**Variation in the strength of local and regional determinants of herbivory across the Neotropics**

**Abstract**

Insect herbivory can vary from an inconsequential biotic interaction to a factor that contributes substantially to the diversity of plants and animals and overall interaction diversity. As herbivory is the result of numerous ecological and evolutionary processes, including complex population dynamics and the evolution of plant defense, it has been difficult to predict variation in herbivory across meaningful spatial scales. In the present work, we characterize patterns of herbivory on plants in a species rich and abundant tropical understory genus (*Piper*) across forests spanning 44° of latitude in the Neotropics. We modeled the effects of geography, climate, resource availability, and *Piper* species richness on the median, dispersion, and skew of generalist and specialist herbivory. By examining these multiple components of the distribution of herbivory, we were able to determine factors that increase biologically meaningful herbivory at the upper ends of the distribution. Site level variables such as latitude, seasonality, and maximum *Piper* richness explained variation in herbivory at the local scale (plot level) better for assemblages of *Piper* congenersthan for a single species. Predictors that varied between local communities, such as resource availability and diversity, best explained the distribution of herbivory within sites, dampening broad patterns across latitude and climate and demonstrating why generalizations about gradients in herbivory have been elusive. The estimated population means, skew, and dispersion of herbivory responded differently to abiotic and biotic factors, illustrating the need for careful studies to explore distributions of herbivory and their effects on forest diversity. Nevertheless, we observed a roughly two-fold increase in median herbivory in humid compared to seasonal forests, and this finding aligns with the hypothesis that precipitation seasonality plays a critical role in shaping interaction diversity within tropical ecosystems.

**Keywords:** Distribution, diversity, herbivore, latitudinal gradient, resource availability, seasonality, tropical forest

**Introduction**

Insect herbivory varies significantly along latitudinal gradients, between distinct biomes, and among individual plants, (Coley et al. 1980; Zhang et al. 2016; Gao et al. 2019). Both central tendencies and ranges of herbivory undergo changes across these scales, and documenting these patterns has been important for elucidating the role of herbivores as selective and diversifying agents within biological communities (Janzen 1970; Langenheim and Stubblebine 1983; Dyer et al. 2010; Endara et al. 2017, 2018). A synthesis of herbivory data on vascular plants estimates that, on average, an individual plant loses 5.3% of its leaf area annually to herbivory, with relatively low variation (95% CI: 4.9-5.7%; Turcotte et al. 2014). However, mean annual herbivory can surpass 25% and fluctuate between 0 and 90% within a single species (Turcotte et al. 2014). Little is known about how distributions of herbivory shift across various gradients (but see <https://herbvar.org>). While many plants are known to exhibit tolerance to herbivory (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999; Massad 2013), high levels of herbivory can impair plant fitness (Marquis 1992; Clark and Clark 1985), modify plant chemistry (Endara et al. 2015), constrain population growth (Katz 2016), and promote community diversity (Carson et al. 2008). Consequently, understanding the factors that influence variation in herbivory contributes to elucidating the ecological and evolutionary roles of herbivores in the formation and structure of plant communities.

Herbivory varies across large-scale environmental gradients, and changes in mean herbivory have been measured across sites that vary in temperature, precipitation, and seasonality (Table 1, Hypotheses 2 and 3; Brenes-Arguedes et al. 2009; Moreira et al. 2015; Galman et al. 2018; Njovu et al. 2018; Hahn et al. 2019; Lynn & Fridley 2019). Within the tropics, herbivores are more species rich closer to the equator (Salazar & Marquis 2012), so herbivory may be responsive to variables associated with latitude even without crossing into temperate zones. Nonetheless, it is difficult to understand the role of specific factors in influencing broad-scale patterns of herbivory, as many factors covary. For example, including mean precipitation in models examining herbivory along a latitudinal gradient suggests that latitude itself is not necessarily an important predictor of herbivory (Loughnan & Williams 2019). Although herbivory is largely considered to be more intense in the tropics (Coley & Aide 1991; Coley & Barone 1996), recent work has shown that herbivory decreases with latitude in the northern but not the southern hemisphere (Zhang et al. 2016). Latitudinal variation in herbivory may also result from the increased specialization and interaction diversity found at lower latitudes (Table 1; Hypothesis 4; Dobzhansky 1950; Mittelbach et al. 2007; Dyer et al. 2007; Schemske et al. 2009; Forister et al. 2015; LaManna et al. 2017; Dyer & Forister 2019), and most of the latitudinal variation in herbivory may be driven by differences between the temperate zone and the tropics (Kozlov et al. 2015).

Beyond large scale gradients, herbivory is influenced at the local level by community attributes such as host plant abundance (Table 1, Hypothesis 5; Root 1973; Whitfeld et al. 2012; Loughnan & Williams 2019), plant species richness (Table 1, Hypothesis 6; Jactel & Brockerhoff 2007; Vehviläinen et al. 2007), population and phylogenetic diversity (Bidart-Bouzat & Kliebenstein 2008; Castagneyrol et al. 2012; Barton et al. 2015), phytochemical diversity (Richards et al. 2015; Salazar et al. 2016; Massad et al. 2017), and plant trait diversity (Schuldt et al. 2014; Coverdale et al. 2018). How these factors might affect the distribution of herbivory among plants in a community is less studied (Zvereva et al. 2020), but it is expected that abundant resources, plant stress, and low plant diversity will favor higher herbivory with distributions exhibiting more positive skew and kurtosis (Cobb et al. 1997; Hunter & Forkner 1999; Pearson et al. 2003a,b; Dyer et al. 2004; Richards & Coley 2008; Dyer et al. 2012; Piper et al. 2018; Lynn & Fridley 2019). Specialist herbivory in particular may increase where species richness is lower as specialists may more easily locate their preferred host plants where resources are concentrated (Janzen 1970; Root 1973).

Elevated levels of herbivory can contribute substantially to ecological and evolutionary processes, including plant growth, survival, reproduction, population dynamics, and the evolution of specialized metabolites (Clark & Clark, 1985; Marquis, 1992; Carson & Root, 2000; Bebber et al., 2004; Fine & Mesones, 2011; Endara et al., 2015). Variation in local environmental conditions, particularly in light (Table 1, Hypothesis 7) and nutrient availability, impact the extent of herbivory and its consequences for plants (Hunter & Forkner, 1999; Pearson et al., 2003a, 2003b; Dyer et al., 2004a; Richards and Coley, 2007, 2008; Piper et al., 2018; Lynn & Fridley, 2019). In addition, specialist and generalist herbivores may respond differently to environmental variation (Massad et al. 2017). Despite considerable empirical data documenting the consequences of high levels of herbivory on individual plants, research characterizing large-scale patterns in herbivory often concentrates on means, ignoring the importance of positively skewed values of herbivory.

Research on patterns of herbivory should supplement comparisons of central tendencies with measures of variation in dispersion, skew, and kurtosis (Rasmann et al. 2014; Gao et al. 2019; Kent et al. 2020), but there are limited attempts to document patterns for these additional moments of herbivory distributions across latitudinal, biotic, and other gradients (https://herbvar.org). It is also challenging to predict how the distribution parameters of herbivory are affected at local scales by factors such as nutrient availability, community richness, or natural enemies. Even as some patterns are documented (for example, distributions of herbivory are characterized by strong positive skew, Massad et al. 2013; Massad et al. 2017; https://herbvar.org; Table 1), it will take careful and detailed study of well understood natural systems to generate clear predictions of how distributions of herbivory are shaped by diverse conditions across multiple scales.

To address the need for both large scale and detailed local level research on herbivory, we collected herbivory data on species in the plant genus *Piper* (Piperaceae) across the Neotropics from the state of São Paulo, Brazil to the Yucatán Peninsula in México using standardized methods. We focused on a single species-rich and abundant plant genus to allow comparisons of herbivory caused by similar assemblages of herbivores across environmental gradients and within communities (Anstett et al. 2016; Zvereva et al. 2020). We asked what factors best explain variation in herbivory and whether the effects of these factors differ across spatial scales or among specialist and generalist herbivores (Table 1). Large-scale variation in herbivory has rarely been studied in datasets examining local diversity and population density as predictors of herbivory. We asked: I. What variables affect the distribution parameters of herbivory? II. Are there site specific effects on the distribution of herbivory? III. Does herbivory vary more at local (within a plot) scales or regionally (between multiple plots across a forest)? In the context of these questions, the “distribution of herbivory” denotes a statistical summary of damage on individual plants. The distribution of herbivory across individual plants is summarized by central tendency, dispersion, skewness, and kurtosis, which are collectively known as the moments of the distribution.

