

Research article

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

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Insect herbivory can be an important selective pressure and contribute substantially to local plant richness. As herbivory is the result of numerous ecological and evolutionary processes, such as complex insect population dynamics and evolution of plant antiherbivore defenses, 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 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 (indicated by skew and dispersion). We observed a roughly twofold increase in median herbivory in humid relative to seasonal forests, which aligns with the hypothesis that precipitation seasonality plays a critical role in shaping interaction diversity within tropical ecosystems. Site level variables such as latitude, seasonality, and maximum *Piper* richness explained the positive skew in herbivory at the local scale (plot level) better for assemblages of *Piper* congeners than 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, dispersion, and skew 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.

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

Introduction

Insect herbivory varies significantly along latitudinal gradients, between distinct biomes, between plant populations, and among individual plants (Coley et al. 1980, Zhang et al. 2016, Gao et al. 2019). Both central tendencies and ranges of herbivory vary 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, Langeheim 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 (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 (Robinson et al. 2023, <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 (Clark and Clark 1985, Marquis 1992), 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 differences in herbivory have been measured across latitude (Lim et al. 2015, Zhang et al. 2016, Loughnan and Williams 2019) and sites that vary in temperature, precipitation, and seasonality (Brenes-Arguedes et al. 2009, Moreira et al. 2015, Galmán et al. 2018, Njovu et al. 2019, Hahn et al. 2019, Lynn and Fridley 2019). Within the tropics, herbivores are more species rich closer to the equator (Salazar and 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 and Williams 2019). Although herbivory is largely considered to be more intense in the tropics (Coley and Aide 1991, Coley and Barone 1996), recent work has shown that herbivory decreases with latitude in the Northern but not in the Southern Hemisphere (Zhang et al. 2016). Latitudinal variation in herbivory may also result from increased herbivore specialization and greater trophic interaction diversity at lower latitudes (Dobzhansky 1950, Mittelbach et al. 2007,

Dyer et al. 2007, Schemske et al. 2009, Forister et al. 2015, LaManna et al. 2017, Dyer and 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 (Root 1973, Whitfeld et al. 2012, Loughnan and Williams 2019), plant species richness (Jactel and Brockerhoff 2007, Vehviläinen et al. 2007), population and phylogenetic diversity (Bidart-Bouzat and 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 more concentrated resources, plant stress, and low plant diversity will favor higher herbivory with distributions exhibiting more positive skew and kurtosis (Cobb et al. 1997, Hunter and Forkner 1999, Pearson et al. 2003a, b, Dyer et al. 2004, 2012, Richards and Coley 2008, Piper et al. 2018, Lynn and Fridley 2019). Specialist herbivory 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). In addition to biotic factors, variation in local environmental conditions, particularly light and nutrient availability, can impact the extent of herbivory and its consequences for plants (Hunter and Forkner 1999, Pearson et al. 2003a, b, Dyer et al. 2004, Richards and Coley 2007, 2008, Piper et al. 2018, Lynn and Fridley 2019).

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 therefore supplement comparisons of central tendencies with measures of variation in dispersion, skew and kurtosis (Rasman et al. 2014, Gao et al. 2019, Kent et al. 2020). These elevated levels of herbivory can affect ecological and evolutionary processes, including plant growth, survival, reproduction, population dynamics, and the evolution of specialized metabolites (Clark and Clark 1985, Marquis 1992, Carson and Root 2000, Bebbler et al. 2004, Fine and Mesones 2011, Endara et al. 2015). High levels of herbivory, for example, have long-lasting effects on plant reproduction (Marquis 1992, Ishizaki et al. 2010).

Nonetheless, there are limited attempts to document patterns in these additional moments of herbivory distributions across gradients that span a range of latitudes, seasonality, nutrient availability, or the diversity and strength of biotic

interactions (Robinson et al. 2023; <https://herbvar.org>). It is also challenging to predict how the distribution of herbivory is 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 generally characterized by a strong positive skew, Massad et al. 2013, 2017, Robinson et al. 2023; <https://herbvar.org>), 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 variation in herbivory, we collected herbivory data on 147 species and morphospecies 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 within communities and across environmental gradients (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. Large-scale variation in herbivory has rarely been studied in datasets examining local diversity and population density as predictors of herbivory. We asked: 1) does herbivory vary more at local (within a plot) scales or regionally (between multiple plots across a forest)? 2) What abiotic and biotic

variables affect the distribution of herbivory? 3) Are there site-specific community effects on the distribution of herbivory (local scale hypotheses in Table 1)? In the context of these questions, the ‘distribution of herbivory’ refers to a statistical distribution of damage on individual plants. The distribution of herbivory across individual plants is summarized by central tendency, dispersion, skewness and kurtosis, which are collectively referred to as the moments of the distribution.

