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Plant size, latitude, and phylogeny explain within-population variability in herbivory

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Title: Plant size, latitude, and phylogeny explain within-population variability in herbivory

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Abstract: Interactions between plants and herbivores are central in most ecosystems, but their strength is highly variable. The amount of variability within a system is thought to influence most aspects of plant–herbivore biology, from ecological stability to plant defense evolution. Our understanding of what influences variability, however, is limited by sparse data. We collected standardized surveys of herbivory for 503 plant species at 790 sites across 116° of latitude. With these data, we show that within-population variability in herbivory increases with latitude, decreases with plant size, and is phylogenetically structured. Differences in the magnitude of variability are thus central to how plant–herbivore biology varies across macroscale gradients. We argue that increased focus on interaction variability will advance understanding of patterns of life on Earth.

One-Sentence Summary: The level of variability in herbivory is a key feature differentiating plant–herbivore systems at macroscales.

Plant–herbivore interactions, which involve more than half of macroscopic biodiversity and 90% of macroscopic biomass (*1*), are believed to shape macroscale biological patterns and processes, such as plant and herbivore biodiversity gradients, biomass distributions, community structure, species coexistence, and trait evolution (*2–4*). Biologists have studied the role of herbivory at macroscales by quantifying how the mean herbivore damage level covaries with latitude, biome, functional traits, and phylogeny (*5–7*). However, macroscale patterns have not always matched expectations. For example, despite the paradigm that herbivore pressure increases towards the equator owing to more benign environmental conditions, empirical patterns have been weak or inconsistent (*8–10*). Similarly, despite the expectation that closely related plant species should face similar pressures from herbivores, phylogenetic signal in mean herbivore damage is often undetectable or restricted to certain groups (*5*, *11*). We suggest that our understanding of macroscale patterns in herbivory can be improved by considering patterns in the magnitude of variability in herbivory, rather than only mean interaction strength.

Variability is a hallmark of plant-herbivore interactions (*12*). Within populations, patterns in damage are often highly skewed, with most plant individuals receiving very low levels of damage and a few plants receiving high levels (*13*). Although there are limited data on the drivers and consequences of this variability, theory indicates that within-species variation in traits or interactions can be as important as the mean for biological processes ranging from population viability to evolutionary dynamics (*14*, *15*). For example, spatial variability can stabilize plant–herbivore dynamics by giving plants refuges from overexploitation (*16*), increase the importance of competition among herbivores (*17*), maintain diversity by facilitating the evolutionary coexistence of alternative strategies (*18*), and drive disease dynamics by causing superspreading events (*19*). Variation in damage among plant individuals also indicates the potential pattern of selection by herbivores, which drives plant defense evolution (*20*). Indeed, variability has been hypothesized to favor inducible plant defenses over constitutively expressed defenses, a central dichotomy in defense evolution (*21*). Despite the central role that variability likely plays in the ecology and evolution of plants and herbivores, macroscale patterns of variability remain uncharacterized. Here we propose and test three hypotheses for patterns in the magnitude of variation in herbivore damage among individuals within plant populations.

First, we hypothesize that herbivory variability within populations increases with distance from the equator, owing to shorter growing seasons and less stable abiotic conditions at higher latitudes reducing the time available for herbivore foraging. A latitudinal variability gradient could help explain how herbivores have influenced global patterns of plant biodiversity despite the weak latitudinal gradient in mean herbivory (*22*, *23*). Herbivory may maintain plant diversity at low latitudes not just by being more intense on average, but also by being a more consistently important force within plant populations. Second, we hypothesize that herbivory is more variable among small plants than large plants. Large plants, which represent a greater sampling area, should average over small-scale random variation in herbivory, resulting in values closer to the population mean, while small plants should be more likely to escape herbivory entirely or be highly damaged by a few events. If supported, this hypothesis would expand our understanding of long-studied differences in defenses between trees and herbs (*24*), with consistent damage on large plants explaining why trees invest a greater proportion of their biomass in constitutive defenses (*25*). Third, we hypothesize that variability in herbivory is phylogenetically structured, with more closely related plants displaying more similar levels of variability. This pattern, which has been documented for mean herbivory (*5*), would indicate that variability is influenced by species-level traits, and is not simply random as it has often been treated.

To characterize macroscale patterns in population-level mean and variability in herbivory, 127 research teams in 34 countries used a standardized protocol (26) to sample plants and quantify aboveground herbivore damage for 790 populations of 503 species in 135 families. This sample comprised more than 50,000 plant individuals distributed across six continents and 116° of latitude. Past macroscale studies that have focused on differences in means typically examined relatively few individuals per population (*5*). In contrast, we sampled 60 individuals per population, allowing us to analyze patterns in population-level variability. For each plant individual, we recorded plant size (height for most species or canopy diameter for prostrate species) and visually estimated the cumulative proportion of leaf tissue damaged by invertebrate and vertebrate herbivores. We quantified the variability in herbivory among individuals within populations using the Gini coefficient, a commonly used scale-invariant metric that ranges from 0–1 (perfectly even to perfectly uneven) (*27*). We tested our hypotheses by quantifying associations between each macroscale factor and the Gini coefficient or mean herbivory using Bayesian phylogenetic beta regressions.

Overall, within-population variation in herbivore damage was very high (mean Gini coefficient = 0.61; 95% CI: 0.40–0.78; Fig. 1). On average, the most-damaged individual in each plant population lost 34.2% (32.4–36.0%) of its leaf area to herbivory, while 27.9% (25.9–29.9%) of individuals completely or essentially escaped herbivory (< 0.5% damage). Indeed, half of the damage in each population was concentrated on 11.3% (10.7–11.9%) of its individuals on average. The level of variation within populations also varied significantly across populations and species, with the Gini coefficient ranging from 0.03, an almost perfectly even distribution of damage, to 1.0, a perfectly uneven distribution with all damage on one plant (Fig. 1B–C). Even though the Gini coefficient normalizes by the mean, it can nevertheless be correlated with it. Indeed, mean herbivory and the Gini coefficient were negatively correlated, with Gini coefficients being low for the 3.9% of populations with very high (> 25%) mean herbivory, whereas populations with lower mean herbivory exhibited the full range of Gini coefficients ($\boldsymbol{\rho}$ = -0.46, Fig. S1).

Geographic patterns of variability

We found strong support for the latitudinal variability gradient hypothesis (Fig. 2A–B). Variation was lowest at the equator (Gini = 0.51 [0.33–0.69]) and increased towards 70° N/S (Gini = 0.70 [0.54–0.84], R^2 = 5%, p_p = 1.0, BF = 2.0e4). Mean herbivory, in contrast, declined with latitude, from 8.0% (4.1–12.3%) at the equator to 2.9% (1.4–4.7%) at 70° N/S; this relationship was less predictable than the one for the Gini coefficient (R^2 = 2%, p_p = 1.0, BF = 2.9e4, Figs. 2C and S2–S3, Tables S1–S3). Thus, plants at higher latitudes, with shorter growing seasons and lower temperatures (26), receive less herbivory on average, and that herbivory is concentrated on fewer individuals. This result could conceivably be an artifact of the negative mean–Gini coefficient correlation. We therefore repeated our analysis with mean herbivory included as a covariate. The estimated latitudinal variability gradient was still strongly positive, though lower in magnitude, with a 20% (6–38%) increase in the Gini coefficient from the equator to 70° N/S (R^2 = 23%, p_p = 1.0, BF = 14.5, Fig. S4). This relationship captured differences among biomes: higher latitude and higher elevation biomes had higher Gini coefficients and lower mean herbivory (Fig. 2D, Fig. S5). While there was a negative correlation between the mean and Gini coefficient among biomes ($\boldsymbol{\rho}$ = -0.68 [-0.95 – -0.10]), there were also large differences in the Gini coefficient

between biomes with similar mean herbivory. This suggests that interaction variability could be a fundamental characteristic differentiating biological systems across macroscales.

Debate over the contribution of herbivory to global patterns of plant evolution has been contentious (*3*, *6*, *8*, *10*, *22*, *23*). Our data show strong evidence of a meaningful, although noisy, latitudinal decline in mean levels of herbivore damage. They also show that herbivory becomes more variable with increasing latitude. This pattern is consistent with our hypothesis that herbivory influences plant evolution at low latitudes not just by being more intense on average, but also by being more consistently important within a plant population. Indeed, theory predicts that the relationship between the strength of antagonistic interactions and the intensity of selection is concave-down (saturating) at low mean interaction strengths (*28*), meaning that variability at high latitudes, where mean herbivory is low, should erode selection via nonlinear averaging (*14*), all else being equal. Our finding is also consistent with the hypothesis that inducible defenses are more common among temperate than tropical plants (*29*, *30*), since greater variation in herbivory is predicted to select for inducibility (*21*). In addition to seasonality and climate, other mechanisms for the latitudinal variability gradient could include greater predation pressure on herbivores at low latitudes (*3*) suppressing localized outbreaks and high tropical herbivore diversity and specialization (*31*) evening out damage patterns across plant individuals. More generally, our results confirm the long-held view that biotic interactions are more consistent in the tropics, perhaps owing to longer growing seasons or greater species diversity and specialization (*3*).

Variability and plant size

We also found strong support for the size-mediated variability hypothesis. Populations of larger individuals exhibit less variability in herbivory among individuals. A 2 m increase in mean plant size (from 0.05–2.05 m, encompassing ~90% of our populations) resulted in a 32.7% (20.6–44.7%) decrease in the Gini coefficient (from 0.70 [0.54–0.85] to 0.47 [0.29–0.66], R^2 = 13.3%, p_p = 1.0, BF = 4.6e7, Figs. 3A and S6). This relationship held even after accounting for the decline in plant size with increasing latitude and differences in plant abundance (which ranged from 2–100% cover in our dataset) (Tables S4–S5) (*32*). Woody species, which averaged 4.1 times larger than herbs in our dataset, had 10.9% (2.9–19.1%) lower Gini coefficients than herbaceous species (0.56 [0.37–0.76] vs. 0.63 [0.44–0.81], BF = 4.25). However, the overall variance explained by growth form, including climber and graminoid categories, was low (R^2 = 2.8%, Figs. 3B and S7), suggesting that mean size is a more important determinant of herbivory patterns than growth form. Mean herbivory, in contrast, was unrelated to mean size or growth form (Figs. S8 and S9).

We posit that lower among-individual variability in herbivory on large plants results from the law of large numbers, which tells us that processes that involve more random events produce values closer to the overall mean. In other words, large plants, which have a greater number of potential herbivory events, average over within-plant variability and receive values closer to the population mean on average. Small plants, in contrast, are more likely to escape herbivory entirely or be severely damaged by a few events, resulting in high variability. A key implication of this phenomenon is that larger species (and larger stages within species) should experience greater selection for high concentrations of constitutive defenses or tolerance. Smaller species (and stages), in contrast, should experience greater selection for inducible defenses and low concentrations of metabolically cheap toxins to save resources in the absence of herbivory and repel herbivores when encountered. This dichotomy in defense evolution has been the focus of

decades of research on differences in defenses between trees and herbs (*24*) and across ontogenetic stages (*33*). Whereas previous work has invoked complex biological explanations for these differences, such as how "apparent" plants are to herbivores (*24*), our results suggest patterns are more parsimoniously explained by the statistical consequences of mean plant size.