The research was guided by the following specific hypotheses which are summarized in Table 1. H1) Herbivory may exhibit greater variability across a forest (between all congeners measured in multiple plots in a forest) compared to local *Piper* assemblages (between congeners measured in the same plot) or in subpopulations of individual species (between conspecifics in a plot). H2) At the regional scale, specialist and generalist herbivory may be higher in seasonal habitats, where leaves may be shorter lived and less well defended (Coley and Barone 1996). This result may be weaker for specialists as they are more locally abundant across their range (Sudta et al. 2022) and are better adapted to higher defenses. H3) Elevated temperatures generally increase metabolism, phenology, population dynamics, and host plant quality (e.g., Dyer et al. 2013), all of which contribute to a positive correlation between temperature and herbivory for both generalists and specialists. Since specialists are more locally abundant than generalists, the distribution of generalist herbivory may be more susceptible to outliers, yielding higher variance and positive skew for generalists versus specialists across the ranges of temperature (Sudta et al. 2022). H4) Herbivory may be elevated (both mean and skew) at lower latitudes. H5) Community level parameters, such as the abundance and richness of congeners (resource availability; Root 1973), may be better predictors of variation in herbivory than large scale factors that differ across sites. Specialist herbivory in particular may increase where resources are more concentrated. H7) Both mean herbivory and variation in herbivory may increase with local host plant abundance and decrease with species richness, particularly for specialists. H5) At the local scale, herbivory in plots with more open canopies may be less positively skewed as herbivore abundance decreases in harsher environments (Richards & Windsor 2007; refer to Table 1 for detailed predictions of all hypotheses).

**Methods**

*Field methods.* Data were collected in standardized plots that were surveyed across 16 sites in the Neotropics, from the Yucatán Peninsula in México to the Mata Atlântica of Brazil (Fig. 1). Plots were surveyed between 2013 and 2020 in the following ecosystems: three seasonally dry sites in the Yucatán, one site in a Costa Rican lowland wet forest, two sites in wet forest of the central Amazon in Brazil, one cloud forest site in the eastern Andes in Ecuador, two mid-elevation wet forest sites and one cloud forest site in Perú, one seasonal forest in the middle-northern Mata Atlântica, one gallery forest in the cerrado, and two seasonal and two wet forest sites in the middle-southern Mata Atlântica (Supporting Information Table 1).

Plots consisted of 10 m diameter (78.5 m2) circles that were centered on a haphazardly selected *Piper* individual at least 20 m from any forest edge. Within the plots, all *Piper* individuals were searched for caterpillars, and herbivory was measured by eye as estimated percent leaf area missing. Herbivory was measured as a continuous variable for entire individuals (not subsets of leaves). Specialist and generalist herbivory were separated as accurately as possible based on typical patterns of herbivore damage on *Piper* (Dyer et al. 2010). For example, much herbivory on *Piper* comes from specialist *Eois* caterpillars and specialist Chrysomelidae and Curculionidae; the damage from these groups is easily differentiated from damage from generalist Acrididae or generalist caterpillars (Dyer et al. 2010). For these measures of herbivory, specialists feed only on *Piper* but may consume multiple congeners, while generalists feed on plants that include species outside the Piperaceae (i.e. at least two families of plants). *Piper* leaves are long-lived (most species in this study have leaves that can live over 5 years), so while some insect herbivores may be seasonal, measures of standing herbivory on a given plant should not be affected by season (Dyer and Palmer 2004). To standardize data collection, the same researcher (TJM) was present at ten of the sites, and she trained researchers who collected data at four of the other sites, as well as researchers who worked directly with her. At the remaining two sites, researchers with extensive experience working with *Piper* collected the data (HGL, WS). All *Piper* individuals were identified to species or morphospecies, and the number of leaves was counted for each plant. Leaf area was measured on a minimum of ten randomly selected leaves per species using a gridded transparency. Canopy openness was measured with a spherical densiometer in the center of plots at all sites except in Ecuador and Perú. Understory richness was measured as the number of woody morphospecies with leaves between 50 cm and 2 m in height in plots at all sites except México. Each plot was evaluated once.

*Climate data.* To describe seasonality in precipitation, data from 2011 through 2019 were extracted from https://climatedataguide.ucar.edu/climate-data/gpcc-global-precipitation-climatology-centre for all sites, and the coefficient of variation in precipitation was calculated. The coefficient of variation in precipitation is a standard means of describing seasonality (e.g., https://www.worldclim.org/data/bioclim.html), and our group has used this as an informative predictor in statistical models (Stireman et al. 2005). Throughout the paper, ‘seasonality’ refers to the coefficient of variation in precipitation. Data on temperature and precipitation for the Reserva Adolfo Ducke are annual averages from 2000-2014 and were provided by the Instituto Nacional de Pesquisas da Amazônia. Data for Mogi-Guaçu are from January 2017-December 2019 and are from the Centro Integrado de Informações Agrometeorológicas of São Paulo. Data from São Bento de Sapucaí and Parque Nacional de Itatiaia were derived from: https://pt.climate-data.org/. Data from the Parque Estadual de Serra do Mar were collected from: http://www.bv.fapesp.br/pt/bolsas/89914/fenologia-de-vegetacao-de-duna-da-praia-da-fazenda-parque-estadual-da-serra-do-mar-nucleo-picinguaba. Data from other reserves in the Mata Atlântica of São Paulo, Costa Rica, and Ecuador were provided by the reserves. Data from Serra Bonita are from Matos et al. (2010). Data for the Perú sites are from nearby San Ramón (https://en.climate-data.org/south-america/peru/junin/san-ramon-28556/). Data on temperature for México are annual averages from December 2017- February 2019 and are from the Servicio Metereológico Nacional CONAGUA (https://smn.conagua.gob.mx/es/climatologia/temperaturas-y-lluvias/mapas-diarios-de-temperatura-y-lluvia).

*Data analyses.* The distribution of herbivory was examined in local *Piper* communities across the Neotropics. Given the skewed nature of herbivory distributions, with most individuals experiencing little damage and a few suffering high herbivory (Table 1), the mean is not an appropriate composite variable for herbivory. We therefore sought to estimate statistics that comprise three components of the distribution of herbivory: central tendency, skew, and dispersion. We calculated the 25th, 50th (median), 75th, 80th, and 90th quantiles and the mean, geometric mean (Turcotte et al. 2014 utilized geometric means), and variance of specialist and generalist herbivory for all *Piper* assemblages (defined as all *Piper* individuals in a given plot). We used a factor analysis of z-score transformed values of these metrics to create latent variables related to central tendency, skew, and dispersion for specialist and generalist herbivory.

We used a longstanding and common approach to creating latent variables: factor analysis (Thompson and Daniel 1996). There are well-established justifications for such an approach, but most relevant here are: 1) dimension reduction: quantiles and other measured variables from a distribution are numerous, and factor analysis reduces the number of these variables making it easier to understand relationships between predictor and response variables; 2) reducing potential multicollinearity: factor analysis reduces multicollinearity via dimension reduction; 3) estimating latent constructs: factor analysis estimates latent constructs that may be causing the values of measured variables. This last point is important with respect to metrics that are used in statistics, such as means and standard deviations, since these do not necessarily directly measure the most relevant summaries of central tendencies or spread of the data.

