001–2000 and 2001–3000 m),
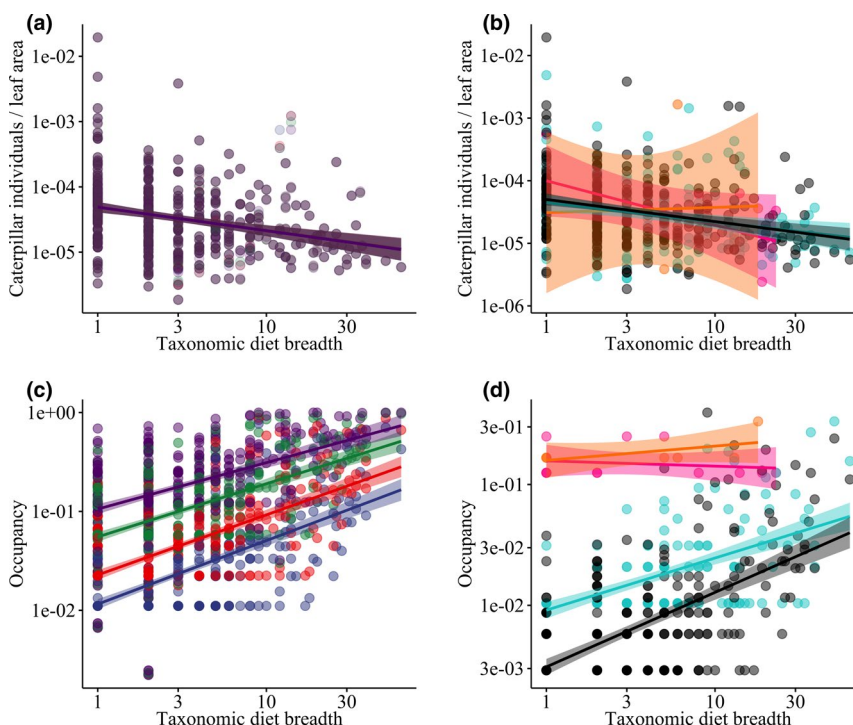

FIGURE 2 Relationship among taxonomic diet breadth and caterpillar abundance per available host area (cm^2) and occupancy (landscape presence) at different scales of observation: (a) and (c) depict plot scales, and (b) and (d) depict elevation scales. Plot-level data were combined for each caterpillar species (points) for various plot aggregates (blue: 5 plots, red: 25, green: 50 and purple: 250) to evaluate the effect of scale. For the elevation analysis, discrete elevation bands included: 0–1000 m (orange), 1001–2000 m (cyan), 2001–3000 m (black) and above 3000 m (pink). Points were set to a transparency value given the quantity of points, such that darker hues indicate a high density of points

while weak positive and negative relationships between occupancy and diet breadth were observed at the low (0–1000 m) and high (>3000 m) elevation bands, respectively (Figure 2d, Table 1). The positive relationship between occupancy and diet breadth provided evidence that more generalized species occupy more places across the landscape. When density was calculated based on plot area, the patterns at both plot and elevation scales were

similar to trends observed for occupancy (Figures S1C and S2; Table S2).

At our largest spatial scale, using all data, including plots and general collections, we detected a much noisier negative relationship between density and diet breadth ($\beta = -0.076$, 95% CI [−0.15, −0.0061]; Figure 3). Nevertheless, the raw effect size indicates an appreciable decrease in density with diet breadth, with a change from feeding on 1 to 10 host plant species yielding a 29% (95% confidence interval: 10% to 48%) decrease in abundance per host plant species.

Inferences about associations between diet breadth and abundance were robust to the use of different specialization indices, specifically ordinated diet breadth and phylogenetic diet breadth. Our results using ordinated diet breadth (Figures S3 and S4; Table S3) and phylogenetic diet breadth (Figures S5 and S6; Table S4) both recovered the same relationships with caterpillar abundance that were found for taxonomic diet breadth. Importantly, more specialized species have greater local abundance and that relationship is not sensitive to the measure of diet breadth used.

TABLE 1 Point estimates for beta coefficients (bold) and associated 95% credible intervals for relationship between taxonomic diet breadth and density per available host plant area and occupancy at plot and elevation levels. Plot levels include different cluster sizes, which represent the number of aggregated 10-m plots.