Phylogenetic patterns of variability

Finally, we tested the hypothesis that variability in herbivory is phylogenetically structured. The Gini coefficient exhibited significant phylogenetic signal (Pagel's $\lambda = 0.51$ [0.45–0.52], $P < 0.001$), indicating that more closely related species display more similar variability levels (Figs. 4 and S10). Mean herbivory, in contrast, did not show meaningful phylogenetic signal ($\lambda = 0.07$ [0.06–0.08], $P = 1.0$). These results were robust to tree topology and species sampling (Supplementary Materials). Our findings suggest that the mean damage level across species changes relatively rapidly in response to evolutionarily labile plant traits, whereas the variability is more strongly determined by traits that are phylogenetically conserved. Indeed, traits thought to influence the amount of herbivore damage, such as chemical defenses, diverge as plants escape their herbivores by evolving novel defenses (*2*, *34*), whereas characteristics such as geographic location and plant size, which we find relate to variability, tend to be less labile. High variability in some families (e.g., Apocynaceae and Plantaginaceae) invites further investigation and could help reveal drivers of these conserved patterns. To examine macroevolutionary patterns, we fit Brownian motion and Ornstein-Uhlenbeck models to test for differences in rates of evolution and the strength of stabilizing selection. The best-fitting models included optima for variability and mean herbivory in tropical vs. temperate systems and woody vs. herbaceous growth forms (Tables S6–S7), indicating that the evolution of variability in herbivory seems driven by conserved plant traits and therefore is a biologically informative feature rather than random noise.

Conclusion

The assumption that plant–herbivore interactions are highly variable has long dominated ecology and evolution, with foundational works on "variable plants and herbivores" (*12*) and theory exploring the consequences of variable herbivory (*21*). Our data confirm this assumption but also reveal a pattern that had not been previously documented: strong differentiation across systems in the level of variability itself. Variation in herbivory covaried with factors central to the ecology and evolution of plant–herbivore interactions such as latitude, biome, plant size, and phylogeny. These macroscale patterns were often stronger than patterns for mean herbivory levels. This suggests that the level of variability could be important for driving differences in plant–herbivore biology around the planet, between species with different traits, and across phylogeny. While the importance of variability in interactions has been recognized by a few fields, such as epidemiology (*19*), the central role of interaction variability in shaping macroscale patterns of life on Earth has been underappreciated. Our global dataset is evidence for the ubiquity and predictability of variability in one biotic interaction and highlights the promise of further explorations of the causes and consequences of interaction variability.

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Competing interests: Authors declare that they have no competing interests.

Data and materials availability: The dataset generated and analyzed in the current study is available at Data Dryad (35). Our code is archived at Zenodo (36).

Supplementary Materials

Herbivory Variability Network Authors

Materials and Methods

Supplementary Text

Figs. S1 to S10

Tables S1 to S7

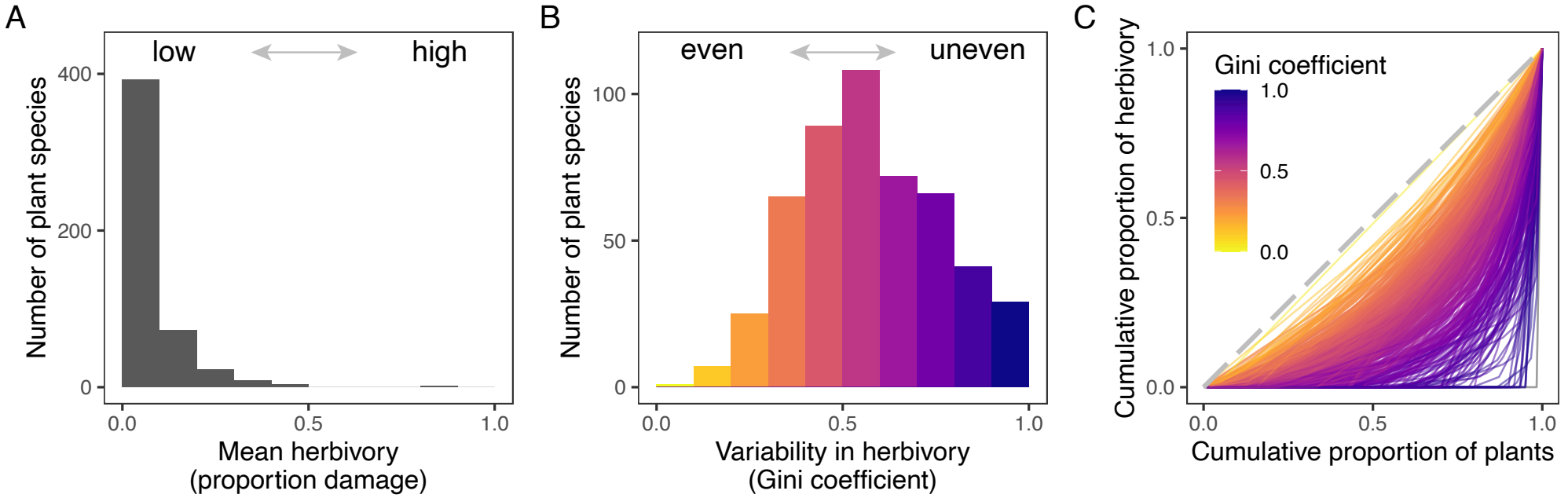
References (*37*–*58*)

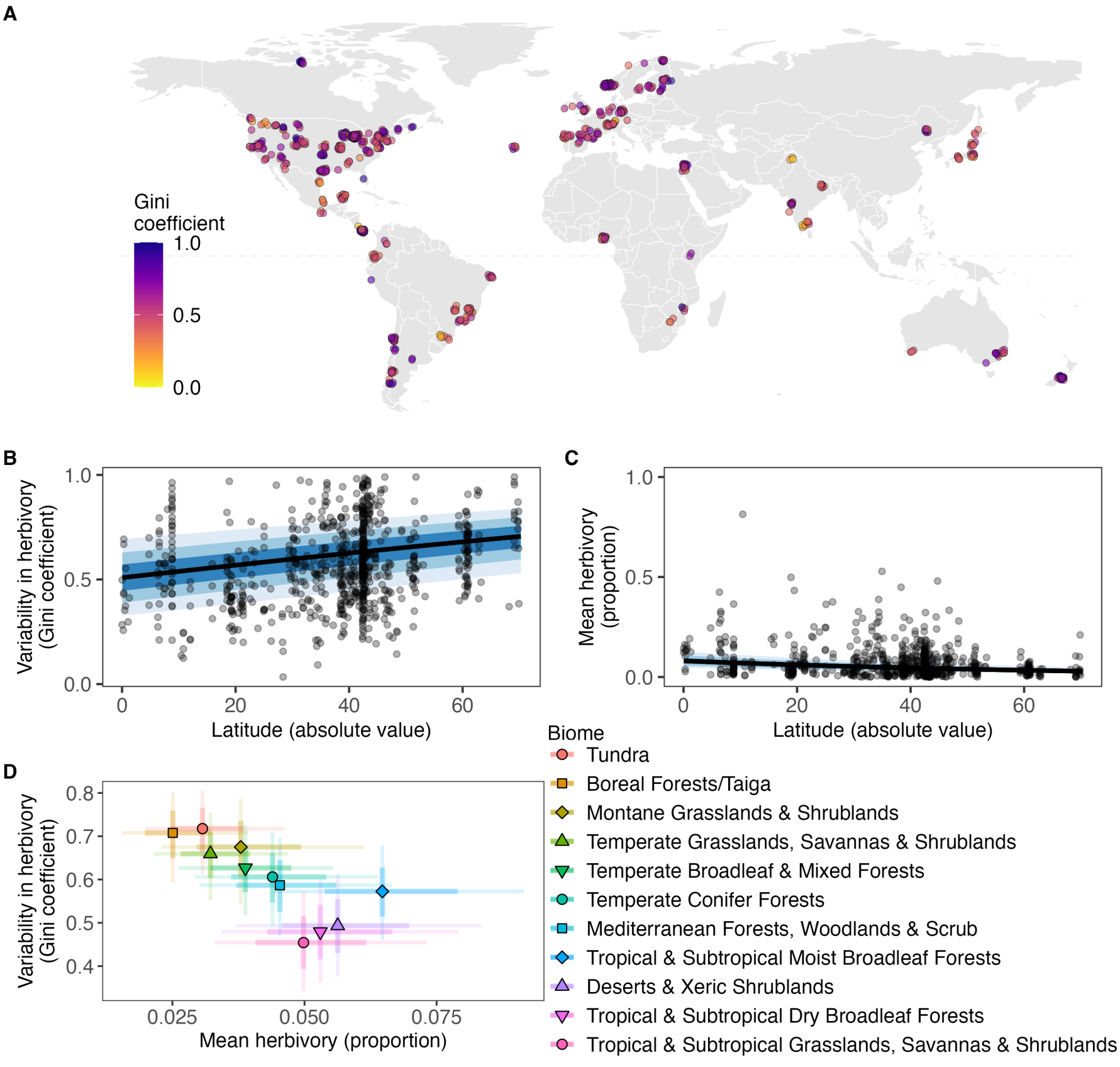
Fig. 1. Mean and variability in plant-herbivore interactions. (**A**) Histogram of the number of plant species with different mean proportion leaf area damaged by herbivores. (**B**) Histogram of the Gini coefficient values for all plant species in our dataset. (**C**) Lorenz curves from all 790 population surveys in our dataset. Each curve shows the cumulative proportion of herbivory across the cumulative proportion of plants, ordered by increasing herbivory, for one plant population. Curves closer to the 1:1 line (gray dashes) indicate more even distributions. Lorenz curves form the basis for the calculation of the Gini coefficient of inequality, which ranges from 0 (a perfectly even distribution) to 1 (a perfectly uneven distribution). Curves are colored by their Gini coefficient (as in 1b). Sample sizes are 790 surveys of 503 plant species.