The first factor represented skew and was loaded most heavily by the 75th, 80th, and 90th quantiles. The second factor represented the central tendency; the mean, geometric mean, median, and the 25th quantile contributed most strongly to it. The third factor represented dispersion and was loaded most heavily by the variance. The three factors (latent variables) were used as responses in Bayesian structural equation models (SEM) to test specific causal hypotheses about the effects of geographic, climatic, and biotic variables on the distribution of herbivory. These models correspond to Question I, regarding variables that affect the distribution of herbivory. SEM was used because it allows for estimation of direct and indirect causal relationships among interacting variables. Exogenous predictors in the SEM included: (i) precipitation seasonality, (ii) average annual temperature, and (iii) the absolute value of latitude (Hypotheses 2-4). Endogenous predictors were (i) the total amount of *Piper* leaf area available in a plot (Hypotheses 5 and 6), (ii) *Piper* diversity in a plot (calculated as Simpson’s index of species equivalents (Jost 2006) based on leaf area rather than the number of *Piper* individuals to better represent the diversity of resources available (Hypotheses 5 and 6), and (iii) the richness of *Piper* species in a plot (Hypotheses 5 and 6). Predictors were normalized as z-scores, and models were run using the lavaan package (Rosseel 2012). The model selection process, starting with the full model and running to the best fit model is documented in Supplementary Table 2. Bayesian posterior probabilities of the parameter estimates of modeled relationships were calculated for the best fit SEM with the blavaan package (Merkle and Rosseel 2016). Bayesian analyses were run with two chains of 10,000 samples using a burn-in of 20 iterations and an adaptation of 1000 iterations. Trace plots and effective sample sizes were used to assess convergence and mixing of the chains to ensure reliable results. Bayesian posterior probabilities are presented with the marginal log-likelihood and posterior predictive *P*-values (PPP values). AIC scores and X2 goodness of fit statistics were compared to determine the best fit model (note that for the X2 goodness of fit, larger *P-*values indicate the models are a better fit to the data). For model selection, we used *a priori* causal models then worked towards the most parsimonious model that fit the data. The variance-covariance matrix of the best fit model is in Supplementary Table 3.

As we were particularly interested in variables that drive extremes in herbivory, we also analyzed the skew of the data, calculated as 80th quantiles of herbivory, for each geographic region separately (combining three sites in México, three sites in Perú, two in the Amazon Basin, and four in the southern Mata Atlântica) using SEM. These analyses allowed us to explore Question II regarding site specific effects on the distribution of herbivory. Higher values of the 80th quantile indicate more plants in a dataset received greater herbivory (Supporting Information Fig. 1). We note that the use of the 80th quantile for herbivory at population and community levels is somewhat arbitrary (as opposed to the 75th or the 90th quantiles), but it was found to be useful in exploration of the data, and other quantiles yielded similar inferences. Predictor variables in the SEM were (i) the total leaf area of each species of *Piper* in a plot, (ii) total leaf area of all *Piper* individuals in a plot, (iii) the relative leaf area of a given species in plot (dividing species level leaf area by total *Piper* leaf area; i-iii are measures of resource abundance; Hypotheses 5 and 6), (iv) *Piper* richness in a plot (Hypotheses 5 and 6), (v) *Piper* diversity in a plot (based on leaf area as described above; Hypotheses 5 and 6). These models included canopy cover (Hypothesis 7) and understory richness when data were available (Hypothesis 5). Data were normalized as z-scores, and all models were run using the lavaan package (Rosseel 2012). The model selection process was similar to that described in Supplementary Table 2.

Finally, to answer Question III concerning whether herbivory varies more at local or regional scales, we qualitatively compared summary statistics of the 80th quantiles of specialist and generalist herbivory at the level of a (i) population (all individuals of a given *Piper* species in a plot), (ii) community (all *Piper* individuals in a plot), and (iii) forest (all *Piper* individuals measured at a given site). To determine the predictive power of site level variables on the distribution of specialist and generalist herbivory at the level of a population and a community (Hypothesis 1), we also ran linear regression models of the 80th quantiles of specialist and generalist herbivory at the population and community level. Predictor variables included the absolute value of latitude, site level seasonality in precipitation, and the maximum *Piper* richness recorded in a plot at each site. Generalist herbivory at the population level was log-transformed for normality. All analyses were conducted with R version 4.0.3.

Our data were collected to test the hypotheses summarized in Table 1; thus our statistical analyses were designed for specific hypothesis tests and a relatively small number of models rather than model selection or prediction approaches. We tested simpler nested SEM, but all were aligned with hypotheses in Table 1. Furthermore, although we include both Bayesian and null-hypothesis-testing approaches, we do not utilize strict cutoffs or "significance" for probability distributions, rather we report measures of variance, credibility intervals, and probability values associated with our parameter estimates (Wasserstein and Lazer 2016; Tredennick et al. 2021). We also note when effect sizes were small but still fit mechanistic hypotheses.

**Results**

Across sites, median plot level *Piper* richness was 4.0 (range: 1-12), and median plot level *Piper* abundance was 26.5 (range: 3-222). The highest number of *Piper* species in a plot was found in the Mata Atlântica, while the seasonally dry forests in México had the lowest maximum number of *Piper* species in a plot (three species; Supporting Information Table 1). Mean herbivory across the dataset was 7.9 ± 0.13% (SE), and the geometric mean was 4.3%. Mean specialist herbivory was 3.5 ± 0.05% (geometric mean = 1.7%), and mean generalist herbivory was 4.4 ± 0.10% (geometric mean = 2.1%).

*What variables affect the distribution parameters of herbivory?*

The best fit Bayesian SEM describing the distribution of herbivory supported the hypotheses that seasonality, *Piper* richness, and resource availability (leaf area) affect herbivory (X2 = 25.74, df = 33, *P* = 0.81; AIC = 4551.64; Bayesian MLL = -2376.82; PPP = 0.72; Fig. 2; Supporting Information Fig. 2). Strongly seasonal sites had less skewed distributions of specialist herbivory and lower mean generalist herbivory. Higher *Piper* richness led to increased variation in specialist and generalist herbivory, greater skew for generalists, and lower mean herbivory for specialists. Where *Piper* leaf area was greater, there was a narrower skew of generalist herbivory. The skew of generalist herbivory was the best described variable in our model (r2 = 0.16), while mean specialist herbivory was the least well described variable (r2 = 0.02). In addition, the SEM showed *Piper* richness was greater in less seasonal sites.

*Are there site-specific effects on the distribution of herbivory?*

The distribution of herbivory was analyzed separately within each site using the 80th quantiles of herbivory, similar to the latent variable describing skew in the multisite analysis. The best predictors of the distribution of herbivory differed between sites (Fig. 3; Supporting Information Table 3). Our southernmost sites had the most herbivory at the population and community scales, and more seasonal sites had the least herbivory. The forest with the most specialist herbivory was our southernmost site in Brazil (24.3 °S) with an 80th quantile of 10% herbivory. Similarly, our second most southern site had the highest generalist herbivory (80th quantile of 13.4% herbivory; Supporting Information Fig. 3). Both of these sites were tropical wet forests with ~2400 mm of precipitation per year. The site with the lowest specialist herbivory was our second most seasonal site, a gallery forest in the Brazilian cerrado (80th quantile of 1.6% herbivory). Our driest, most seasonal site in México had the lowest generalist herbivory (80th quantile of 1.8% herbivory).

Generalist and specialist herbivory decreased on *Piper* species with more plot-level leaf area (species per plot leaf area) in the tropical dry forests of México and in the Amazon Basin. In contrast, specialist herbivory increased with leaf area in Ecuadorian cloud forest, which was among our least seasonal sites. Total *Piper* leaf area in a plot (including all *Piper* species) led to more generalist and specialist herbivory in the cerrado gallery forest and to more generalist herbivory in Ecuador. Plots with greater *Piper* species richness received more generalist herbivory in Costa Rica, where *Piper* richness was relatively high (5.2 ± 0.5 (SE) species per plot). In contrast, generalist damage decreased with *Piper* richness in the Amazon Basin sites, where overall *Piper* richness was lower (4.2 ± 0.3 species per plot), but increased with *Piper* diversity (based on leaf area). Understory plant richness increased generalist herbivory in the Amazon Basin, where richness was high (60.3 ± 2.9 species per plot), and in the Mata Atlântica, where understory richness was lower (32.0 ± 2.0 species per plot). In the cerrado gallery forest, generalist herbivory decreased with canopy openness (Fig. 3; Supporting Information Table 3).