The research was guided by the following hypotheses (summarized in Table 1 with specific predictions). While contrasting predictions are possible for the hypotheses, the directions of predicted effects were guided by existing empirical and theoretical studies (Table 1). H1) Herbivory may exhibit greater variability among *Piper* assemblages (between plots) than within local assemblages (between congeners or 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 (Sudta et al. 2022) and are better adapted to higher defenses. H3) Elevated temperatures generally increase herbivore metabolism and population dynamics, as well as phenological asynchrony with enemies, all of which contribute to a positive correlation between temperature and herbivory. 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. H4) Herbivory may be elevated (both mean and

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 herbivore metabolism, developmental rates, population growth, and host plant quality, leading to a positive correlation between temperature and herbivory for both generalists and specialists Prediction: The mean and skew of herbivory will increase with temperature. As specialists are more locally abundant than generalists (Sudta et al. 2022), the distribution of generalist herbivory will be more susceptible to outliers, yielding higher variance and positive skew for generalists across the ranges of temperature
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 concentration	H5. The Janzen–Connell hypothesis (Janzen 1970, Connell 1971) predicts that specialist herbivory is greater where plant richness is lower. Similarly, the resource concentration hypothesis (Root 1973) proposes that 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
Canopy openness	H6. 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

skew) at lower latitudes. H5) Community level parameters, such as abundance and species richness (resource availability: Root 1973, richness: Janzen 1970, Connell 1971), may better predict variation in herbivory than large-scale factors that differ across sites. Specialist herbivory may increase more than generalist damage where resources are more concentrated. H6) At the local scale, herbivory in plots with more open canopies may be less positively skewed as herbivore abundance decreases in hotter, drier environments found in canopy gaps (Richards and Windsor 2007).

The research focused on changes in moments of the distribution of herbivory because these hypotheses address variation in herbivory, with a focus on extreme levels of herbivory, which have greater impacts on plants. Thus, we examined the median and geometric mean, measures of central tendency that are appropriate for positively skewed distributions. We also estimated the dispersion of herbivory across neighboring plants, which captures the spread of herbivory values within a community. Finally, we assessed positive skew in herbivory values through a latent variable construct, which was most heavily influenced by the upper quantiles of herbivory in populations and communities.

Material and 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 Atlántica 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 the 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 Atlántica, one gallery forest in the cerrado, and two seasonal and two wet forest sites in the middle-southern Mata Atlántica (Supporting information).

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; these species typically consume 1–3 species within *Piper*, and the damage from these taxa is easily differentiated from damage by 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 five