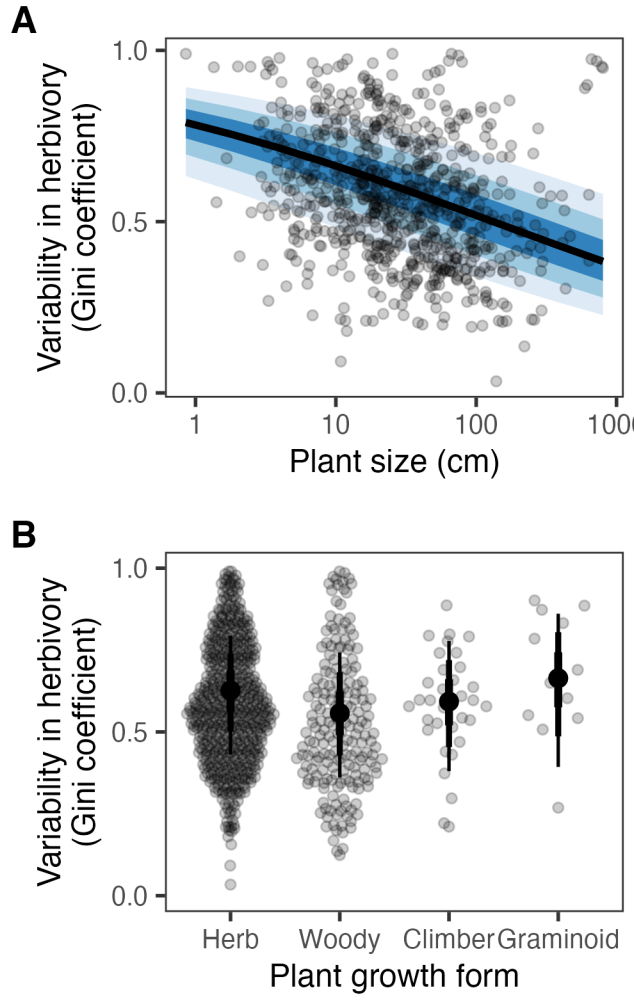
Fig. 2. Global patterns of variability in herbivory within plant populations. (**A**) The geographic distribution of our sampling sites, colored by variability in herbivory among individuals within populations (Gini coefficient). Points are slightly jittered for visibility. (**B**–**C**) Variability in herbivory increased and mean herbivory decreased with latitude across our sampling extent. Lines show predicted means and 50, 80, and 95% credible intervals from Bayesian phylogenetic beta regressions. (**D**) The 11 biomes in our study can be characterized by their mean and variability in herbivory. Herbivory variability and mean showed an inverse relationship across biomes ($\boldsymbol{\rho}$ = -0.67 [-0.94 – -0.08]), but there were also differences in variability between biomes with similar means. Error bars show 50 and 80% credible regions. Sample size is 790 surveys of 503 species. Legend in (D) is ordered by Gini coefficient.

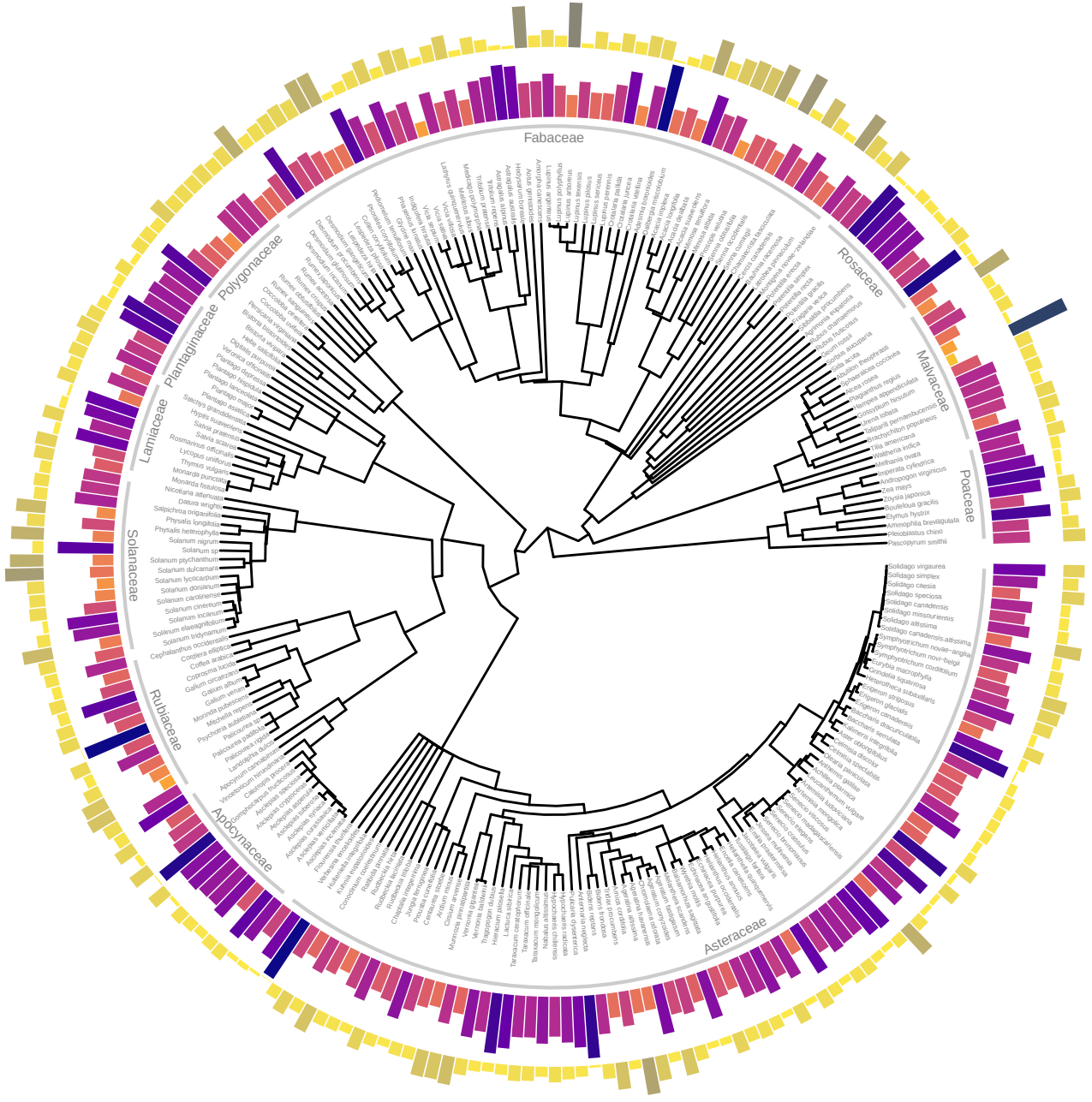
Fig. 3. Plant size shapes variability in herbivory. (**A**) Variability in herbivory among individuals within populations declines with the average size (height or canopy diameter for prostrate species) of plants in the population (R^2 = 13.3%, p_p = 1.0, BF = 4.6e7; 735 surveys of 472 species). (**B**) Variability in herbivory, however, is only weakly related to plant growth form (R^2 = 2.8%), with woody plants having 10.9% (2.9–19.1%) lower Gini coefficients than herbaceous species (790 surveys of 503 species). Lines, shaded regions, and large points show predicted means and 50, 80, and 95% credible intervals from phylogenetic Bayesian beta regressions. Each small grey point is one survey.

Fig. 4. Phylogenetic patterns of mean and variability in herbivory. Variability in herbivory among plants within populations (Gini coefficient) show greater phylogenetic signal (Pagel's λ = 0.51 [0.45–0.52], $P < 0.001$) than mean herbivory levels (Pagel's λ = 0.07 [0.06–0.08], $P > 0.1$). For clarity, this tree includes only the 240 species from the 11 best-represented plant families ($\geq$ 8 species per family). Our analyses included all 503 species in the dataset (see Fig. S10 for the full tree).


A
low
high
Number of plant species
400
200
0
0.0
0.5
1.0
Mean herbivory
(proportion damage)
B
even
uneven
Number of plant species
100
50
0
0.0
0.5
1.0
Variability in herbivory
(Gini coefficient)
C
Gini coefficient
1.0
0.5
0.0
Cumulative proportion of herbivory
1.0
0.5
0.0
0.0
0.5
1.0
Cumulative proportion of plants


A
Gini coefficient
1.0
0.5
0.0
B
Variability in herbivory (Gini coefficient)
1.0
0.5
0.0
0
20
40
60
Latitude (absolute value)
C
Mean herbivory (proportion)
1.0
0.5
0.0
0
20
40
60
Latitude (absolute value)
D
Variability in herbivory (Gini coefficient)
0.8
0.7
0.6
0.5
0.4
0.025
0.050
0.075
Mean herbivory (proportion)
Biome
Tundra
Boreal Forests/Taiga
Montane Grasslands & Shrublands
Temperate Grasslands, Savannas & Shrublands
Temperate Broadleaf & Mixed Forests
Temperate Conifer Forests
Mediterranean Forests, Woodlands & Scrub
Tropical & Subtropical Moist Broadleaf Forests
Deserts & Xeric Shrublands
Tropical & Subtropical Dry Broadleaf Forests
Tropical & Subtropical Grasslands, Savannas & Shrublands


A
Variability in herbivory (Gini coefficient)
1.0
0.5
0.0
1
10
100
1000
Plant size (cm)
B
Variability in herbivory (Gini coefficient)
1.0
0.5
0.0
Herb
Woody
Climber
Graminoid
Plant growth form


Fabaceae
Rosaceae
Malvaceae
Poaceae
Asteraceae
Apocynaceae
Rubiaceae
Solanaceae
Lamiaceae
Plantaginaceae
Polygonaceae
Mean herbivory (proportion)
0.0
0.5
1.0
Variability in herbivory (Gini coefficient)
0.0
0.5
1.0

Science
AAAS

Supplementary Materials for

Plant size, latitude, and phylogeny explain within-population variability in herbivory

The Herbivory Variability Network

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The PDF file includes:

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Materials and Methods

Species and site selection

The Herbivory Variability Network (HerbVar, www.herbvar.org) is a research coordination network of researchers from 34 countries that aims to better understand the role of variability in the ecology and evolution of plant–herbivore interactions. We maximized the geographic and phylogenetic breadth of our dataset for this paper by prioritizing sampling new sites and species from families and clades not yet sampled by us. Using those goals, 127 research teams selected species and sites with which they had familiarity, allowing expert assessment. This effort resulted in 790 population-level surveys encompassing 503 plant species from 135 plant families across 34 countries and six continents. Across the 135 plant families, we sampled a median of 2 species per family, though we had five families with more than 20 species (Asteraceae, Fabaceae, Plantaginaceae, Polygonaceae, and Solanaceae). Of the 503 plant species, 415 (83%) were surveyed once, but three plant species (*Plantago lanceolata*, *P. major*, and *Taraxacum officinale*) were surveyed more than 10 times each. Separate surveys of the same species were grouped in analyses via random effects (see below).

Field surveys

For each species and site, members surveyed cumulative herbivory and other ecological variables using a standardized protocol developed collaboratively by the network. Whereas past macroscale herbivory studies had small sample sizes within species and populations, our protocol established a target of 60 individuals within each population survey, facilitating robust estimation of variation and other patterns within populations. The full protocol can be found in the Supplementary Text (below) or at The Herbivory Variability Network's website (https://herbvar.org). In brief, for each survey, we recorded the geographic coordinates of the site's origin and used randomized transect and subtransect distances to select 30 individuals and each of their nearest conspecific neighbors, for a total of 60 individuals sampled. For small populations (< 90 individuals), we exhaustively surveyed all individuals in the population, rather than randomly selecting 30 individuals. Surveys in our final database had an average of 66 (±2 SE) individuals per population, with a mode of 60, though some surveys had as few as 21 or as many as 869 individuals.