*Does herbivory vary more at local scales or regionally?*

The distributions of herbivory described with 80th quantiles were similar at the level of a population (conspecifics in a plot), community (congeners in a plot), and site (congeners in multiple plots in a forest; Supporting Information Fig. 3). The 80th quantiles at the site level fell within the interquartile range of the population and community level 80th quantiles with rare exceptions (Supporting Information Fig. 4). Site level variables (latitude, seasonality, and maximum *Piper* richness) explained the 80th quantile of generalist herbivory better than specialist herbivory (Table 2). The site level variables also better predicted herbivory at the community rather than population level (Table 2). Damage by generalist herbivores increased farther from the equator, but the opposite was true for specialist herbivory (Table 2). Herbivory by both generalists and specialists increased where *Piper* was more species rich and decreased in more seasonal sites.

**Discussion**

The search for broad patterns of herbivory has uncovered few consistent relationships, despite numerous hypotheses attempting to explain variation in herbivory (Coley and Aide 1991; Coley and Barone 1996; Moles et al. 2011; Lim et al. 2015; Zhang et al. 2016). In the present work, we examined many of these hypotheses (Table 1), and we found that both landscape and local level variables affect the distribution of herbivory. Importantly, not all metrics of the distributions of herbivory were affected by the same variables, and relevant predictors differed between sites and for generalist and specialist herbivores. Interestingly, the distributions of herbivory were similar whether analyzed for a population of a single species, a local assemblage of co-occurring congeners, or all congeners measured in a forest, suggesting variables that influence herbivory on an individual plant may affect patterns of herbivory across an entire forest. *Piper* is a particularly informative genus for understanding broad scale patterns. It is both abundant and species rich across the Neotropics (Dyer and Palmer 2004), and it suffers levels of herbivory similar to estimates of global averages (the geometric mean in our dataset was 4.3%, while the globally reported geometric mean is 5.3%; Turcotte et al. 2014).

*Herbivory is not directly affected by latitude but is lower in more seasonal forests*

A major question in large-scale studies of herbivory is whether herbivory changes with latitude (Moles et al. 2011; Lim et al. 2015; Zhang et al. 2016). Our SEM indicated that latitude did not have direct effects on the distribution of herbivory, but it is important to note that our latitudinal gradient was limited to the tropics, and many ecological changes associated with latitude occur over gradients that extend from the tropical into the temperate zone (Dyer and Forister 2019). In our dataset, seasonality was the best predictor of changes in herbivory. This may explain why the search for latitudinal gradients in herbivory has been inconclusive and why studies incorporating climate are better able to explain variation in herbivory across large spatial scales (Zhang et al. 2016; Loughnan and Williams 2019). In our data, seasonal variation in precipitation directly reduced the skew of specialist herbivory and the mean of generalist herbivory, and temperature alone was not predictive of herbivory. Seasonality also affected the distribution of herbivory indirectly via changes in *Piper* richness.

Herbivory was lower in more seasonal forests for both specialists and generalists, contrary to our initial hypothesis and a previous review that found *Piper* herbivory to be greater in dry than wet forests (Dirzo and Boege 2008). Our findings are consistent, however, with a study showing plants experience more damage in wet than dry forests (Brenes Arguedas et al. 2009). *Piper* species may be near their range limits in the seasonal forests we studied and therefore host fewer specialized herbivores and suffer lower herbivory (Anstett et al. 2016). Within a forest, herbivore occurrence, plant-herbivore-parasitoid networks, and the relative abundance of generalists and specialists on *Piper* change seasonally (Cosmo et al. 2019; Campos-Moreno et al. 2021; authors, pers. obs). Our data were not collected across multiple seasons at all sites, but *Piper* leaves are long-lived, and specialist *Eois* are often found feeding on mature leaves (authors, pers. obs.). Our measurements of standing herbivory are therefore integrative, reflecting herbivory potentially accumulated over multiple seasons and cannot be used to measure seasonal differences. Herbivory may also vary between years, so long-term studies following leaves through their entire lifespan may produce a more nuanced understanding of variation in herbivory across time and space (Filip et al. 1995).

*Environmental variation describes generalist better than specialist herbivory*

Only 7% of the distribution of specialist herbivory at the community level could be explained by latitude, seasonality, and local *Piper* richness, while these site level factors explained 28% of the variation in generalist herbivory. Differences in the importance of variables influencing specialists versus generalists may partially explain why predicting global patterns of total herbivory has been elusive. For example, local interactions, plant traits, and phylogenetic diversity are known to particularly affect specialist herbivory (Schuldt et al. 2014; Massad et al. 2017; Jactel et al. 2021), while our data show site level factors explain much of the variation in generalist herbivory. Specialist herbivory is the result of a potentially long co-evolutionary history between lineages of plants and herbivores (Ehrlich and Raven 1964; Agrawal et al. 2012; Volf et al. 2018), so it makes sense that specialist damage is more difficult to predict based on factors varying at regional scales. In contrast, generalist herbivores are less constrained by species specific traits and may respond more to environmental variation. A previous study focused on two species of *Piper* found that generalist herbivores increase in richness toward the equator, although herbivory itself did not vary with latitude (Salazar and Marquis 2012). In contrast, our data show mean generalist damage was lower in more seasonal sites, farther from the equator, despite well documented patterns of increasing diet breadth at higher latitudes (Dyer et al. 2007; Forister et al. 2015). Seasonality and distance from the equator were not invariably correlated, however, as two of our Mata Atlântica sites, which were the farthest from the equator, were less seasonal than other sites, such as the dry forests in Mexico and the gallery forest in the cerrado.

*Specialists and generalists respond differently to resource availability and diversity*

Generalist herbivory was lower on species with greater leaf area in our plots. Although this contradicts our original hypothesis that herbivory should be more prevalent or intense where resources are abundant, the pattern is similar to experimental results showing herbivory declines with plant density, possibly because damage is spread across many individuals (Germany et al. 2019). In addition, a locally abundant *Piper* species may by chance be suboptimal for a generalist herbivore, resulting in the herbivore moving to another patch of forest or reducing feeding rates to detoxify defensive chemistry. Both possibilities are supported by the fact that the skew of generalist herbivory decreased with leaf area. In contrast, percent specialist herbivory increased where leaf area was more abundant. This may be because specialists more effectively find their hosts when resources are concentrated, increasing herbivory (Jactel et al. 2021). The difference between specialist and generalist herbivory could also be due to changes in plant chemistry post-damage, which may serve to repel generalist herbivores but not affect adapted specialists. Induced defenses are not thought to be especially important in the tropics (Bixenmann et al. 2016; Glassmire et al. 2023), but volatiles emitted by *Piper* change with damage, which could affect herbivore host searching (Stanton, unpublished data).

Locally, herbivory often increases where patches of forest are more uniform or where associational resistance is lacking (Barbosa et al. 2009; Alvarez-Loayza and Terborgh 2011; Massad et al. 2013; Norghauer et al. 2016; Jactel et al. 2021). At the sites included in this study, *Piper* diversity, measured as species richness and Simpson’s index of leaf area, led to greater skew and dispersion of generalist herbivory. Similarly, the skew of specialist herbivory increased with *Piper* richness, although mean specialist herbivory decreased. It is interesting that in natural settings, where biodiversity-ecosystem function relationships can be difficult to discern, our data support an increase in function (as indicated by herbivory) with greater plant diversity. Understanding determinants of generalist herbivory on *Piper* is particularly important as generalist herbivores shared by *Piper* and other genera can increase plant diversity locally (Dyer et al. 2010).

The contrasts uncovered between generalist and specialist herbivory likely reflect differences in host searching and dietary choices between these two groups of herbivores. Generalists appear to favor more diverse communities, where a single potential host plant does not dominate, potentially due to benefits of dietary mixing (Bernays et al. 1994; Singer et al. 2004). Specialists, on the other hand, may be more attracted to areas where their preferred resource is highly abundant (Root 1973). Site by site, however, these patterns vary widely, as we discuss below.