	Measure of density β-coefficient [95% CI]	
Level of observation	**Density per available host plant area**	**Occupancy**
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		
0–1000 m	**0.10** [−1.72, 1.63]	**0.12** [−0.33, 0.50]
1001–2000 m	**−0.31** [−0.49, −0.12]	**0.43** [0.34, 0.53]
2001–3000 m	**−0.35** [−0.48, −0.21]	**0.62** [0.52, 0.71]
>3000 m	**−0.73** [−1.48, 0.068]	**−0.05** [−0.30, 0.20]

DISCUSSION

As a theoretical expectation, the 'jack of all trades is a master of none' paradigm has persisted despite decades of examination with limited consensus, depending on the organisms and the traits being examined (Forister et al., 2012; Futuyma & Moreno, 1988). For
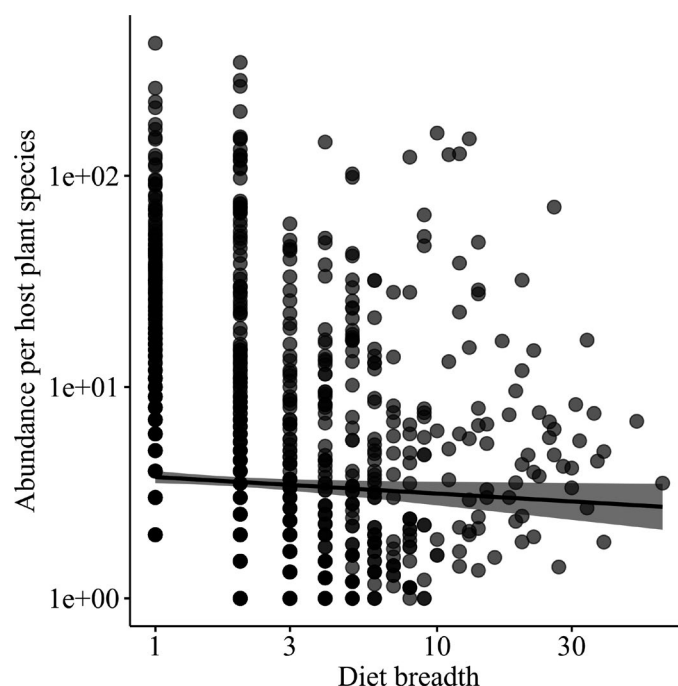

FIGURE 3 Relationship between caterpillar abundance per host plant species and taxonomic diet breadth at a regional scale. Points were set to a transparency value given the quantity of points, such that darker hues indicate a high density of points

many morphological traits, biophysical constraints in vertebrates have produced clear examples where an ecological generalist underperforms specialists when evaluated in a common context or on a shared resource (Oufiero et al., 2012). The story has been more complicated for herbivorous insects, where the focal trait is typically developmental performance for juvenile stages, and specialists have often not outperformed generalists when experimentally evaluated on a common resource (Agrawal, 2020; García-Robledo & Horvitz, 2012; Hardy et al., 2020). In the absence of a single unifying mechanism explaining the causes of ecological specialization, our results confirm that species abundance patterns associated with diet breadth reveal emergent patterns at the community level. Instead of an experimental framework to evaluate performance, 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 we find that specialists tend to be locally more abundant while generalists occupy more places on the landscape.

Despite variation in the strength and direction of the relationship between diet breadth and abundance across different levels of observation and measures of abundance that we have reported here, the raw effect sizes were substantial. At the smallest spatial scale (plot-level), adding an additional host plant species to taxonomic diet breadth results in a 4% decrease in caterpillar abundance per available host plant (Figure 2a; Table 1; Figure S1A). This result raises a possibility (because it is not an inference for caterpillars at all scales or sites) that at local scales specialists are indeed better adapted to their host plants, whereas generalists benefit from being able to colonize more hosts. That general pattern is largely robust to observations taken at different elevational and spatial scales (Figure 2), but the signal was weak or non-existent for lowest (0–1000 m) and highest (>3000 m) elevations, for which sample sizes were considerably smaller (i.e. there were 6 plots at the elevation 0–1000 m, 96 plots at the elevation 1001–2000 m, 345 plots at the elevation 2001–3000 m and 8 plots at elevations >3000 m a.s.l.). Additionally, sampling has occurred across many years at all elevations, and we cannot rule out the possibility of differential caterpillar declines (or other changes) in different locations (Salcido et al., 2020); more focused sampling is needed at the highest and lowest elevations. The signal was also weak at the very largest scale that included general collecting (Figure 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. The positive relationship between diet breadth and occupancy is an interesting contrast to the smaller scale negative relationship, but the patterns are not inconsistent and reflect high turnover of specialist caterpillars across the landscape and low turnover of generalists. In fact, a null model predicts a strong, positive relationship between diet breadth