For each of the plant individuals within a survey, we quantified aboveground herbivory by visually estimating the proportion of surface area of leaves and other photosynthetic tissue damaged by herbivores. We included all visible herbivory, including invertebrate and vertebrate damage and chewing damage, mining, and visible sucking damage that had accumulated across the growing season up to the date of the survey. We standardized visual estimates of herbivory across researchers by disseminating a detailed guide to visually estimating herbivory, providing a printable template that researchers could take to the field, and by having researchers undertake online training before going to the field including the ZAX Herbivory Trainer (*37*). For individuals under 2 m tall, we visually estimated herbivory by examining all aboveground tissue. Because this would not be feasible for individuals over 2 m tall, we randomly sampled 30 leaves per plant, estimated proportion herbivory on each leaf, and averaged those values to estimate whole plant proportion herbivory. Finally, we recorded the size of each individual by recording the linear dimension that best represented the size of individuals of that species, height for most species but canopy diameter for others (e.g., prostrate species). Our final dataset included plants

with an average size (height or diameter) of 0.85–799.8 cm. All data were uploaded to a repository hosted by Michigan State University, where a data team checked the data for consistency, integrated them into the database, and prepared them for analysis.

Full field survey protocol

A protocol for quantifying variability in plant–herbivore interactions
HerbVar: A collaborative network studying global patterns of variability in herbivory

1. Motivation:
Published studies and personal observations suggest the distribution of herbivore feeding damage among individual plants within a population is often highly skewed such that most plants experience relatively low levels of damage, and a small fraction of plants experience disproportionately high levels of damage. Theory suggests that such variability can have dramatic ecological and evolutionary consequences. For example, variability among plants can lead overall herbivore population size to be greater or less than expected based on average plant quality and asymmetric fitness surfaces can lead to over-investment in defensive traits. Surprisingly, despite the theoretical importance and potential generality of variability in herbivory, it has received little empirical attention, limiting our fundamental understanding of how plants and herbivores interact.

We are forming a global collaboration to quantify the distribution of herbivory for diverse plant species in multiple ecosystems across the world. The goal of this work is (1) to assess if variability in herbivory is indeed a common feature of plant–herbivore interactions, and (2) to examine how the amount of variability and skew varies with key ecological and evolutionary factors. Quantifying general patterns in the distribution of herbivore damage within populations would be a major contribution to our fundamental understanding of herbivory. In addition, identifying the factors that relate with variability in herbivory would provide the field with a new paradigm for describing plant–herbivore interactions and allow us to generate novel hypotheses about the ecology and evolution of plant–herbivore interactions.

2. Project goals:
1. Quantify the within-population distribution of plant damage and herbivore density across many systems
2. Quantify how within-population distributions of damage and herbivore density differ across
    a. Plant species
    b. Plant functional traits (from literature)
    c. Latitude
    d. Plant ecology (e.g., rarity)
    e. Herbivore species
    f. Herbivore functional groups
    g. Ecosystem type
    h. And many other potential factors (e.g., seasonality, precipitation...)

3. Overview:

Below, we provide a straight-forward and broadly applicable protocol to achieve these goals. This is the Primary HerbVar Survey Protocol. In brief, 30 randomly-selected plant individuals in a site (~population) are surveyed for herbivore damage and (possibly) herbivore abundance. Data are also collected on the nearest conspecific neighbor of each plant (for a total of N = 60 plants). These methods yield estimates of variability, skew, and spatial patterns (e.g., autocorrelation) in herbivore damage.

The HerbVar Primary Survey Protocol is designed to work for many common plant growth forms and contexts, so we expect most surveys to use this protocol. The primary protocol, however, will not work for every plant growth form or context, so HerbVar has multiple alternative survey protocols. Alternative protocols can be found in the shared Drive in the "Alternative protocols" folder. These include protocols for surveying plants with low density or abundance, mature trees, cacti and other succulents, reproductive (flower/fruit/seed) damage, and vertebrate browsing damage, as well as an optional insect sampling protocol. If the primary protocol is not feasible for a species or site, then we suggest one of these alternative protocols. If none of these alternative protocols fits the situation, then collaborators may deviate from the primary protocol. We trust collaborators to decide how to adapt the primary protocol in ways that works for their systems. We suggest, however, that collaborators strive to follow the spirit of the protocol below: randomly select at least 30 plants from a site and census them and their nearest neighbors for herbivory and herbivore data. For a dataset to be usable in the overall study, it will have to be comparable to data collected using this protocol. Collaborators who deviate from the HerbVar protocols should carefully record their methods.

The primary protocol works best for sites with at least ~90 plant individuals, such that it makes sense to sample individuals randomly. If your site has fewer than ~90 individuals of your plant species, then please consider comprehensively censusing all individuals within the site as suggested in our document on surveying low-density/low-abundance sites. A comprehensive census, when feasible, would be even better than the protocol below. If plants are far enough apart, please take GPS coordinates for each plant. If a comprehensive census is not feasible, then please modify the primary protocol or the low-density/low-abundance guidelines to work efficiently with your species and site. Please reach out to the HerbVar coordinators if you have questions or want to check that your modifications will lead to adequate data.

4. The Primary HerbVar Survey Protocol:
There is a template data sheet for this protocol, and example of a completed datasheet in the HerbVar shared Google Drive

- Pick a plant species (see "6. Guidelines for selecting plant species" below)
- Pick a site (see "7. Delineating a site" below for advice)
- Pick a time to sample (see "8. When to Sample" below for advice)
- Calculate a 'custom' radius for circular quadrats. We developed the following method to create quadrat sizes specific to each plant species and site, given that plant size and density vary immensely. This approach seeks an optimal, intermediate quadrat size that balances the costs associated with a small quadrat size (many empty quadrats) and a large quadrat size (quadrats that require counting many plant individuals).
    - Estimate mean density of plants per square meter by counting the number of plants in 1 m^2 at 10 random locations within the site; calculate mean density (D)

    - Use D to calculate a circular quadrat radius (r) that would on average contain 4 plants:
        - $r = \sqrt{4/(\pi D)}$
- Lay a transect through the middle of the site
    - Record GPS coordinates of origin, length (m), and compass direction (degrees) of transect (need to pick a coordinate system and precision)
- Select center points of circular quadrats. Randomly select 40+ points in the site by selecting pairs of random numbers. One random number represents distance along the transect (0–length of transect); the other represents distance left or right of the transect (left=negative, 0=center, right=positive). These are the center points of quadrats.

For each quadrat:
- Locate a quadrat center point using transect and measuring tape or stick
- Count and record the number of focal plants within r meters of the center point (a circular quadrat)
- Record other quadrat level data:
    - Percent cover of focal plant (ignore non-focal species)
    - Percent cover of all non-focal plant species (ignore focal species)
        - These 2 percent covers could total more than 100% if they overlap
        - If surveying understory plants, ignore forest canopy when estimating percent cover
- If the circular quadrat has 0 plants, record a zero and continue to the next quadrat

If the circular quadrat has > 0 plants:
- Randomly choose 1 of the plants within the quadrat to survey
    - A quicker alternative would be to choose the plant closest to the quadrat center. But this is recommended only if you think it will produce an unbiased sample of plants from your site. Be careful about over-representing large and/or isolated plants (which will be closer to more points relative to small plants in crowded patches).
- Data to record for each selected plant (1 per quadrat):
    - Plant life stage: seedling, vegetative, reproductive
    - Plant size, use judgement to pick best measure for your species
        - E.g., standing plant height (ground to tallest living part), stem length, foliage diameter, stem diameter
    - Herbivore damage (see Damage estimation training document) in 3 ways:
        - (1) Presence/absence of leaf damage: *If a plant has ~60 leaves or less in total*, please record the total number of leaves on the plant, and the number of those leaves that have damage (count leaf as damaged if it has > 0.5% herbivory). *If a plant has more than ~60 leaves*, record presence/absence of herbivory on 60 randomly (arbitrarily) chosen leaves and please note you stopped at 60.
            - If plants have reproductive parts (flowers/fruits/seeds) that could have been damaged by herbivores, please see the HerbVar Flower/Fruit/Seed Damage Protocol. This is optional, but encouraged.
        - (2) Estimated percent damage on 10 randomly (arbitrarily) chosen leaves

            - One estimate per leaf (for a total of 10 estimates)
            - Ideally, chosen leaves will be representative of all leaves (e.g., sample young and old leaves in proportion to frequency on plant)
            - For leaves with herbivore-built leaf shelters (rolls and ties), please carefully peer into or open shelters to estimate damaged area and count resident herbivores
        - (3) Estimated percent damage across the whole plant, optionally also breaking apart damage by type or even species of herbivore if possible (e.g., sucking damage versus chewing damage, add columns as needed)
            - E.g., If a plant has 4 equally-sized leaves and 2 of those leaves are 50% eaten, then whole plant has 25% herbivory
            - But take leaf size into account when leaves vary in size
    - Presence of plant diseases
    - Number of leaf mines and galls per plant (= herbivory + herbivores).
        - If there is reason to believe that galls or mines have accumulated through multiple years (e.g. stem galls on woody perennials), please note this
        - If there are too many mines or galls to count individually, estimate the number per plant by tallying the number per module (e.g. stem, branch) and multiplying by number of modules
    - Optional: abundance of other externally-feeding herbivores (standardized approach; see Herbivore sampling protocol to decide if/how to collect these data)
    - Distance to nearest conspecific neighbor (where the nearest neighbor is the plant with the closest aboveground tissue to any aboveground tissue on the focal plant)

- Data to record for the first nearest conspecific neighbor of selected plant:
    - All the same data as focal plant except nothing for neighbor's neighbor
- Continue visiting the randomly selected points until ≥ 30 focal plants and 30 nearest neighbors have been surveyed

5. Methods notes:
- Modifications of this protocol may be necessary to adapt it to different systems (see "3. Overview" above). If this protocol will not work for your system, please first consult our alternative protocols (see page 2 above and Alternative protocols folder). If our alternative protocols do not solve the issues, then you may adapt the primary protocol as needed. Whatever you do, please record methods carefully and strive to follow the spirit of the protocol and produce comparable data.
- In our experience, 1 survey (of 1 site of 1 plant species) takes 2 well-trained undergraduates 2-8 hours to complete using the methods above (after a species and site have already been selected). This is in old fields, prairies, and deciduous forests in Michigan. Could take longer in other systems.
- We select 40 quadrat center points (instead of 30) so that we have extra points ready in case some quadrats are empty. If you predict that many quadrats will be empty (e.g., in a very spatially clumped population of plants), then select more points (e.g., 60 points). (Remember the goal is to have 30 focal plants sampled).

- Sometimes, especially in small populations, a focal plant ends up being another focal plant's neighbor. This is fine. Just note and keep going. If you have time, you can add an extra focal plant at the end (but this isn't totally necessary).
- For clonal plants, we have been calling stems "plant individuals" if they are not connected aboveground. When looking for aboveground connections, we clear away detritus, but we do not dig or move soil.
- Please see our Damage estimation training document for guidelines on how to estimate herbivore damage. Here are two tips:
    - Sometimes discerning herbivore damage from physical damage (e.g., wind, trampling) is tricky. We do the best we can. We look at things like how jagged the cut edges are and if they travel past the missing area into the remaining leaf tissue (which would suggest the damage may have been physical).
    - Another challenge is old damage that occurred when leaves were still expanding. This could potentially make area removed seem larger than it was. If we suspect something like this happened, then we try to bend the leaf back into shape to see if it seems like the missing area expanded over time.
- We will accept surveys that only assess damage and do not identify herbivores. This will allow people without insect ID skills to participate in the study.