*Effects of resources and richness on herbivory distributions differ between sites*

In the three Mexican dry forests, herbivory was reduced on species with more leaf area in a plot, presumably because there were more resources available for herbivores, and herbivory was therefore less concentrated on single individuals (Schuldt et al. 2014). In contrast, in our second most seasonal location, a cerrado gallery forest, both generalist and specialist herbivory increased with total *Piper* leaf area. Leaf area per species was greater in plots in México than in the cerrado gallery forest, potentially explaining why there may have been a dilution of herbivory in México and not in the gallery forest. In addition, *Piper* is restricted to the narrow confines of gallery forest in the cerrado (Oliveira-Filho and Ratter 2002), and this concentration of resources may have resulted in the higher herbivory measured. Similar to the cerrado site, in the Ecuadorian cloud forest more extreme generalist and specialist damage was found in plots with more *Piper* leaf area. The higher herbivory measured in Ecuador may result from a less seasonal climate and what is therefore more constant herbivore pressure. In the cerrado, another important pattern was that canopy openness limited herbivory, where increased light levels may cause particularly strong reductions in humidity (corroborating results reported by Richards and Windsor 2007).

In lowland humid forests of Costa Rica and the Amazon Basin *Piper* richness had contrasting effects on generalist herbivory. In Costa Rica, *Piper* richness resulted in more generalist damage. In the Amazon, *Piper* richness was associated with less generalist damage. Nonetheless, generalist herbivory increased with *Piper* leaf area diversity in the Amazon Basin. In addition, *Piper* richness and leaf area diversity were positively correlated in Costa Rica (where richness increased generalist damage). When calculating diversity based on leaf area, one captures the diversity of resources available from an herbivore’s point of view, and this may be a more informative description of resource diversity than the richness of individual plants, particularly if richness values include many small individuals.

*Conclusions*

The search for factors that influence variation in herbivory informs both ecology and conservation because herbivores play a strong role in maintaining tropical forest diversity, even at large scales (Levi et al. 2019). Our data demonstrate that seasonality and community level parameters, such as species richness and resource availability, partially explain the distribution of herbivory. Going forward, it will be important to acknowledge that variables operating at both regional and local scales govern patterns of herbivory. Future work may also benefit from addressing interactions between these predictors. Overall, research that addresses the causes and effects of variation in the statistical distributions of herbivory will help determine factors that produce ecologically meaningful levels of herbivory.

**References**

Agrawal, A. A., Petschenka, G., Bingham, R. A., Weber, M. G., & Rasmann, S. (2012). Toxic cardenolides: Chemical ecology and coevolution of specialized plant-herbivore interactions. *New Phytologist*, *194*, 28–45. <https://doi.org/10.1111/j.1469-8137.2011.04049.x>

Alvarez-Loayza, P., & Terborgh, J. (2011). Fates of seedling carpets in an Amazonian floodplain forest: Intra-cohort competition or attack by enemies? *Journal of Ecology*, *99*, 1045–1054. <https://www.jstor.org/stable/23027668>

Anderson, R. M., Dallar, N. M., Pirtel, N. L., Connors, C. J., Mickley, J., Bagchi, R., & Singer, M. S. (2019). Bottom-up and top-down effects of forest fragmentation differ between dietary generalist and specialist caterpillars. *Frontiers in Ecology and Evolution 7*, 452. doi: 10.3389/fevo.2019.00452

Anstett, D. N., Nunes, K. A., Baskett, C., & Kotanen, P. M. (2016). Sources of controversy surrounding latitudinal patterns in herbivory and defense. *Trends in Ecology & Evolution*, *31*, 789–802. <https://doi.org/10.1016/j.tree.2016.07.011>

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology Evolution and Systematics*, *40*, 1–20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>

Barton, K. E., Valkama, E., Vehvilainen, H., Ruohomaki, K., Knight, T. M., & Koricheva, J. (2015). Additive and non-additive effects of birch genotypic diversity on arthropod herbivory in a long-term field experiment. *Oikos*, *124*, 697–706.

Bebber, D. P., N. D. Brown, and M. R. Speight. 2004. Dipterocarp Seedling Population Dynamics in Bornean Primary Lowland Forest during the 1997-8 El Niño-Southern Oscillation. *Journal of Tropical Ecology 20*, 11–19.

Bernays, E. A., Bright, K. L., Gonzalez, N., & Angel, J. (1994). Dietary Mixing in a Generalist Herbivore: Tests of Two Hypotheses. *Ecology, 75*, 1997–2006. https://doi.org/10.2307/1941604

Bidart-Bouzat, M. G., & Kliebenstein, D. J. (2008). Differential levels of insect herbivory in the field associated with genotypic variation in glucosinolates in Arabidopsis thaliana. *Journal of Chemical Ecology*, *34*, 1026–1037. <https://doi.org/10.1007/s10886-008-9498-z>

Bixenmann, R. J., Coley, P. D., Weinhold, A., & Kursar, T. A. (2016). High herbivore pressure favors constitutive over induced defense. *Ecology and Evolution*, *6*, 6037–6049. <http://dx.doi.org/10.1002/ece3.2208>

Brenes-Arguedas, T., Coley, P. D., & Kursar, T. A. (2009). Pests vs. Drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*, *90*, 1751–1761. <https://doi.org/10.1890/08-1271.1>

Campos-Moreno, D. F., Dyer, L. A., Salcido, D., Massad, T. J., Pérez-Lachaud, G., Tepe, E. J., Whitfield, J. B., & Pozo, C. (2021). Importance of interaction rewiring in determining spatial and temporal turnover of tritrophic (*Piper*-caterpillar-parasitoid) metanetworks in the Yucatán Península, México. *Biotropica*, *53*, 1071–1081. <https://doi.org/10.1111/btp.12946>

Carson, W.P. and Root, R.B. (2000). Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, *70*, 73-99.

Carson, W. P., Anderson, J. T., Leigh Jr, E. G., & Schnitzer, S.A. (2008). Challenges associated with testing and falsifying the Janzen-Connell Hypothesis: A review and critique. Pp 210-241 in W. P. Carson & S. A. Schnitzer, eds. Tropical Forest Community Ecology. Blackwell Publishing, Malden, USA.

Castagneyrol, B., Lagache, L., Giffard, B., Kremer, A., & Jactel, H. (2012). Genetic diversity Increases insect herbivory on oak saplings. *PLOS ONE*, *7*, e44247. <https://doi.org/10.1371/journal.pone.0044247>

Clark, D. B., & Clark, D. A. (1985). Seedling dynamics of a tropical tree: Impacts of herbivory and meristem damage. *Ecology*, *66*, 1884–1892. <https://doi.org/10.2307/2937384>

Cobb, N. S., Mopper, S., Gehring, C. A., Caouette, M., Christensen, K. M., & Whitham, T. G. (1997). Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. *Oecologia*, *109*, 389–397. <https://doi.org/10.1007/s004420050098>

Coley, P. D. (1980). Effects of leaf age and plant life history patterns on herbivory. *Nature*, *284*(5756), 545–546.

Coley, P. D., & Aide, T. M. (1991). A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pp 25 – 49 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes, & W. W. Benson, eds. Plant-Animal Interactions? Evolutionary Ecology in Tropical and Temperate Regions. Wiley & Sons, New York.

Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology, Evolution, and Systematics, 27*, 305–335.

Cosmo, L. G., Nascimento, A. R., Cogni, R., & Freitas, A. V. L. (2019). Temporal distribution in a tri-trophic system associated with *Piper amalago* L. in a tropical seasonal forest. *Arthropod-Plant Interactions*, *13*, 647–652. <https://doi.org/10.1007/s11829-019-09687-y>

Coverdale, T. C., Goheen, J. R., Palmer, T. M., & Pringle, R. M. (2018). Good neighbors make good defenses: Associational refuges reduce defense investment in African savanna plants. *Ecology*, *99*, 1724–1736. <https://doi.org/10.1002/ecy.2397>

Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, *38*, 208–221. <https://www.jstor.org/stable/27826306>

Dirzo R, & Boege K. 2008. Patterns of herbivory and defense in tropical dry and rain forests. Pp. 63–78 in W. P. Carson & S. A. Schnitzer, eds. Tropical forest Community Ecology. Wiley-Blackwell, Hoboken, NJ.

Dyer, L. A., Letourneau, D. K., Dodson, C. D., Tobler, M. A., Stireman, J. O., & Hsu, A. (2004). Ecological causes and consequences of variation in defensive chemistry of a Neotropical shrub. *Ecology*, *85*, 2795–2803. https://doi.org/10.1890/03-0233

Dyer L. A., & Palmer, A. D. N. (2004). *Piper*: A Model Genus for Studies of Phytochemistry, Ecology, and Evolution. Springer US, Boston, USA.