and occupancy across the landscape (Forister & Jenkins, 2017), and other work related to these null expectations has suggested that generalism does not cause higher local abundance, instead generalism might itself be a result of a greater abundance, which increases chance encounters with a wider range of species (Fort et al., 2016). These chance encounters increase with greater plant beta diversity across the study area, which could contribute to the pattern here of lower local abundance and greater landscape occupancy; if plant beta diversity were low, then the low local abundances of more generalized species would be associated with low landscape occupancy.

It is important to note that the results reported here do not directly test specific mechanisms generating the observed relationships between diet breadth and abundance or occupancy. As discussed above, the idea of genetic trade-offs as an expectation associated with the jack-of-all trades hypothesis (Agosta & Klemens, 2009; Levins, 1968) has a long history with only minimal support for herbivorous insects (Gompert & Messina, 2016). Other equally powerful ideas have received less attention, including the hypothesis that narrow niches are associated with more efficient selection for beneficial alleles, and generalists are less well adapted to any one resource because selection is effectively diluted across multiple environments (Whitlock, 1996). Diet breadth also has a positive association with body size in some lepidopterans (Davis et al., 2013) and variation in body size can help increase the degree of generalism across the landscape (Morris et al., 2021); however, associations between caterpillar size classes and degree of generalism were not detected in our study (Figure S7).

Regardless of the mechanisms explaining the tendency towards higher local densities of more specialized species, an important finding from our work is not only the sign and magnitude of that relationship, but also the shape of the variance. In particular, the range of densities observed for specialists is orders of magnitude greater than the range for densities of generalists (Figure 2a). This broad distribution of densities for specialists counterintuitively raises the possibility that being a host specialist is a more multifaceted condition than host generalization. Specialists, for example, likely contend with a different or more variable suite of natural enemies that affect local abundance in ways that are heterogeneous and warrant further study (Singer & Stireman, 2005). It would be interesting to examine differences in the ratio of specialists to generalists among some common host genera (Figure S8) with an eye towards measuring the effects of natural enemies and plant chemistry on those ratios. Understanding shifts in specialist to generalist ratios across different scales of observation for selected host taxa could provide considerable insight into the causes and consequences of the ubiquity of specialist herbivores and other parasites (Forister & Jenkins, 2017; Novotny et al., 2002).

The diet breadth of rare species, defined as those that were found as single individuals (singletons) in extensive sampling, is complicated and poses particular challenges. Rare species in tropical forests represent a high proportion of insect herbivores, contributing to high species richness in tropical insect communities (Price et al., 1995), and singleton records are made up of both specialist and generalist herbivores (Novotný & Basset, 2000). Species are rare for various reasons, including sampling bias and host specificity (Novotný & Basset, 2000). For instance, there may be insufficient spatial and seasonal replication of sampling, as certain insect species may occupy different host plants in different seasons. Insect herbivores depend on the quality of their host plants, and their preferred host plants may not be sampled, limiting the possibility of knowing their diet breadth. We removed over 2000 singletons from the analyses in the present study because they were found once in the 18 years of data collection. The data were collected all year-round; therefore, it is unlikely that the collections do not incorporate seasonal and spatial variation. Increasing sampling effort over time could potentially increase mean diet breadth simply by adding more discovery of host associations, but our data did not support this idea (Figure S9).

In conclusion, the results reported here confirm the long-standing, but rarely observed assumptions of a negative correlation between abundance and diet breadth and a positive correlation between landscape occupancy and diet breadth. These results are a reminder that many decades are often needed for the evaluation of basic assumptions that underlie ecological theory, especially when that theory is applied to complex traits such as digestion and juvenile development. It is also the case that such relationships are likely dependent on the taxa and communities being studied. A similar investigation was recently conducted with field data for armoured scale insects, with the conclusion that diet breadth and abundance are not linked (Peterson et al., 2020). Although Peterson et al. (2020) did not detect an overall abundance–diet breadth relationship, it is the case that the most abundant species tended to be extreme specialists (consistent with the high variance we observed in our specialized species). Another interesting contrast in the literature comes from a study of British moths, where more generalized species were more common at individual light traps (Quinn et al., 1997). The difference between that result and ours might be explained by the resolution: light traps pull adults from an area that is broader than the hyper-local plots where we collected caterpillars, thus reinforcing the complexity and importance of both geographic and taxonomic scale (Hughes, 2000). There is clearly much yet to be learned about ecological and dietary specialization, and the observations reported here are made more relevant in the midst of ongoing reports of declining insect abundances from around the world (Halsch et al., 2021; van Klink et al., 2020; Salcido et al., 2020; Wagner, 2020). One might expect that generalist insects would be less sensitive to Anthropocene stressors because of their wider presence across the landscape. However, the lower local abundances of generalists might predispose them to extirpation, which could have cascading effects on metapopulations, putting generalist species at risk. Increased investment in long-term data sets, particularly those of tropical insect herbivore systems, will be important to test long-standing and unresolved ideas about ecological specialization, and importantly, how we may best conserve habitat to preserve these diverse interactions.