6. Guidelines for picking plant species:
We are hoping for a broad sampling of plant species, so data on any plant species will be valuable. However, we have developed a sampling plan structured around 1) gathering data for as many plant families as possible; 2) in-depth sampling of plant species within five focal families (Apocynaceae, Asteraceae, Fabaceae, Rubiaceae, and Solanaceae); and 3) sampling of three globally-distributed taxa: *Taraxacum officinale* (dandelion), *Plantago lanceolata* (narrowleaf plantain), *Plantago major* (broadleaf plantain). You can read more about our sampling plan on our website (https://herbvar.org/protocols.html; ""HerbVar species selection plan").

Thus, contributed surveys would ideally include one new family that is not currently in the database, one species from a focal family, and one survey of a focal species. Additional surveys would be the collaborator's choice and could include re-sampling the same species through time or across a gradient. While this stratified sampling approach is preferred, all plant populations are of interest and collaborators are welcome to select plants based on criteria that make sense to them (familiarity with taxa, location & feasibility, etc). Also, feel free to re-sample species that have already been sampled. It will be interesting to have estimates of how consistent our data are within species. But once a species has been surveyed 2-3 times, it is probably preferable to survey a new species.

We have charts in tabs in the Completed surveys document that are constantly updating to indicate gaps in sampling. In addition to the guidelines above, other features of a plant species that would make it a valuable addition to the dataset include:

- Occurs in a novel ecosystem
- Possesses a novel or underrepresented growth form, life history, or other set of traits

Other species selection notes:

- We have been surveying both native and non-native plant species.

- We are interested in agricultural and other cultivated plants and have already sampled a handful. When surveying cultivated plants, make sure the plants have been free of insecticides for an ecologically meaningful time before your survey.

7. Delineating a site:
We realize that defining the edges of a site can be subjective and not easy. We search for an area where a given plant species occurs at a high enough density to easily select 30 focal plants and 30 unique neighbors with our method. This is usually a relatively dense patch. Walk around and see if you see the density drop off to well below the mean density that is used to calculate radius size. This is usually quite simple, e.g., when we walk out from the center of a site and don't see any individuals of the focal species within 5 m, we decide we're at the edge of a patch. In some systems, delineating a single, sampleable population simply might not be possible (e.g., where a species covers a vast area). In these cases, collaborators should simply do their best to select a reasonable, representative area to sample.

Response variables
Our analyses focused on two response variables, the amount of variation in herbivory among individuals within a population and the mean herbivory within a population. We summarized variation in herbivory across individuals within populations by calculating the sample-size corrected Gini coefficient of variation in proportion aboveground herbivory among individuals in each population using R package DescTools (*38*). The Gini coefficient is a widely used metric that represents the level of variation or unevenness of a distribution of a variable among units. It is analogous to the more widely known coefficient of variation except calculated with L-moments instead of conventional moments, making it more robust to outliers and more reliable at small sample sizes (*39*). The Gini coefficient has been used extensively in ecology, including recent work describing the distribution of abundances and changes in abundances among species within communities (*40*, *41*) and the distribution of size hierarchies in plant populations (*42*). Although it is normalized by the mean, the Gini coefficient, all else equal, typically displays a negative relationship with the mean, like the coefficient of variation. Thus, in addition to models quantifying total variation in the Gini coefficient, we also accounted for this relationship and asked if variation in the Gini coefficient could be related to variation in the mean by adding mean herbivory to models as a covariate.

Our second response variable, mean herbivory, allowed us to ask what factors influence the average or relative total herbivory across individuals and to examine how they complement or differ from factors that influence variability. For mean herbivory, we averaged the proportion of aboveground herbivory across all individuals surveyed in a population. An alternative metric for describing the center of a distribution is the median. In our dataset, mean herbivory and median herbivory, however, had a correlation of 0.964 across species. Given this high correlation, we present the mean to enable comparison with past studies, which all report patterns in mean herbivory.

Site- and species-level predictors
In addition to latitude, we used the geographic coordinates of each site to extract the site's biome type using a 2017 global assessment of biomes (*43*). Our surveys spanned 11 biomes. Nine of those contained at least 25 surveys: desert and xeric shrublands; Mediterranean forests,

woodlands and scrub; temperate broadleaf and mixed forests; temperate conifer forests; temperate grasslands, savannas and shrublands; tropical & subtropical dry broadleaf forests; tropical and subtropical grasslands, savannas and shrublands; tropical and subtropical moist broadleaf forests; and tundra. Two biomes, boreal forests/taiga and montane grasslands and shrublands, contained nine and eight surveys, respectively.

In our data set, latitude is strongly correlated with many temperature variables from the bioclim database (mean annual temperature: $r = -0.50$, $p < 0.001$; temperature seasonality: $r = 0.63$, $p < 0.001$; annual temperature range: $r = 0.55$, $p < 0.001$), and to a lesser degree with precipitation (mean annual precip: $r = -0.22$, $p < 0.001$; precipitation seasonality: $r = -0.32$, $p < 0.001$).

For each plant species in our dataset, we determined growth form by recording them in the field or extracting them from the literature (*44–46*). Plant species were grouped into one of four categories: herb/forb (306 species); woody shrub/tree (157); climber (using other plants for physical support, 29 species); and graminoid (grasses and sedges, 11 species). Climbers included both herbaceous vines and woody lianas. Species that could span multiple categories were placed in the best-fitting category based on species descriptions in the literature.

Statistical modeling

We modeled our response variables – mean herbivory and variability in herbivory among plant individuals within a population – as a function of our predictors using Bayesian phylogenetic generalized linear mixed models in R in the brms package, which uses Hamiltonian Monte Carlo estimation via the Stan platform (*47–49*). We used a beta response distribution because it is well suited to represent variables on the 0–1 interval (*50*). We accounted for correlations among surveys of the same species and phylogenetic correlations among plant species by including random effects for plant species and phylogeny, based on a phylogenetic covariance matrix built using a phylogenetic tree of our species (see below for phylogenetic methods). We modeled differences across biomes by using the Gini coefficient and mean herbivory as response variables together in a single multivariate (multi-response) model, allowing us to estimate the correlation between the Gini coefficient and mean herbivory across biomes.

Because the beta distribution is undefined for 1 and three surveys had Gini coefficient values of 1, we truncated those values to 0.99 (the next highest Gini coefficient value was 0.985). This can be thought of as representing the limits to our ability to detect extremes and allows the use of beta models, thereby avoiding the need for zero/one hurdle models, which we feel is justified because we do not think that zero or one values arose from fundamentally separate processes from values close to zero or one (*50*). We log transformed plant size before using it as a predictor.

Models ran across at least seven chains for at least 40,000 iterations total, using the first half of each chain as a warm up. We assessed runs by ensuring all Rhat values were < 1.03, and visually checked fits via posterior predictive checks (*51*). We used weakly informative priors on all parameters: N(0, 2) for slopes and intercepts, gamma(1, 0.05) for the φ dispersion parameter of the beta distribution, and half-Cauchy(0, 1) for the standard deviations associated with the random effects.

For each model, we report effect sizes, 95% credible intervals (CIs), and marginal Bayesian R^2 values in the main text and parameter posteriors, 95% CIs, posterior predictive checks, and diagnostics in Figs. S2–S9. Marginal Bayesian R^2 values represent the percent of the variance in the response explained by the population-level parameters (fixed effects). For each of our directional hypotheses, we also report the proportion of the posterior on the hypothesized side of zero (p_p) and the Bayes factor (BF) estimated with the Savage-Dickey density ratio, restricting the prior and posterior to the hypothesized side of zero. Values of p_p closer to one indicate stronger support. BF values greater than one can be interpreted as evidence against the null, with higher values indicating stronger evidence.

When examining latitudinal gradients, we first asked whether the relationship between latitude and herbivory (mean herbivory or variability in herbivory) differed between the Northern and Southern Hemispheres by testing for an interaction between latitude and hemisphere. Neither the Gini coefficient nor the mean showed a significant interaction with hemisphere (Tables S1–S2). Moreover, Gini coefficients and means were similar on average in the Northern and Southern Hemispheres ($Gini_{Northern}$ = 0.58 [0.22–0.95], $Gini_{Southern}$ = 0.54 [0.21–0.90]; $mean_{Northern}$ = 0.070 [0.00–0.29], $mean_{Southern}$ = 0.070 [0.00–0.29]). Because of the similarity of these patterns north and south of the equator, we used the absolute value of latitude (degrees from equator) as our predictor variable for latitude in all analyses. We examined the potential for latitudinal differences in plant abundance and plant size to drive the latitudinal gradient in herbivory variability by re-fitting our latitudinal model of the Gini coefficient with either focal plant abundance (percent cover) as a covariate (Table S3) or mean plant size as a covariate (Table S4). We also examined the potential for differences in focal plant abundance to drive the plant size–variability relationship by re-fitting our plant size model with focal plant abundance (percent cover) as a covariate (Table S5).

Patterns of herbivory mean and variability across the plant tree of life

We generated a phylogenetic tree for the 503 plant species in the dataset using R package V.PhyloMaker2 (*52*). This method uses the most recent dated phylogenies for both seed- and spore-bearing plants to infer the largest dated mega-tree of vascular plants available (*53*, *54*). This megatree was then pruned to match a list of provided taxa. If taxa were missing from the megatree they were bound to the node of a congener or, if no congeners were present, to the ½ or upper ⅓ point of the family branch (V.PhyloMaker2 scenario S3). In our dataset, 338 species were present in the megatree, and 165 required binding. Of bound species, 134 had a congener in the megatree, and were thus bound at the genus level; the remaining 31 species did not have a congener in the megatree and were bound at the family level.

We estimated phylogenetic signal in the Gini coefficient and mean herbivory using Pagel's λ in R package phytools (*55*). Both the Gini coefficient and mean herbivory were logit-transformed prior to analysis (*50*). To account for uncertainty in tree inference, we estimated phylogenetic signal for mean and variability in herbivory in a distribution of 1,000 trees with different placement of missing taxa. For each tree, missing taxa were bound to a random node at or below the corresponding genus or family-level node in R package V.PhyloMaker2 (scenario S2) (*52*). We report the mean and 95% CI for λ across this distribution of trees, as well as percent of trees with significant phylogenetic signal. We also tested the sensitivity of λ to species sampling effects in two ways. First, we ensured that sparse sampling within some families was not driving

our results by re-running our analyses on a tree pruned to families with ≥ 8 species (11 families and 240 species). Second, we quantified phylogenetic signal after resampling trees 1,000 times with random exclusion of 10–50% of species using R package sensiPhy (*56*) (see Supplementary Text below).