Dyer, L. A., Singer, M. S., Lill, J. T., Stireman, J. O., Gentry, G. L., Marquis, R. J., Ricklefs, R. E., Greeney, H. F., Wagner, D. L., Morais, H. C., Diniz, I. R., Kursar, T. A., & Coley, P. D. (2007). Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, *448*, 696-699. <https://doi.org/10.1038/nature05884>

Dyer, L. A., Letourneau, D. K., Chavarria, G. V., & Amoretti, D. S. (2010). Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. *Ecology*, *91*, 3707–3718. <https://doi.org/10.1890/08-1634.1>

Dyer, L. A., Carson, W. P, & Leigh, E. G. (2012). Insect outbreaks in tropical forests: Patterns, mechanisms, and consequences. Pp 219-245 in P. Barbosa, D. K. Letourneau, & A. A. Agrawal, eds. Insect Outbreaks Revisited, first edition. Blackwell Publishing Ltd, Hoboken, NJ.

Dyer, L. A., & Forister, M. L. (2019). Challenges and advances in the study of latitudinal gradients in multitrophic interactions, with a focus on consumer specialization. *Current Opinion in Insect Science*, *32*, 68–76. <https://doi.org/10.1016/j.cois.2018.11.008>

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

Endara, M.-J., Weinhold, A., Cox, J. E., Wiggins, N. L., Coley, P. D., & Kursar, T. A. (2015). Divergent evolution in antiherbivore defences within species complexes at a single Amazonian site. *Journal of Ecology*, *103*, 1107–1118. <https://doi.org/10.1111/1365-2745.12431>

Endara, M.-J., Coley, P. D., Ghabash, G., Nicholls, J. A., Dexter, K. G., Donoso, D. A., Stone, G. N., Pennington, R. T., & Kursar, T. A. (2017). Coevolutionary arms race versus host defense chase in a tropical herbivore-plant system. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, E7499–E7505. <https://doi.org/10.1073/pnas.1707727114>

Endara, M.-J., Nicholls, J. A., Coley, P. D., Forrister, D. L., Younkin, G. C., Dexter, K. G., Kidner, C. A., Pennington, R. T., Stone, G. N., & Kursar, T. A. (2018). Tracking of host defenses and phylogeny during the radiation of Neotropical Inga-feeding sawflies (Hymenoptera; Argidae). *Frontiers in Plant Science*, *0*. <https://doi.org/10.3389/fpls.2018.01237>

Eveleigh, E. S., McCann, K. S., McCarthy, P. C., Pollock, S. J., Lucarotti, C. J., Morin, B., McDougall, G. A., Strongman, D. B., Huber, J. T., Umbanhowar, J., & Faria, L. D. B. (2007). Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proceedings of the National Academy of Sciences*, *104*(43), 16976–16981. <https://doi.org/10.1073/pnas.0704301104>

Filip, V., Dirzo, R., Maass, J. M., & Sarukhan, J. (1995). Within- and Among-Year Variation in the Levels of Herbivory on the Foliage of Trees from a Mexican Tropical Deciduous Forest. *Biotropica*, *27*(1), 78–86. <https://doi.org/10.2307/2388905>

Fine, P. V. A., & Mesones, I. (2011). The role of natural enemies in the germination and establishment of *Pachira* (Malvaceae) trees in the Peruvian Amazon. *Biotropica 43*, 265–269.

Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Drozd, P., Fox, M., Glassmire, A. E., Hazen, R., Hrcek, J., Jahner, J. P., Kaman, O., Kozubowski, T. J., Kursar, T. A., … Dyer, L. A. (2015). The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences*, *112*, 442–447. <https://doi.org/10.1073/pnas.1423042112>

Galmán, A., Abdala‐Roberts, L., Zhang, S., Teran, J. C. B.-M. y, Rasmann, S., & Moreira, X. (2018). A global analysis of elevational gradients in leaf herbivory and its underlying drivers: Effects of plant growth form, leaf habit and climatic correlates. *Journal of Ecology*, *106*(1), 413–421. <https://doi.org/10.1111/1365-2745.12866>

Gao, J., Fang, C., & Zhao, B., (2019). The latitudinal herbivory hypothesis revisited: To be part is to be whole. *Ecology and Evolution*, *9*, 3681-3688.

Gentry, G. L., & Dyer, L. A. (2002). On the conditional nature of neotropical caterpillar defenses against their natural enemies. *Ecology, 83*(11), 3108–3119. https://doi.org/10.1890/0012-9658(2002)083[3108:OTCNON]2.0.CO;2

Germany, M. S., Bruelheide, H., & Erfmeier, A. (2019). Janzen-Connell effects in a forest BEF experiment: Strong distance-dependent seedling establishment of multiple species. *Ecology*, *100*(8), e02736. <https://doi.org/10.1002/ecy.2736>

Glassmire, A. E., Carson, W. P., Smilanich, A. M., Richards, L. A., Jeffrey, C. S., Dodson, C. D., Philbin, C. S., Garcia Lopez, H., and Dyer, L. A. (2023). Multiple and contrasting pressures determine intraspecific phytochemical variation in a tropical shrub. *Oecologia, 201*, 991–1003.

Hahn, P. G., Agrawal, A. A., Sussman, K. I., & Maron, J. L. (2019). Population variation, environmental gradients, and the evolutionary ecology of plant defense against herbivory. *The American Naturalist*, *193*(1), 20–34. <https://doi.org/10.1086/700838>

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, *94*(879), 421–425. <https://www.jstor.org/stable/2458808>

Hunter, M. D., & Forkner, R. E. (1999). Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology*, *80*(8), 2676–2682. [https://doi.org/10.1890/0012-9658(1999)080[2676:HDIFPA]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5b2676:HDIFPA%5d2.0.CO;2)

Jactel, H., & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters*, *10*(9), 835–848. <https://doi.org/10.1111/j.1461-0248.2007.01073.x>

Jactel, H., Moreira, X., & Castagneyrol, B. (2021). Tree diversity and forest resistance to insect pests: Patterns, mechanisms, and prospects. In A. E. Douglas (Ed.), *Annual Review of Entomology, Vol 66, 2021* (Vol. 66, pp. 277–296). Annual Reviews. <https://doi.org/10.1146/annurev-ento-041720-075234>

Janzen, D. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist 104*:501-528.

Johnson, M. T. J., & Rasmann, S. (2011). The latitudinal herbivory-defence hypothesis takes a detour on the map. *New Phytologist*, *191*(3), 589–592. <https://doi.org/10.1111/j.1469-8137.2011.03816.x>

Jost, L. (2006). Entropy and diversity. *Oikos 113*:363-375.

Katz, D. S. W. (2016). The effects of invertebrate herbivores on plant population growth: A meta-regression analysis. *Oecologia*, *182*(1), 43–53. <https://doi.org/10.1007/s00442-016-3602-9>

Kent, D.R., Lynn, J.S., Pennings, S.C., Souza, L.A., Smith, M.D. and Rudgers, J.A., (2020). Weak latitudinal gradients in insect herbivory for dominant rangeland grasses of North America. *Ecology and evolution*, *10*(13), 6385-6394.

Langeheim, J. H., & Stubblebine, W. H. (1983). Variation in leaf resin composition between parent tree and progeny in *Hymenaea*: Implications for herbivory in the humid tropics. *Biochemical Systematics and Ecology 11*:97–106.

Levi, T., Barfield, M., Barrantes, S., Sullivan, C., Holt, R. D., & Terborgh, J. (2019). Tropical forests can maintain hyperdiversity because of enemies. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(2), 581–586. <https://doi.org/10.1073/pnas.1813211116>

Lim, J. Y., Fine, P. V. A., & Mittelbach, G. G. (2015). Assessing the latitudinal gradient in herbivory. *Global Ecology and Biogeography*, *24*(10), 1106–1112. <https://doi.org/10.1111/geb.12336>

Loughnan, D., & Williams, J. L. (2019). Climate and leaf traits, not latitude, explain variation in plant–herbivore interactions across a species’ range. *Journal of Ecology*, *107*, 913–922. <https://doi.org/10.1111/1365-2745.13065>

Lynn, J. S., & Fridley, J. D. (2019). Geographic patterns of plant–herbivore interactions are driven by soil fertility. *Journal of Plant Ecology 12*:653–661.