AUTHORSHIP
CS wrote the first draft of the manuscript. DMS, MLF and LAD contributed substantially to consequent drafts and revisions. LAD, TRW, SV and DMS collected field data. CS, MLF and LAD generated research questions and designed statistical analyses. CS, DMS, LAD and MLF conducted statistical analyses.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13972.

DATA AVAILABILITY STATEMENT
Data supporting the results are archived in the Zenodo open repository (https://doi.org/10.5281/zenodo.5839171).

ORCID
Chanchanok Sudta https://orcid.org/0000-0001-7459-1331
Danielle M. Salcido https://orcid.org/0000-0001-6970-7387
Lee A. Dyer https://orcid.org/0000-0002-0867-8874

REFERENCES
Agosta, S.J. & Klemens, J.A. (2009) Resource specialization in a phytophagous insect: no evidence for genetically based performance trade-offs across hosts in the field or laboratory. *Journal of Evolutionary Biology*, 22, 907–912.

Agrawal, A.A. (2020) A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, 101, e02924.

Brown, J.H. (1984) On the relationship between abundance and distribution of Species. *The American Naturalist*, 124, 255–279.

Davies, T.J., Barraclough, T.G., Chase, M.W., Soltis, P.S., Soltis, D.E. & Savolainen, V. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 1904–1909.

Davis, R.B., Õunap, E., Javoiš, J., Gerhold, P. & Tammaru, T. (2013) Degree of specialization is related to body size in herbivorous insects: a phylogenetic confirmation. *Evolution*, 67, 583–589.

Dyer, L., Massad, T. & Forister, M. (2015) The question of scale in trophic ecology. In: Hanley, T. & La Pierre, K. (Eds.) *Trophic ecology: bottom-up and top-down interactions across aquatic and terrestrial systems*. Cambridge, MA: Cambridge University Press, pp. 288–317.

Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J. et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, 448, 696–699.

Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, 18, 586–608.

Fordyce, J.A., Nice, C.C., Hamm, C.A. & Forister, M.L. (2016) Quantifying diet breadth through ordination of host association. *Ecology*, 97, 842–849.

Forister, M.L., Dyer, L.A., Singer, M.S., Stireman III, J.O. & Lill, J.T. (2012) Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. *Ecology*, 93, 981–991.

Forister, M.L. & Jenkins, S.H. (2017) A neutral model for the evolution of diet breadth. *The American Naturalist*, 190, E40–E54.

Fort, H., Vázquez, D.P. & Lan, B.L. (2016) Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma. *Ecology Letters*, 19, 4–11.

Fox, L.R. & Morrow, P.A. (1981) Specialization: species property or local phenomenon? *Science*, 211, 887–893.

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

García-Robledo, C. & Horvitz, C.C. (2012) Jack of all trades masters novel host plants: positive genetic correlations in specialist and generalist insect herbivores expanding their diets to novel hosts. *Journal of Evolutionary Biology*, 25, 38–53.

Gompert, Z. & Messina, F.J. (2016) Genomic evidence that resource-based trade-offs limit host-range expansion in a seed beetle. *Evolution*, 70, 1249–1264.

Halsch, C.A., Shapiro, A.M., Fordyce, J.A., Nice, C.C., Thorne, J.H., Waetjen, D.P. et al. (2021) Insects and recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2002543117.

Hardy, N.B., Kaczvinsky, C., Bird, G. & Normark, B.B. (2020) What we don't know about diet-breadth evolution in herbivorous insects. *Annual Review of Ecology Evolution and Systematics*, 51, 103–122.

Hughes, J.B. (2000) The scale of resource specialization and the distribution and abundance of lycaenid butterflies. *Oecologia*, 123, 375–383.