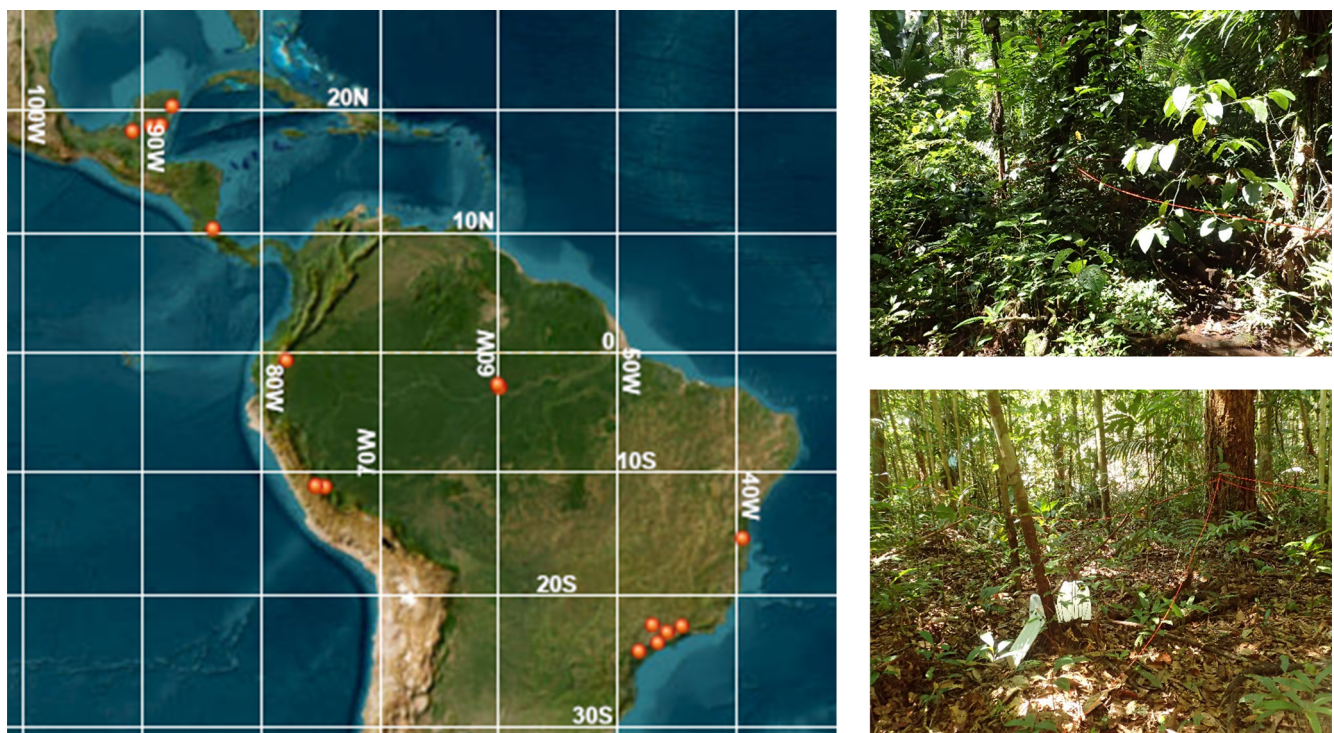


Figure 1. Map of 16 study sites spanning 44° latitude from 20°N in México to 24°S and examples of two study plots from the Reserva Adolfo Ducke

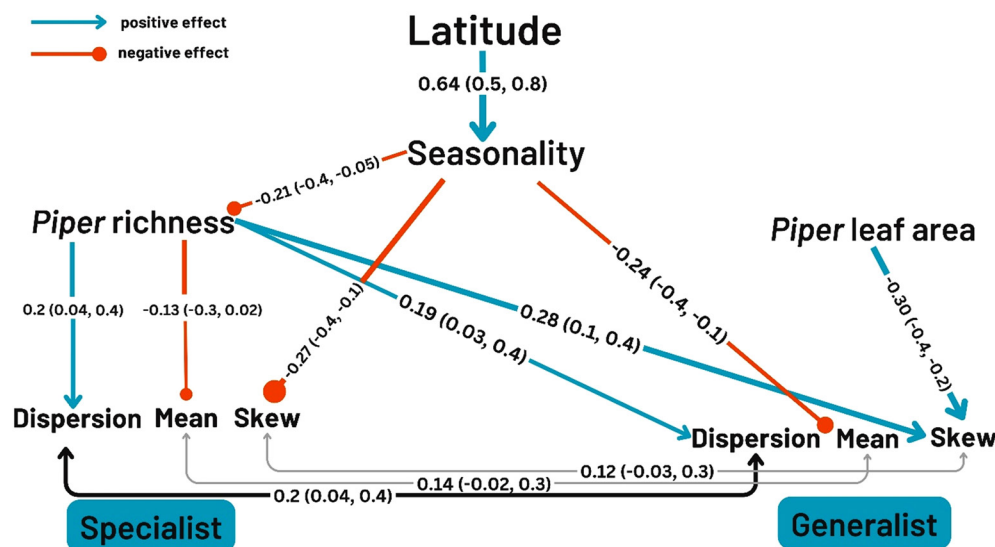


Figure 2. Bayesian structural equation model explaining the distribution of generalist and specialist herbivory in 164 plots across 16 forests. Blue arrows indicate positive causal relationships; red circles show negative causal relationships. Values shown are standardized regression coefficients estimated as means of Bayesian posterior distributions of SEM parameters and 95% equal-tailed credible intervals. See the Supporting information for distributions of the posteriors. The only causal path in which the 95% equal-tailed credible intervals included zero was between *Piper* richness and mean specialist herbivory. Black double-headed arrows indicate positive associations, and gray double-headed arrows indicate associations for which the 95% equal-tailed credible intervals included zero. The thickness of the lines indicates the relative strength of the relationships.