Marino, P.C., & Landis, D. A. (1996). Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications, 6,* 276-284.

Marquis, R. J. (1992). A bite is a bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). *Ecology*, *73*, 143–152. <https://doi.org/10.2307/1938727>

Massad, T. J. (2013). Ontogenetic differences of herbivory on woody and herbaceous plants: A meta-analysis demonstrating unique effects of herbivory on the young and the old, the slow and the fast. *Oecologia*, *172*, 1–10. https://doi.org/10.1007/s00442-012-2470-1

Massad, T. J., Balch, J. K., Davidson, E. A., Brando, P. M., Mews, C. L., Porto, P., Quintino, R. M., Vieira, S. A., Marimon Junior, B. H., & Trumbore, S. E. (2013). Interactions between repeated fire, nutrients, and insect herbivores affect the recovery of diversity in the southern Amazon. *Oecologia*, *172*, 219–229. <https://doi.org/10.1007/s00442-012-2482-x>

Massad, T. J., de Moraes, M. M., Philbin, C., Oliveira, C., Torrejon, G. C., Yamaguchi, L. F., Jeffrey, C. S., Dyer, L. A., Richards, L. A., & Kato, M. J. (2017). Similarity in volatile communities leads to increased herbivory and greater tropical forest diversity. *Ecology 98*:1750–1756.

Massad, T. J., L. A. Richards, C. Philbin, L. Fumiko Yamaguchi, M. J. Kato, C. S. Jeffrey, C. Oliveira Jr, K. Ochsenrider, M. M. de Moraes, E. J. Tepe, G. Cebrian Torrejon, M. Sandivo, & Dyer, L. A. (2022). The chemical ecology of tropical forest diversity: Environmental variation, chemical similarity, herbivory, and richness. *Ecology* n/a:e3762.

Matos, F. B., Amorim, A. M., & Labiak, P. H. (2010). The ferns and lycophytes of a montane tropical forest in southern Bahia, Brazil. *Journal of the Botanical Research Institute of Texas,* *4*, 333–346.

Merkle, E. C., & Rosseel, Y. (2016). blavaan: Bayesian structural equation models via parameter expansion. arXiv 1511.05604. URL <https://arxiv.org/abs/1511.05604>.

Moreira, X., Abdala-Roberts, L., Parra-Tabla, V., & Mooney, K. A. (2015). Latitudinal variation in herbivory: influences of climatic drivers, herbivore identity and natural enemies. *Oikos, 124,* 1444–1452.

Moles, A. T., Bonser, S. P., Poore, A. G. B., Wallis, I. R., & Foley, W. J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, *25*, 380–388. <https://doi.org/10.1111/j.1365-2435.2010.01814.x>

Murphy, S. M., Lill, J. T., Bowers, M. D. & Singer, M. S. (2014) Enemy-free space for parasitoids. *Environmental Entomology, 43,* 1465–1474.

Njovu, H. K., Peters, M. K., Schellenberger Costa, D. Brandl, R., Kleyer, M., Steffan‐Dewenter, I., & Si, X. (2019). Leaf traits mediate changes in invertebrate herbivory along broad environmental gradients on Mt. Kilimanjaro, Tanzania. *The Journal of Animal Ecology, 88,* 1777–1788.

Norghauer, J. M., Free, C. M., Landis, R. M., Grogan, J., Malcolm, J. R., & Thomas, S. C., (2016). Herbivores limit the population size of big-leaf mahogany trees in an Amazonian forest. *Oikos, 125,* 137–148.

Oliveira-Filho, A. T., & Ratter, J. A. (2002). 6. Vegetation Physiognomies and Woody Flora of the Cerrado Biome. In The Cerrados of Brazil (pp. 91-120). Columbia University Press.

Pacala, S. W. & Hassell, M. P. (1991) The Persistence of Host-Parasitoid Associations in Patchy Environments. II. Evaluation of Field Data. *The American Naturalist 138,* 584-605.

Pearson, T. R. H., Burslem, D., Goeriz, R. E., & Dalling, J. W. (2003a). Interactions of gap size and herbivory on establishment, growth and survival of three species of neotropical pioneer trees. *Journal of Ecology*, *91*, 785–796. <https://doi.org/10.1046/j.1365-2745.2003.00803.x>

Pearson, T. R. H., Burslem, D., Goeriz, R. E., & Dalling, J. W. (2003b). Regeneration niche partitioning in neotropical pioneers: Effects of gap size, seasonal drought and herbivory on growth and survival. *Oecologia*, *137*, 456–465. <https://doi.org/10.1007/s00442-003-1361-x>

Piper, F. I., S. H. Altmann, & Lusk, C. H. (2018) Global patterns of insect herbivory in gap and understorey environments, and their implications for woody plant carbon storage. *Oikos 127*, 483–496.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980) Interactions among three trophic levels: influence of plants on interaction between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, *11*, 41-65.

Rasmann, S., Pellissier, L., Defossez, E., Jactel, H., & Kunstler, G. (2014). Climate‐driven change in plant–insect interactions along elevation gradients. *Functional Ecology*, *28*, 46-54.

Richards, L. A., & Windsor, D. M. (2007). Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Ecology*, *23*, 169–176. <https://doi.org/10.1017/S0266467406003907>

Richards, L. A., & Coley, P. D. (2008). Combined Effects of Host Plant Quality and Predation on a Tropical Lepidopteran: A Comparison between Treefall Gaps and the Understory in Panama. *Biotropica*, *40*, 736–741. <https://doi.org/10.1111/j.1744-7429.2008.00438.x>

Richards, L. A., L. A. Dyer, M. L. Forister, A. M. Smilanich, C. D. Dodson, M. D. Leonard, & Jeffrey, C. S. (2015). Phytochemical diversity drives plant-insect community diversity. *Proceedings of the National Academy of Sciences of the United States of America, 112*, 10973–10978.

Root, R. (1973). Organization of a plant-arthropod association in simple and diverse habitats—fauna of collards (*Brassica oleracea*). *Ecological Monographs*, *43*, 95–120. <https://doi.org/10.2307/1942161>

Rosenthal, J. P., & Kotanen, P. M. (1994). Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution*, *9*, 145–148. <https://doi.org/10.1016/0169-5347(94)90180-5>

Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software, 48*, 1-36. URL <http://www.jstatsoft.org/v48/i02/>.

Salazar, D., & Marquis, R. J. (2012). Herbivore pressure increases toward the equator. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 12616–12620. <https://doi.org/10.1073/pnas.1202907109>

Salazar, D., Jaramillo, A., & Marquis, R. J. (2016). The impact of plant chemical diversity on plant-herbivore interactions at the community level. *Oecologia*, *181*, 1199–1208. <https://doi.org/10.1007/s00442-016-3629-y>

Schuldt, A., Assmann, T., Bruelheide, H., Durka, W., Eichenberg, D., Härdtle, W., Kröber, W., Michalski, S. G., & Purschke, O. (2014). Functional and phylogenetic diversity of woody plants drive herbivory in a highly diverse forest. *New Phytologist*, *202*, 864–873. <https://doi.org/10.1111/nph.12695>

Singer, M. S., Carriere, Y., Theuring, C., & Hartmann, T. (2004). Disentangling food quality from resistance against parasitoids: Diet choice by a generalist caterpillar. *American Naturalist*, *164*, 423–429. <https://doi.org/10.1086/423152>

Stireman, J. O. III & Singer, M. S. (2003). Determinants of parasitoid-host associations: insights from a natural tachinid-lepidopteran community. *Ecology*, 84, 296–310.

Stireman, J. O., Dyer, L. A., Janzen, D. H., Singer, M. S., Lill, J. T., Marquis, R. J., Ricklefs, R. E., Gentry, G. L., Hallwachs, W., Coley, P. D., Barone, J. A., Greeney, H. F., Connahs, H., Barbosa, P., Morais, H. C., & Diniz, I. R. (2005). Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proceedings of the National Academy of Sciences*, *102*, 17384–17387. <https://doi.org/10.1073/pnas.0508839102>

Strauss, S. Y., & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*, *14*, 179–185. <https://doi.org/10.1016/S0169-5347(98)01576-6>

Sudta, C., Salcido, D. M., Forister, M. L., Walla, T. R., Villamarín‐Cortez, S. & Dyer, L.A., (2022). Jack‐of‐all‐trades paradigm meets long‐term data: Generalist herbivores are more widespread and locally less abundant. *Ecology Letters*, *25*, 948-957.