We also fit different macroevolutionary models to our data to explore whether the evolution of herbivory (Gini coefficient and mean) could be modeled as driven by plant growth form (herbaceous vs. woody; woody includes woody shrubs and trees, but vines were not considered) or biome affinity (temperate vs. tropical; temperate: latitude ≤23°; tropical: latitude >23°). The subset of dataset for this analysis had 306 herbaceous species and 157 woody species and 638 temperate surveys and 152 tropical surveys We implemented models that considered herbivory evolving under a Brownian Motion dynamic in which the rate of evolution (σ^2) parameter was shared across trait states (BM1 model) or allowed to vary depending on the state of the trait being examined (BMS); that is, whether herbivory evolved at different rates in herbaceous and woody (or temperate and tropical) taxa. We also examined models to explicitly evaluate whether (variability or mean) herbivory is evolving under a regime that pulls with strength α towards one or many evolutionary optima (parameter θ), known collectively as Ornstein-Uhlenbeck (OU) models. Of these, we only considered OU1 models (single evolutionary optimum θ while keeping rate and strength of pull towards the optimum as constant), and OUM models, which allow for herbivory to evolve towards different optima, depending on the state of the trait (i.e, herbaceous vs. woody, or tropical vs. temperate). We did not consider models that allow multiple rates or strengths of pull towards the optima because they did not produce reliable parameter estimates for our data. To implement these models, mean herbivory data were logit-transformed.

For each plant character trait, we mapped its evolution onto a phylogeny using continuous-time reversible Markov models (*57*), evaluated models of evolution, and iterated this process across 100 phylogenies to account for uncertainty in both trait mapping and phylogeny estimation. Stochastic maps of trait evolution were generated with the *make.simmap* function in the 'phytools' R package (*55*). Plant phylogenies were derived from a megatree (*53*) with the 'V.Phylomaker2' R package (*52*). Because some taxa were not present in the megatree, we bound missing tips to randomly selected nodes in respective genera or families with each iteration (V.PhyloMaker2 scenario 2).

All models of evolution were implemented using the 'OUwie' package in R (*58*). The algorithm was set to "invert" for which all models converged and reached a reliable solution. To compare models, we used the average Bayesian Information Criterion (BIC) across the 100 iterations described above (Tables S6 and S7).

Sample size sensitivity analyses

While our target sample size within each survey was 60 plant individuals, some surveys had fewer than 60 individuals due to logistical constraints. Other surveys reached more than 60 individuals. We ensured that our results were not influenced by differences in within-survey sample size using a sampling procedure and rerunning our analyses. First, we excluded 14 of our 790 surveys with fewer than 30 individuals. Next we sampled 30 plant individuals from each survey without replacement. We repeated this 100 times, giving us 100 replicate datasets with 30 plant individuals per survey. Finally, we repated our analyses for each of these 100 replictate

datasets, including calculations of mean herbivory and the Gini coefficient, phylogenetic generalized linear mixed models, and other phylogenetic analyses. We present the results of this sensivity analysis in the Supplementary Text.

Gini asymmetry coefficient

Whereas the Gini coefficient describes the amount of variation or uneveness of the distribution of a variable among units within a population, the Gini asymmetry coefficient, a metric designed to supplement the Gini coefficient describes the contribution of individuals with low or high values to the observed Gini coefficient value. The Gini asymmetry coefficient is thus an additional descriptor of the shape of variation among individuals within a population. When the Gini asymmetry coefficient is less than one, it indicates that a distroportionately high number of individuals with low values contributes to observed unevenness. When the Gini asymmetry coefficient is greater than one, it indicates that individuals with disproportionately high herbivory contribute most to uneveness. Finally, when the Gini asymmetry coefficient is close to one, it indicates that individuals with low values and individuals with high values contribute similarly to observed unevenness and that the Lorenz curve (Fig. 1C) is symmetric.We calculated the Gini asymmetry coefficient using the ineq package in R and examined its relationship with latitude and plant size using Bayesian phylogenetic linear mixed models. We present these results in the Supplementary Text (below).

Supplementary Text

Pagel's lambda sensitivity analyses

Pagel's λ was significantly greater than zero for all 1,000 trees with randomized placement of missing taxa for the Gini coefficient (μ [95% CI] = 0.48 [0.45–0.52], $P < 0.001$) and never significant for mean herbivory (μ [95% CI] = 0.069 [0.06–0.08], $P > 0.1$), suggesting our results are not sensitive to uncertainty in tree topology.

Our results were also robust to species sampling effects. As with the full tree, the subtree with only families with ≥ 8 species (11 families and 240 species) displayed significant phylogenetic signal for the Gini coefficient ($\lambda = 0.21$, $P = 0.049$) but not for mean herbivory ($\lambda = 0.057$, $P = 0.21$). Moreover, these results were not highly sensitive to the random removal of species from the tree and dataset. We found significant phylogenetic signal for the Gini coefficient in 100% of 1,000 simulations with random removal of 10% of species, in 99% of simulations with random removal of 20% of species, in 91% of simulations with random removal of 30% of species, and in 75% of simulations with random removal of 40% of species. For mean herbivory, phylogenetic signal was non-significant in > 98% of all simulations for 10, 20, 30, and 40% random species removal.

Sample size sensitivity analyses

The results of the analyses on the datasets subsampled to have 30 plant individuals per survey were essentially identical to the results on the full dataset presented in the main text. The model-estimated mean Gini coefficient averaged across the 100 subsampled datasets was 0.60 [95% CI = 0.57–0.64], which is nearly identical to the estimate from the full dataset (0.61). Similarly, the mean slope for the latitudinal gradient of herbivory variability across the subsampled datasets was 0.17 [0.14–0.19], which is very close to the slope estimated using the full dataset (0.18). Moreover, 100% of the subsampled datasets yielded latitudinal slopes with credible intervals that did not overlap zero. The estimated relationship between plant size and the Gini coefficient was also highly similar between the subsampled dataset (-0.26 [-0.24–-0.28]) and full data set (-0.26), and all subsampled data sets yielded slopes with credible intervals that did not overlap zero. These results indicate that our results were not influenced by differences in within-survey sample sizes across surveys.

Gini asymmetry coefficient

The model-estimated mean Gini asymmetry coefficient was slightly less than one on average but had a 95% credible interval that overlapped one (0.94 [0.89–1.02]). Gini asymmetry coefficient values close to one indicate that a disproportionately high number of indivduals with low values and individuals with disproportionately high values both contributed similarly to the observed Gini coefficient value. This result therefore suggests that observed evenness is a function of both a high number of plant individuals that escape herbivory and a number of plants that receive disproportionately high herbivory. However, the fact that most of the credible interval was slightly below one suggests that on average observed Gini coefficients are driven slightly more by a disproportionately high number of plants that escape herbivory than they are by plants that receive very high herbivory. When we modeled the Gini asymmetry coefficient as a function of latitude or plant size, we found flat relationships. This included a slope of 0.00 (-0.01–0.02) for

latitude and 0.01 (-0.01–0.02) for plant size. These results indicate that the shape of the variability may be less predictable than the amount of variability itself.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

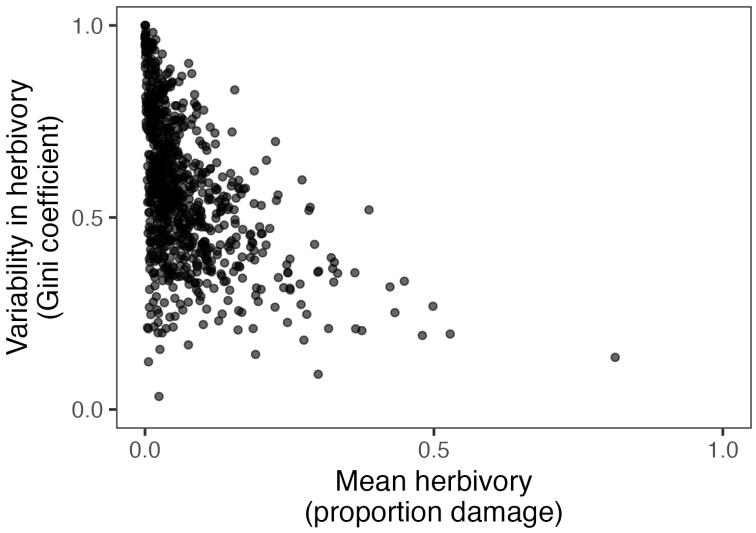
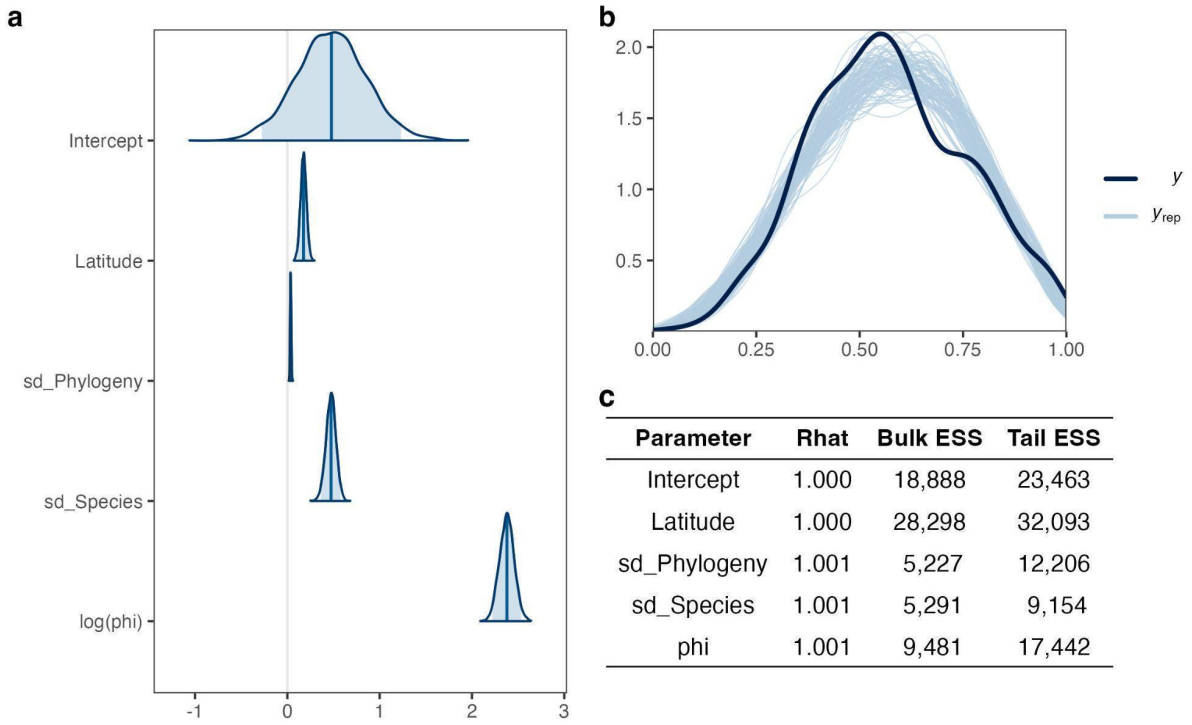