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 of 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, thus sample sizes were small, especially given the focus on moments of the distribution such as skew. To get estimates that were somewhat less susceptible to distributions of small sample sizes, we utilized a latent variable approach, described below, to estimate distribution parameters.

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. 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 to 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 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 to February 2019 and are from the Servicio Meteorológico 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. To answer Question I concerning whether herbivory varies more at local or regional

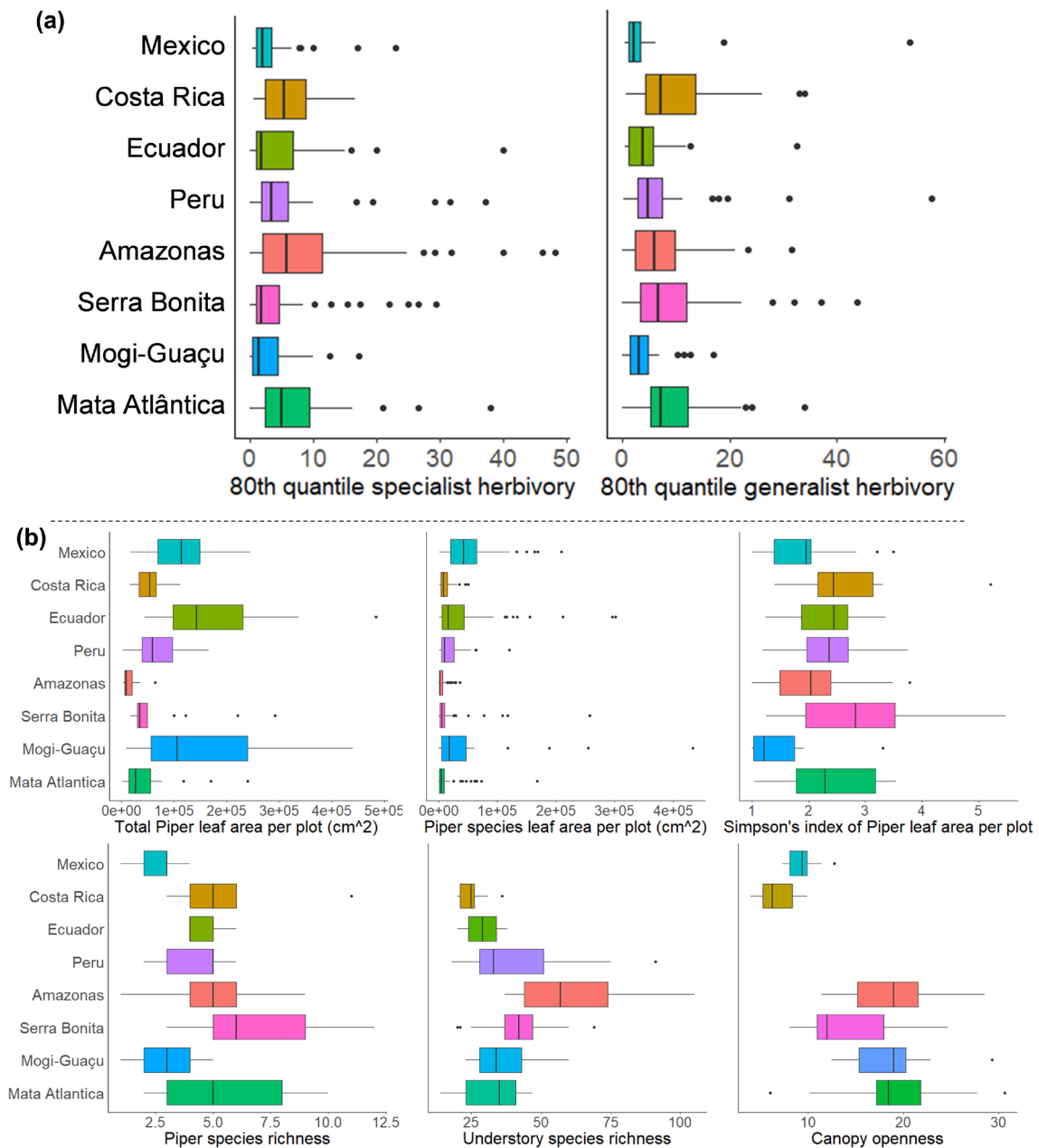


Figure 3. (a) Distributions of 80th quantiles of specialist and generalist herbivory per site. (b) Distributions of predictor variables that had direct effects on specialist and generalist herbivory in the site level SEM. *Piper* species leaf area per plot is the leaf area of each *Piper* species in a plot in cm². Total *Piper* leaf area per plot is the combined leaf area of all *Piper* species in cm². Simpson's index of *Piper* leaf area treats leaf area as though it were species abundance to calculate resource diversity. Understory species richness and canopy openness were not measured at all sites. See Table 3 for standardized parameter estimates of direct effects of these variables on herbivory, and Supporting information for scatterplots of the direct effects on specialist and generalist herbivory. Sites are arranged from north to south (México, Costa Rica, Ecuador, Perú, Amazonas, Serra Bonita, Mogi-Guaçu, and the central-southern Mata Atlântica).

scales, we qualitatively compared summary statistics of the 80th quantiles of specialist and generalist herbivory at the level of a 1) population (all individuals of a given *Piper* species in a plot), 2) community (all *Piper* individuals in a plot) and 3) 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.

Given the skewed nature of herbivory distributions, with most individuals experiencing little damage and a few suffering high herbivory (Table 1), the arithmetic mean is not the most appropriate composite variable for herbivory and the degree of positive skew should be a focal statistic to estimate. We therefore sought to estimate statistics that comprise three components of the distribution of herbivory: central tendency, skew and dispersion. We calculated the 25, 50 (median), 75, 80 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; and 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: 1) precipitation seasonality, 2) average annual