Thompson, B. & Daniel, L. G., (1996). Factor analytic evidence for the construct validity of scores: A historical overview and some guidelines. *Educational and Psychological Measurement*, *56*, 197-208.

Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology, 102(6), e03336. https://doi.org/10.1002/ecy.3336

Turcotte, M. M., Davies, T. J., Thomsen, C. J. M., & Johnson, M. T. J. (2014). Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. *Proceedings of the Royal Society B: Biological Sciences*, *281,* 1787. <https://doi.org/10.1098/rspb.2014.0555>

Vehvilainen, H., Koricheva, J., & Ruohomaki, K. (2007). Tree species diversity influences herbivore abundance and damage: Meta-analysis of long-term forest experiments. *Oecologia*, *152*, 287–298. <https://doi.org/10.1007/s00442-007-0673-7>

Volf, M., S. T. Segar, S. E. Miller, B. Isua, M. Sisol, G. Aubona, P. Simek, M. Moos, J. Laitila, J. Kim, J. Zima, J. Rota, G. D. Weiblen, S. Wossa, J.-P. Salminen, Y. Basset, & Novotny, V. (2018). Community structure of insect herbivores is driven by conservatism, escalation and divergence of defensive traits in *Ficus*. *Ecology Letters, 21,* 83–92.

Wasserstein, R. L., & Lazar, N. A. (2016). The ASA Statement on p-Values: Context, Process, and Purpose. The American Statistician, 70(2), 129–133. https://doi.org/10.1080/00031305.2016.1154108

Whitfeld, T. J. S., Novotny, V., Miller, S. E., Hrcek, J., Klimes, P., & Weiblen, G. D. (2012). Predicting tropical insect herbivore abundance from host plant traits and phylogeny. *Ecology*, *93*, S211–S222. <https://doi.org/10.1890/11-0503.1>

Zhang, S., Zhang, Y., & Ma, K. (2016). Latitudinal variation in herbivory: Hemispheric asymmetries and the role of climatic drivers. *Journal of Ecology*, *104*, 1089–1095. <https://doi.org/10.1111/1365-2745.12588>

Zvereva, E.L., Zverev, V., Usoltsev, V.A. & Kozlov, M.V. (2020). Latitudinal pattern in community‐wide herbivory does not match the pattern in herbivory averaged across common plant species. *Journal of Ecology*, *108*, 2511-2520.

**Table 1.** Hypothesized responses of specialist and generalist herbivory to local and regional variation in abiotic and biotic conditions

|  |  |
| --- | --- |
| **Predictor** | **Relevant hypotheses** |
| Scale at which the distribution of herbivory is assessed | H1: Variation in herbivory may increase with scale (spatially and phylogenetically).  Prediction: The dispersion and skew of specialist and generalist herbivory will be greater across congeners in a forest as compared to congeners within a local community or members of a subpopulation. |
| ***Regional scale*** |  |
| Precipitation seasonality | H2: At the regional scale, specialist and generalist herbivory may be higher in seasonal habitats, where leaves may be shorter lived and less well defended (Coley and Barone 1996).  Prediction: While specialist and generalist herbivory will be higher in seasonal forests, the pattern may be weaker for specialists as they are more locally abundant across their range (Sudta et al. 2022) and are better adapted to higher defenses. |
| Average temperature | H3: Elevated temperatures may increase metabolism, phenology, population dynamics, and host plant quality (Dyer et al. 2013), which may result in a positive correlation between temperature and herbivory for both generalists and specialists.  Prediction: The mean and skew of herbivory will increase with temperature, but as specialists are more locally abundant than generalists, the distribution of generalist herbivory will be more susceptible to outliers, yielding higher variance and positive skew for generalists across the ranges of temperature (Sudta et al. 2022). |
| Latitude | H4: Generalist and specialist herbivory may be higher at lower latitudes as herbivory is greater in the tropics (Coley and Barone 1996), negative density dependence is stronger in the tropics (LaManna et al. 2017), and generalist herbivore richness decreases with latitude (Salazar and Marquis 2012).  Prediction: The mean and skew of herbivory may increase toward the equator, particularly for generalists. |
| ***Local scale*** | |
| Resource availability | H5: The resource concentration hypothesis (Root 1973) suggests herbivory should increase in plots where host plants are relatively more abundant. Specialist damage may be especially affected by associational resistance.  Prediction: The mean, dispersion, and skew of herbivory will increase in plots where resources are more concentrated, especially for specialists. |
| Species richness | H6: The Janzen-Connell hypothesis (Janzen 1970; Connell 1971) predicts specialist herbivory is greater where plant richness is lower. Generalist herbivory should also be greater where richness is lower (Massad et al. 2022).  Prediction: The mean and skew of herbivory will increase where species richness is lower, particularly for specialists. |
| Canopy openness | H7: Herbivory may be less positively skewed in plots with more light as herbivores decrease in gaps during the dry season (Richards and Windsor 2007).  Prediction: The dispersion and skew of herbivory will decrease in high light environments. |

**Table 2.** Linear regression results of 80th quantiles of herbivory calculated at the community (*Piper* congeners in a plot) and population (*Piper* conspecifics per plot) levels. Latitude is the absolute value of latitude, *Piper* richness is the maximum richness recorded at each site. Values are parameter estimates (PE; ±SE) and *P*-values. Adjusted r2 values are presented

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response variable** | | **Latitude** | ***Piper* richness** | **Seasonality** | **Overall model** |
| Community level 80th quantile | Generalist herbivory | PE = 0.12 ±0.05  *P* =0.01 | PE = 0.82 ±0.12  *P* < 0.001 | PE = -9.04 ±2.45  *P* < 0.001 | F3,160 = 21.61  *P* < 0.001  r2 = 0.28 |
| Specialist herbivory | PE = -0.03 ±0.05  *P* =0.53 | PE = 0.13 ±0.12  *P* = 0.30 | PE = -6.09 ±2.60  *P* = 0.02 | F3,160 = 5.26  *P* = 0.002  r2 = 0.07 |
| Population level 80th quantile | Generalist herbivory | PE = 0.04 ±0.009  *P* < 0.001 | PE = 0.11 ±0.02  *P* < 0.001 | PE = -2.42 ±0.44  *P* < 0.001 | F3,495 = 19.71  *P* < 0.001  r2 = 0.10 |
| Specialist herbivory | PE = -0.08 ±0.05  *P* =0.11 | PE = 0.10 ±0.11  *P* = 0.40 | PE = -2.38 ±2.44  *P* = 0.33 | F3,495 = 3.44  *P* = 0.02  r2 = 0.01 |

**Fig. 1.** Map of 16 study sites spanning 44° latitude from 20 °N in México to 24 °S and examples of two study plots from the Reserva Adolfo Ducke

**Fig. 2.** Bayesian structural equation model describing the distribution of generalist and specialist herbivory across 164 plots in 16 forests. Blue arrows indicate positive causal relationships; red circles show negative causal relationships; none of the Bayesian 95% equal-tailed credible intervals included zero. Black double-headed arrows indicate a positive correlation, and grey double-headed arrows indicate a correlation in which the Bayesian 95% equal-tailed credible intervals included zero. Values shown are Bayesian posteriors. The thickness of the lines indicates the relative strength of the relationships

**Fig. 3.** Site level SEM path coefficients describing the 80th quantiles of specialist and generalist herbivory. Distributions of variables are shown in the table margins across sites from N to S (México, Costa Rica, Ecuador, Perú, Amazonas, Serra Bonita, Mogi-Guaçu, and the central-southern Mata Atlântica). R2 values are the amount of herbivory explained by the models. Grey values were non-significant but were included in the best fit models. Relationships between other variables in the models are in Supporting Information Table 2

|  |  |
| --- | --- |
|  |  |

**Fig. 1.**



**Fig. 2.**



**Fig. 3.**