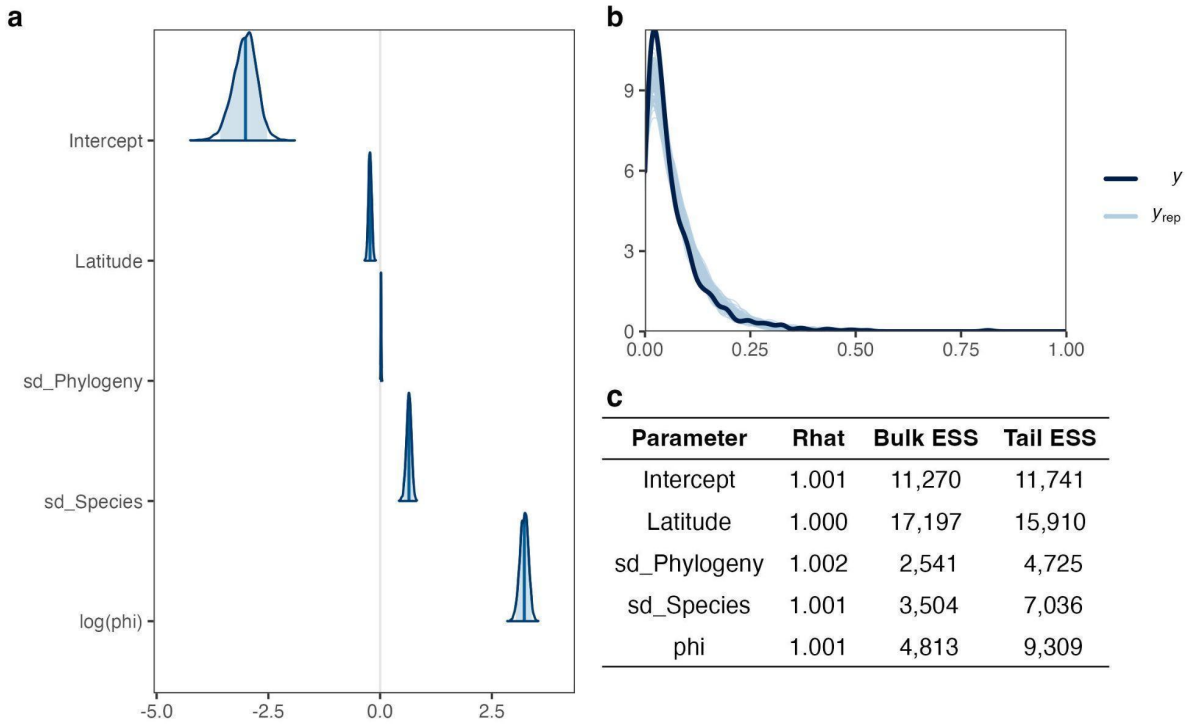
Fig. S1. The relationship between the Gini coefficient and mean herbivory. For low to moderate mean herbivory levels, populations exhibit a large range of Gini coefficients, whereas populations with high herbivory levels exhibit low Gini coefficients. This triangular relationship between the Gini coefficient and mean herbivory resulted in a correlation of -0.46 in the raw data. Each point is one survey (790 surveys of 503 plant species).



c

Parameter	Rhat	Bulk ESS	Tail ESS
Intercept	1.000	18,888	23,463
Latitude	1.000	28,298	32,093
sd_Phylogeny	1.001	5,227	12,206
sd_Species	1.001	5,291	9,154
phi	1.001	9,481	17,442

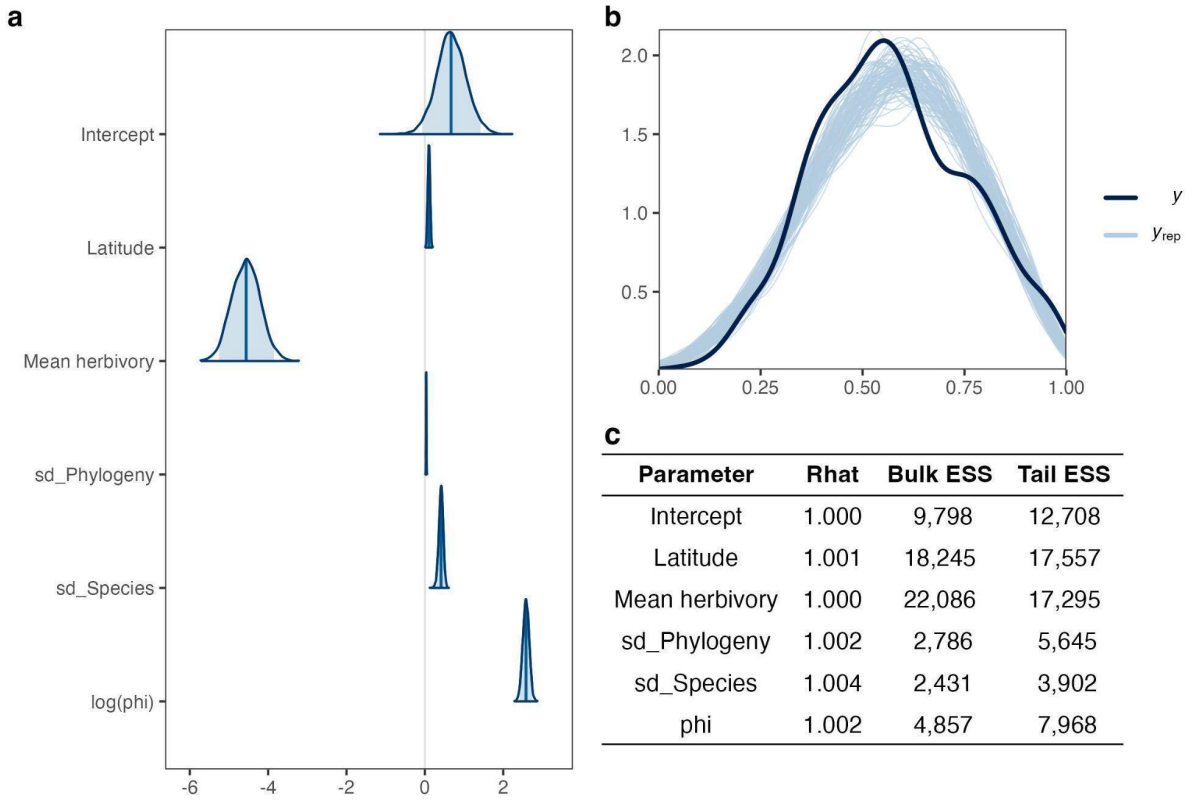
Fig. S2. Summary of the model of the relationship between the Gini coefficient of herbivory and latitude. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. Latitude is absolute value and scaled. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b)** and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.



c

Parameter	Rhat	Bulk ESS	Tail ESS
Intercept	1.001	11,270	11,741
Latitude	1.000	17,197	15,910
sd_Phylogeny	1.002	2,541	4,725
sd_Species	1.001	3,504	7,036
phi	1.001	4,813	9,309

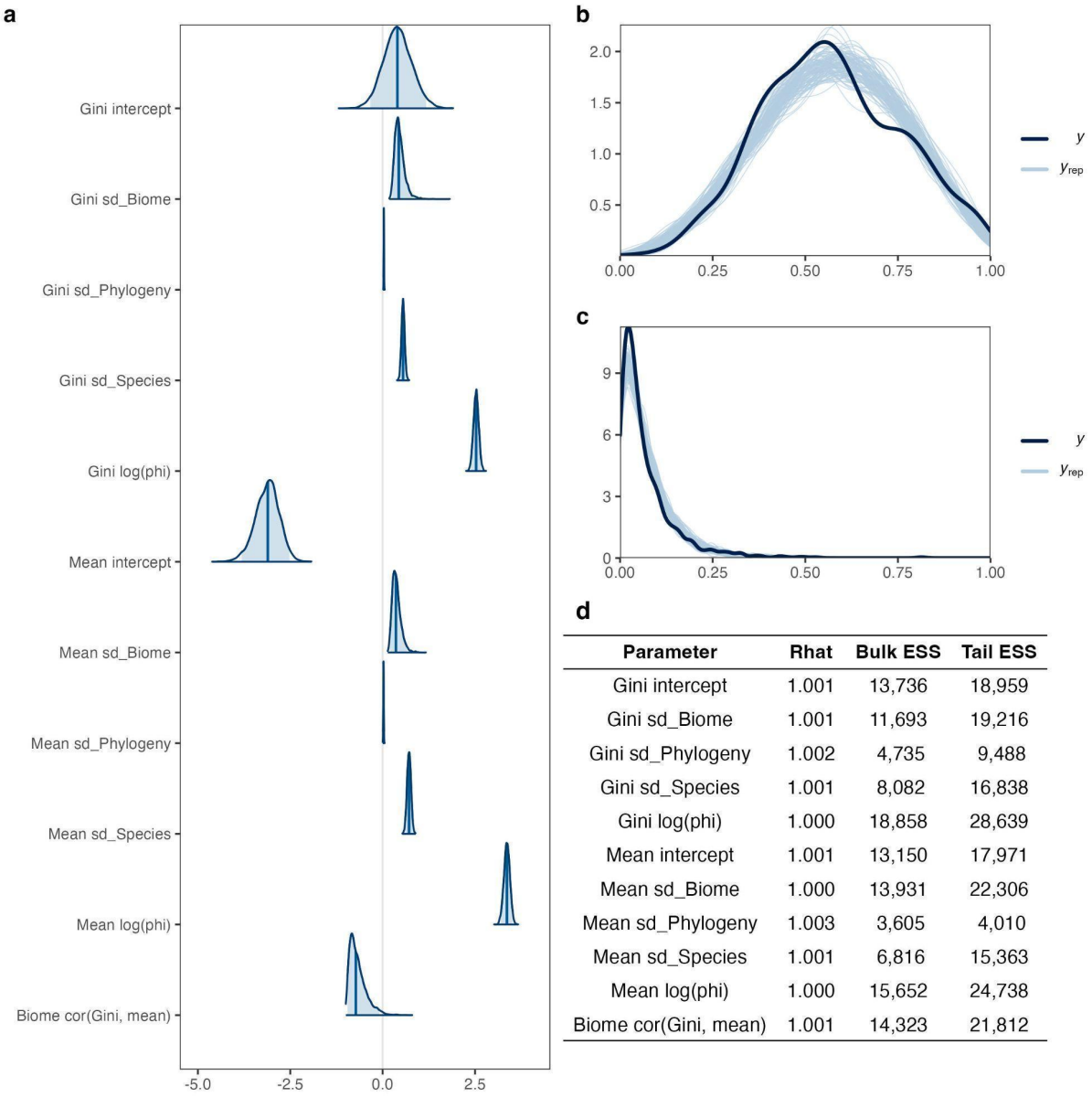
Fig. S3. Summary of the model of the relationship between mean herbivory and latitude. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. Latitude is absolute value and scaled. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b**) and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.



c

Parameter	Rhat	Bulk ESS	Tail ESS
Intercept	1.000	9,798	12,708
Latitude	1.001	18,245	17,557
Mean herbivory	1.000	22,086	17,295
sd_Phylogeny	1.002	2,786	5,645
sd_Species	1.004	2,431	3,902
phi	1.002	4,857	7,968