temperature, and 3) the absolute value of latitude (hypotheses 2–4). Endogenous predictors were 1) the total amount of *Piper* leaf area available in a plot (hypotheses 5 and 6; this is likely correlated with measures of plant cover, such as the leaf area index, but it includes all *Piper* leaves in a plot and thus quantifies resources available to herbivores), 2) *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 3) 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). See the Supporting information for the model selection process, starting with the full model and running to the best fit model. Bayesian posterior probabilities of the parameter estimates of modeled relationships were calculated for the best fit SEM with using the 'lavaan' package in R (www.r-project.org, Merkle and Rosseel 2018). 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 χ^2 goodness of fit statistics were compared to determine the best fit model (note that for the χ^2 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. See the Supporting information for the variance-covariance matrix of the best fit model.

As we were particularly interested in variables that drive extremes in herbivory, we also analyzed the approximate skew of the data, using 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 Atlántica) using SEM. We used this particular upper quantile as a focal metric because it loaded most heavily on the skew factor and is a good summary statistic for extreme values of herbivory. 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). 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 1) the total leaf area of each species of *Piper* in a plot, 2) total leaf area of all *Piper* individuals in a plot, 3) the relative leaf area of a given species in a plot (dividing species level leaf area by total *Piper* leaf area; hereafter referred to as *Piper* species dominance; predictors i–iii are measures of resource abundance; hypotheses 5 and 6), 4) *Piper* richness in a plot (hypotheses 5 and 6), and 5) *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 the Supporting information.

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. All analyses were conducted with R ver. 4.0.3 (www.r-project.org).

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). Mean herbivory across the dataset was $7.9 \pm 0.13\%$ (SE), and the geometric mean was 4.3%. Mean specialist herbivory was $3.5 \pm 0.05\%$ (geometric mean = 1.7%), and mean generalist herbivory was $4.4 \pm 0.10\%$ (geometric mean = 2.1%). For all sites, specialist herbivory was almost exclusively from *Eois*, Chrysomelidae, and Curculionidae, as in previous studies (Dyer and Palmer 2004, Dyer et al. 2004, Connahs et al. 2009).

Does herbivory vary more at local scales or regionally (Question 1; hypothesis 1)?