Jorge, L.R., Novotny, V., Segar, S.T., Weiblen, G.D., Miller, S.E., Basset, Y. et al. (2017) Phylogenetic trophic specialization: a robust comparison of herbivorous guilds. *Oecologia*, 185, 551–559.

Joshi, A. & Thompson, J.N. (1995) Trade-offs and the evolution of host specialization. *Evolutionary Ecology*, 9, 82–92.

Kelly, C.A. & Bowers, M.D. (2016) Preference and performance of generalist and specialist herbivores on chemically defended host plants. *Ecological Entomology*, 41, 308–316.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D. et al. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.

Krasnov, B.R., Poulin, R., Shenbrot, G.I., Mouillot, D. & Khokhiova, I.S. (2004) Ectoparasitic "jacks-of-all-trades": relationship between abundance and host specificity in fleas (Siphonaptera) parasitic on small mammals. *The American Naturalist*, 164, 506–516.

Levins, R. (1968) *Evolution in changing environments*. Princeton, NJ: Princeton University Press.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. New York: Harper & Row.

Mani, M.S. (1968) *Ecology and biogeography of high altitude insects*. Series Entomologica, 1st edition. The Hague, Netherlands: Dr. W. Junk N.V. Publishers.

Morris, J.R., Allhoff, K.T. & Valdovinos, F.S. (2021) Strange invaders increase disturbance and promote generalists in an evolving food web. *Scientific Reports*, 11, 21274.

Novotný, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, 89, 564–572.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. et al. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416, 841–844.

Oufiero, C.E., Holzman, R.A., Young, F.A. & Wainwright, P.C. (2012) New insights from serranid fishes on the role of trade-offs in suction-feeding diversification. *Journal of Experimental Biology*, 215, 3845–3855.

Peterson, D.A., Hardy, N.B., Morse, G.E., Itioka, T., Wei, J. & Normark, B.B. (2020) Nonadaptive host-use specificity in tropical armored scale insects. *Ecology and Evolution*, 10(23), 12910–12919.

Poisot, T., Bever, J.D., Nemri, A., Thrall, P.H. & Hochberg, M.E. (2011) A conceptual framework for the evolution of ecological specialisation. *Ecology Letters*, 14, 841–851.

Price, P.W., Diniz, I.R., Morais, H.C. & Marques, E.S.A. (1995) The abundance of insect herbivore species in the tropics: the high local richness of rare species. *Biotropica*, 27, 468–478.

Pyrcz, T., Wojtusiak, J. & Garlacz, R. (2009) Diversity and distribution patterns of Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in northwestern Ecuador. *Neotropical Entomology*, 38, 716–726.

Quinn, R., Gaston, K., Blackburn, T. & Eversham, B. (1997) Abundance–range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. *Ecological Entomology*, 22, 453–461.

Ravigné, V., Dieckmann, U. & Olivieri, I. (2009) Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *The American Naturalist*, 174, E141–E169.

Salcido, D.M., Forister, M.L., Lopez, H.G. & Dyer, L.A. (2020) Loss of dominant caterpillar genera in a protected tropical forest. *Scientific Reports*, 10, 1–10.

Scriber, J.M. (2010) Integrating ancient patterns and current dynamics of insect–plant interactions: taxonomic and geographic variation in herbivore specialization. *Insect Science*, 17, 471–507.

Singer, M.S. & Stireman, J.O. (2005) The tri-trophic niche concept and adaptive radiation of phytophagous insects. *Ecology Letters*, 8, 1247–1255.

Sklenář, P. & Ramsay, P.M. (2001) Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions*, 7, 113–124.

Tapia, D.H., Silva, A.X., Ballesteros, G.I., Figueroa, C.C., Niemeyer, H.M. & Ramírez, C.C. (2015) Differences in learning and memory of host plant features between specialist and generalist phytophagous insects. *Animal Behavior*, 106, 1–10.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, 368, 417–420.

Wagner, D.L. (2020) Insect declines in the anthropocene. *Annual Review of Entomology*, 65, 457–480.

Whitlock, M.C. (1996) The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *The American Naturalist*, 148, S65–S77.

Wilson, D.S. & Yoshimura, J. (1994) On the coexistence of specialists and generalists. *The American Naturalist*, 144, 692.

Zhong, S., Khodursky, A., Dykhuizen, D.E. & Dean, A.M. (2004) Evolutionary genomics of ecological specialization. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 11719–11724.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.