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). 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). 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.

What variables affect the distribution of herbivory (Question 2; hypotheses 2–7)?

The best fit Bayesian SEM describing the distribution of herbivory at the plot level ($n = 164$ plots) supported the hypotheses that seasonality, *Piper* richness, and resource availability (leaf area) affect herbivory ($\chi^2 = 25.74$, $df = 33$, $p = 0.81$; $AIC = 4551.64$; Bayesian $MLL = -2376.82$; $PPP = 0.72$; Fig. 2, Supporting information). 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

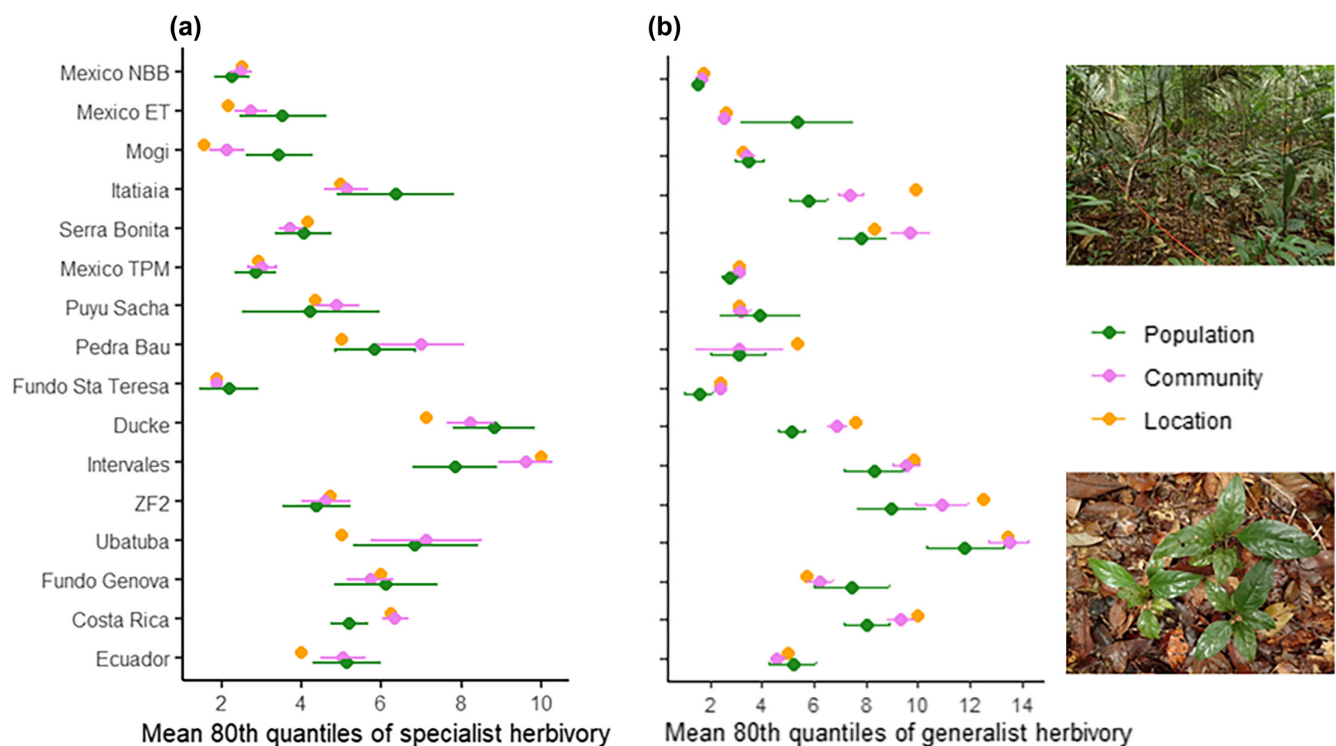


Figure 4. Means and SE of 80th quantiles of (a) specialist and (b) generalist herbivory at the level of local populations, communities and sites. Sites are organized in order of decreasing seasonality

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; $\pm$ SE) and p-values. Adjusted R^2 values are presented.

Response variable		Latitude	<i>Piper</i> richness	Seasonality	Overall model
Community level 80th quantile	Generalist herbivory	PE=0.12	PE=0.82	PE=−9.04	$F_{3,160}=21.61$
		± 0.05	± 0.12	± 2.45	$p < 0.001$
		$p=0.01$	$P < 0.001$	$p < 0.001$	$R^2=0.28$
	Specialist herbivory	PE=−0.03	PE=0.13	PE=−6.09	$F_{3,160}=5.26$
		± 0.05	± 0.12	± 2.60	$p=0.002$
		$p=0.53$	$p=0.30$	$p=0.02$	$R^2=0.07$
Population level 80th quantile	Generalist herbivory	PE=0.04	PE=0.11	PE=−2.42	$F_{3,495}=19.71$
		± 0.009	± 0.02	± 0.44	$p < 0.001$
		$p < 0.001$	$p < 0.001$	$p < 0.001$	$R^2=0.10$
	Specialist herbivory	PE=−0.08	PE=0.10	PE=−2.38	$F_{3,495}=3.44$
		± 0.05	± 0.11	± 2.44	$p=0.02$
		$p=0.11$	$p=0.40$	$p=0.33$	$R^2=0.01$

($r^2=0.16$), while mean specialist herbivory was the least well described variable ($r^2=0.02$). In addition, the SEM showed *Piper* richness was greater in less seasonal sites.

Are there site-specific effects on the distribution of herbivory (Question 3; hypotheses 2–7)?

The distribution of herbivory at the plot level was analyzed separately for each study site using the 80th quantiles of herbivory, similar to the latent variable describing skew in the multisite analysis (sample sizes for each site are the number of plots listed in the Supporting Information and range from 15 to 38). The best predictors of the distribution of specialist and generalist herbivory differed between sites (Table 3, Fig. 3, Supporting information).

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

Table 3. Standardized path coefficients describing direct effects of predictor variables on the 80th quantiles of specialist and generalist herbivory included in best-fit structural equation models. Full model results and other relationships included in the best-fit models are in the Supporting information. Bold path coefficients indicate relationships with p-values < 0.05 . R^2 values indicate the total variance in the 80th quantiles of specialist and generalist herbivory explained by all predictors in each SEM. SPLA=*Piper* species per plot leaf area; TPLA=total *Piper* leaf area in a plot; SILA=Simpson's index of leaf area; PR=*Piper* richness; UR=understory richness; CO=canopy openness.

		Predictor variables with direct effects on 80th quantiles of specialist and generalist herbivory						R^2
	Study sites	SPLA	TPLA	SILA	PR	UR	CO	
80th quantiles of specialist herbivory	México	−0.29		−0.15				0.08
	Costa Rica			0.22				0.05
	Ecuador	0.31						0.09
	Perú		−0.23		0.13			0.05
	Amazonas	−0.32			−0.19		0.18	0.10
	Serra Bonita	0.14		0.19				0.04
	Mogi-Guaçu		0.61					0.38
	Mata Atlântica				−0.16	0.13		0.03
80th quantiles of generalist herbivory	México	−0.26		−0.16				0.06
	Costa Rica				0.25			0.06
	Ecuador		0.19					0.04
	Perú	−0.11	−0.16					0.05
	Amazonas			0.29	−0.31	0.22		0.10
	Serra Bonita	−0.12				−0.19		0.05
	Mogi-Guaçu		0.38				−0.40	0.31
	Mata Atlântica				−0.16	0.32		0.10

decreased with canopy openness (Table 3, Fig. 3, Supporting information).

Our southernmost sites had the most herbivory at the population (intraspecific 80th quantiles of herbivory within a plot) and community (80th quantile of all *Piper* in a plot) 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; Parque Estadual de Intervales) with an 80th quantile of 10% herbivory (Fig. 4). Similarly, our second most southern site had the highest generalist herbivory (80th quantile of 13.4% herbivory; Parque Estadual de Serra do Mar, Picinguaba; Fig. 4). Both 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 (Mogi-Guaçu; 80th quantile of 1.6% herbivory; Fig. 4). Our driest, most seasonal site in México had the lowest generalist herbivory (Nuevo Becal and San Felipe de Bacalar; 80th quantile of 1.8% herbivory; Fig. 4).

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). *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). In the present work, we examined many of these hypotheses (Table 1), and we found that both large-scale and local-level environmental variation 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. 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 that the same variables influencing herbivory on an individual plant may affect patterns of herbivory across an entire forest (Table 1: H1).

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 (Table 1: H4; 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 (direct effects were not retained in the best fit model; Supporting information), 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.

The skew of specialist and the mean of generalist herbivory were lower in more seasonal forests, contrary to our initial hypothesis (Table 1: H3) and a previous review that found *Piper* herbivory to be greater in dry than in wet forests (Dirzo and Boege 2008). Our findings are consistent, however, with a study showing plants experience more damage in wet than in 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; Massad et al. unpubl.). 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 (Massad et al. unpubl.). 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 drivers of specialist versus generalist herbivory 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 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 (Hiura and Nakamura 2013, Anstett et al. 2014). 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 in our study; the two Mata Atlântica sites farthest from the equator were less seasonal than sites closer to the equator, such as the dry forests in Mexico and the gallery forest in the cerrado.

Specialists and generalists respond differently to resource concentrations and diversity

Generalist herbivory was lower on species with greater leaf area (greater dominance) in our plots. Although this contradicts our original hypothesis that herbivory should be more prevalent or intense where resources are abundant (Table 1: H5), 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 dominant *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 consistent with the skew of generalist herbivory decreasing with *Piper* species dominance (Fig. 2).

Locally, herbivory often increases where patches of forest are less diverse 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 both species richness and Simpson's index of leaf area, actually led to greater skew and dispersion of generalist herbivory (Fig. 2, Table 3 – Amazonas). Similarly, the dispersion of specialist herbivory increased with *Piper* richness, although mean specialist herbivory decreased (Fig. 2). Plant diversity thus appears to have complex effects on herbivory that vary among herbivore taxa, inhibiting host searching by some species and facilitating host location for others (Table 1: H5).

The contrasts uncovered between generalist and specialist herbivory likely reflect differences in host searching and dietary choices between these two groups of herbivores. 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). Generalists appear to favor more diverse communities, where a single potential host plant does not dominate, potentially due to benefits of dietary mixing (Table 1: H5; 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.

Effects of resources and richness on herbivory distributions differ between sites

In the three Mexican dry forests, herbivory was reduced on dominant *Piper* species (Table 1: H5; Table 3), 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 (Mogi-Guaçu), both generalist and specialist herbivory increased with total *Piper* leaf area (Table 3). *Piper* species dominance 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. 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 (Table 3). The higher herbivory measured in Ecuadorian plots with greater *Piper* leaf area may result from a less seasonal climate that allows for more constant herbivore pressure throughout the year. In the cerrado, another important pattern was that canopy openness limited generalist herbivory (Table 3), where increased light levels may cause particularly strong reductions in humidity (Table 1: H6; corroborating results reported by Richards and Windsor 2007). Local conditions, such as resource concentration and canopy gaps, may therefore confound the search for broad patterns in herbivory.

In the Amazon, *Piper* richness was associated with less generalist damage (Table 1: H5). Nonetheless, generalist herbivory increased with *Piper* leaf area diversity in the Amazon Basin (Table 3), as it does in the Mata Atlântica (Massad et al. 2022). In Costa Rica, richness increased generalist damage, and *Piper* richness and leaf area diversity were positively correlated. 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 descriptor 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 within populations and between congeners of a diverse tropical plant genus. 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.

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Author contributions

Tara Joy Massad: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (supporting); Writing – original draft (equal); Writing – review and editing (equal). **André Rangel Nascimento:** Data curation (equal); Investigation (equal). **Diego Fernando Campos Moreno:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Wilmer Simbaña:** Investigation (equal). **Humberto Garcia Lopez:** Investigation (equal). **Lidia Sulca:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Cintia Lepesqueur:** Investigation (equal). **Lora A. Richards:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Matthew L. Forister:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **John O. Stireman III:** Funding acquisition (equal); Writing – review and editing (equal). **Eric J. Tepe:** Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Kathryn A. Uckele:** Writing – review and editing (equal). **Laura Braga:** Investigation (equal). **Thomas R. Walla:** Writing – review and editing (equal). **Angela M. Smilanich:** Funding acquisition (equal); Writing – review

and editing (equal). **Ari Grele:** Writing – review and editing (equal). **Lee A. Dyer:** Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Digital Repository: <https://zenodo.org/records/10150241> (Massad et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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