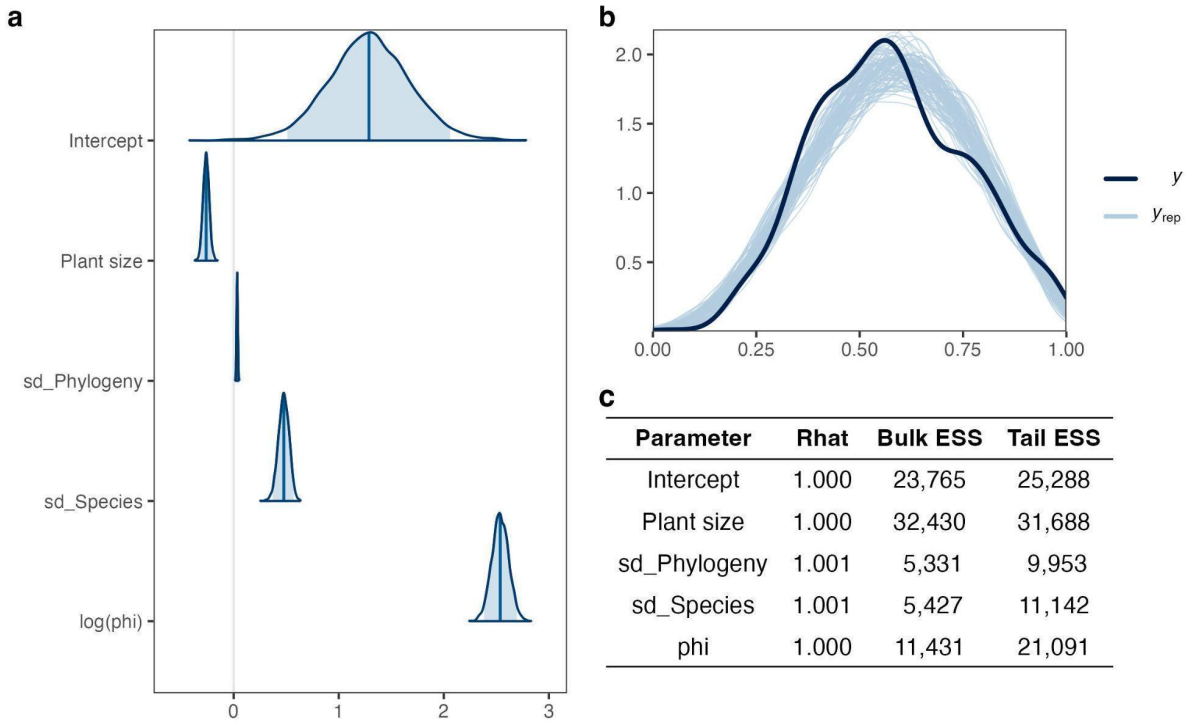
Fig. S4. Summary of the model of the relationship between the Gini coefficient of herbivory and latitude with mean herbivory as a covariate. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. Latitude is absolute value and scaled. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b)** and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.



d

Parameter	Rhat	Bulk ESS	Tail ESS
Gini intercept	1.001	13,736	18,959
Gini sd_Biome	1.001	11,693	19,216
Gini sd_Phylogeny	1.002	4,735	9,488
Gini sd_Species	1.001	8,082	16,838
Gini log(phi)	1.000	18,858	28,639
Mean intercept	1.001	13,150	17,971
Mean sd_Biome	1.000	13,931	22,306
Mean sd_Phylogeny	1.003	3,605	4,010
Mean sd_Species	1.001	6,816	15,363
Mean log(phi)	1.000	15,652	24,738
Biome cor(Gini, mean)	1.001	14,323	21,812

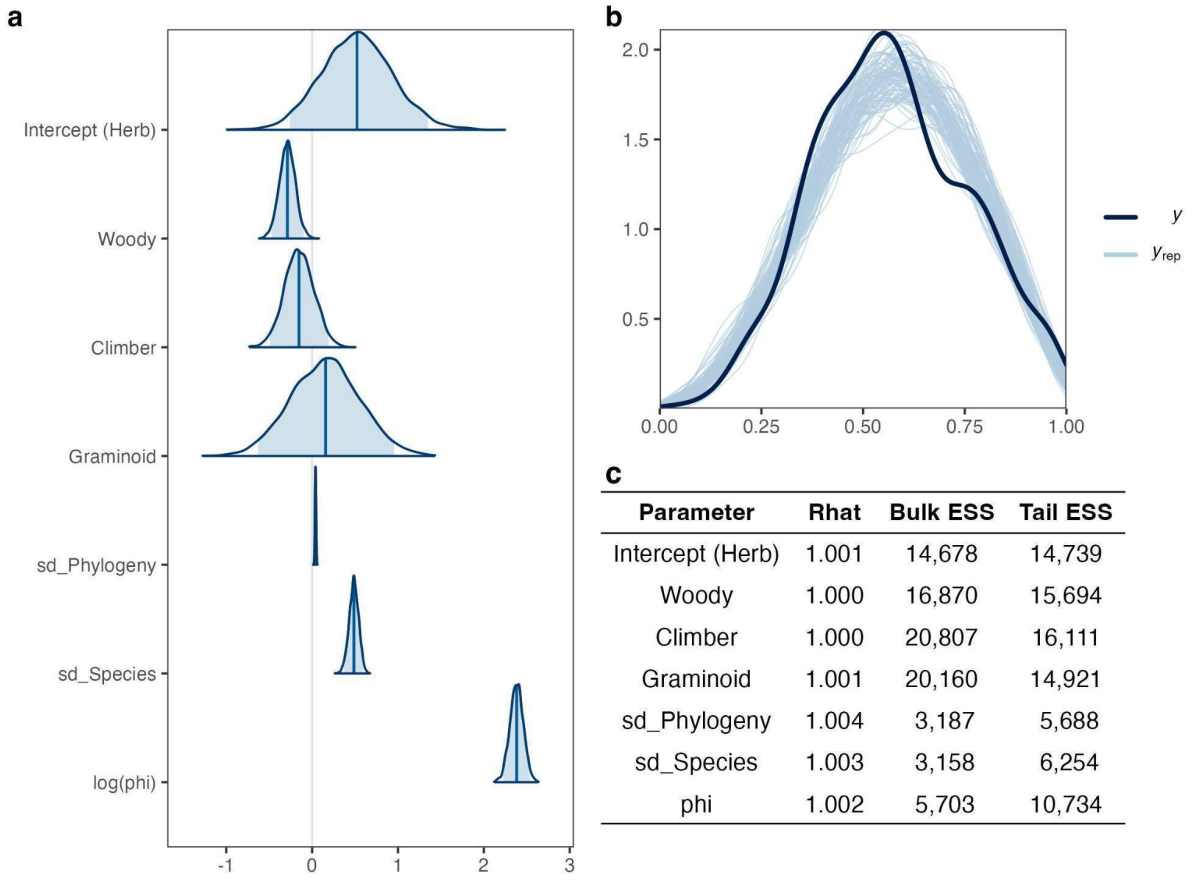
Fig. S5. Summary of the model of the relationship between the Gini coefficient of herbivory and mean herbivory as responses and biome as a random grouping variable. (**a**) Posterior distributions of parameters from this multivariate phylogenetic beta regression. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Biome cor(Gini, mean) is the estimated correlation between the Gini coefficient and mean herbivory across biomes. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b**), (**c**), and (**d**), Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.



c

Parameter	Rhat	Bulk ESS	Tail ESS
Intercept	1.000	23,765	25,288
Plant size	1.000	32,430	31,688
sd_Phylogeny	1.001	5,331	9,953
sd_Species	1.001	5,427	11,142
phi	1.000	11,431	21,091

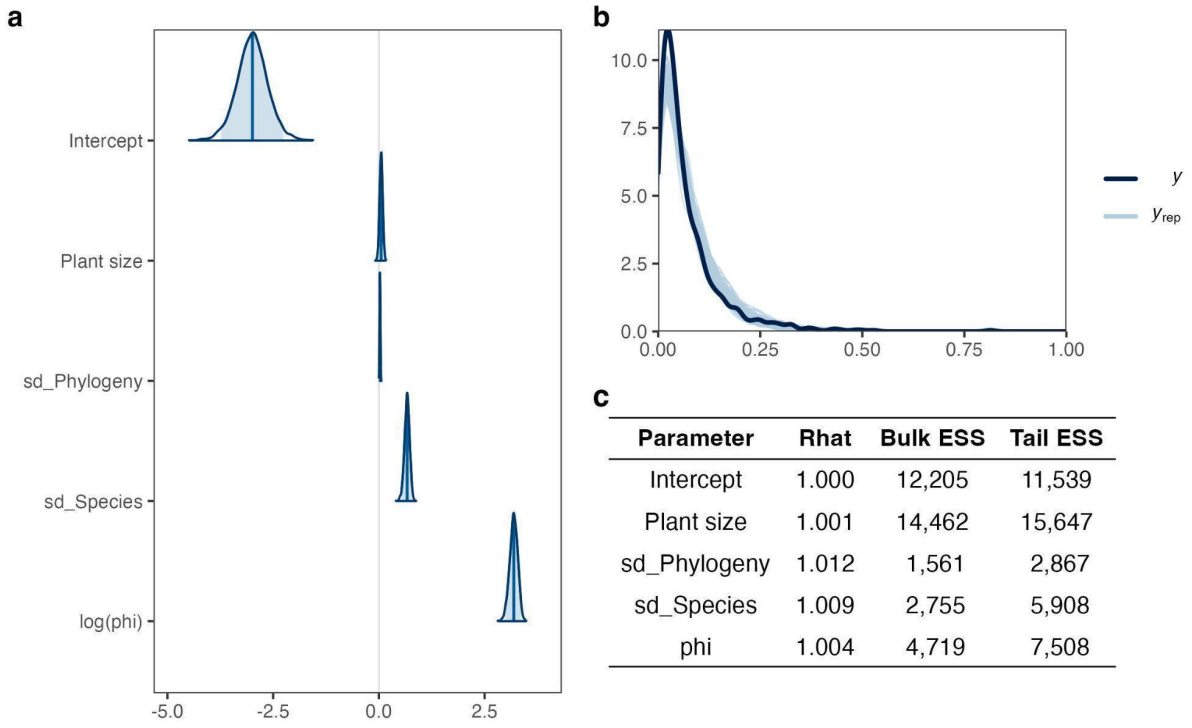
Fig. S6. Summary of the model of the relationship between the Gini coefficient of herbivory and plant size. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. Plant size is log transformed plant diameter. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b)** and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 735 surveys of 472 species.



c

Parameter	Rhat	Bulk ESS	Tail ESS
Intercept (Herb)	1.001	14,678	14,739
Woody	1.000	16,870	15,694
Climber	1.000	20,807	16,111
Graminoid	1.001	20,160	14,921
sd_Phylogeny	1.004	3,187	5,688
sd_Species	1.003	3,158	6,254
phi	1.002	5,703	10,734

Fig. S7. Summary of the model of the relationship between the Gini coefficient of herbivory and plant growth form. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. The intercept is the predicted mean for herbs, whereas parameters for other growth forms are differences from herbs. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b)** and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.



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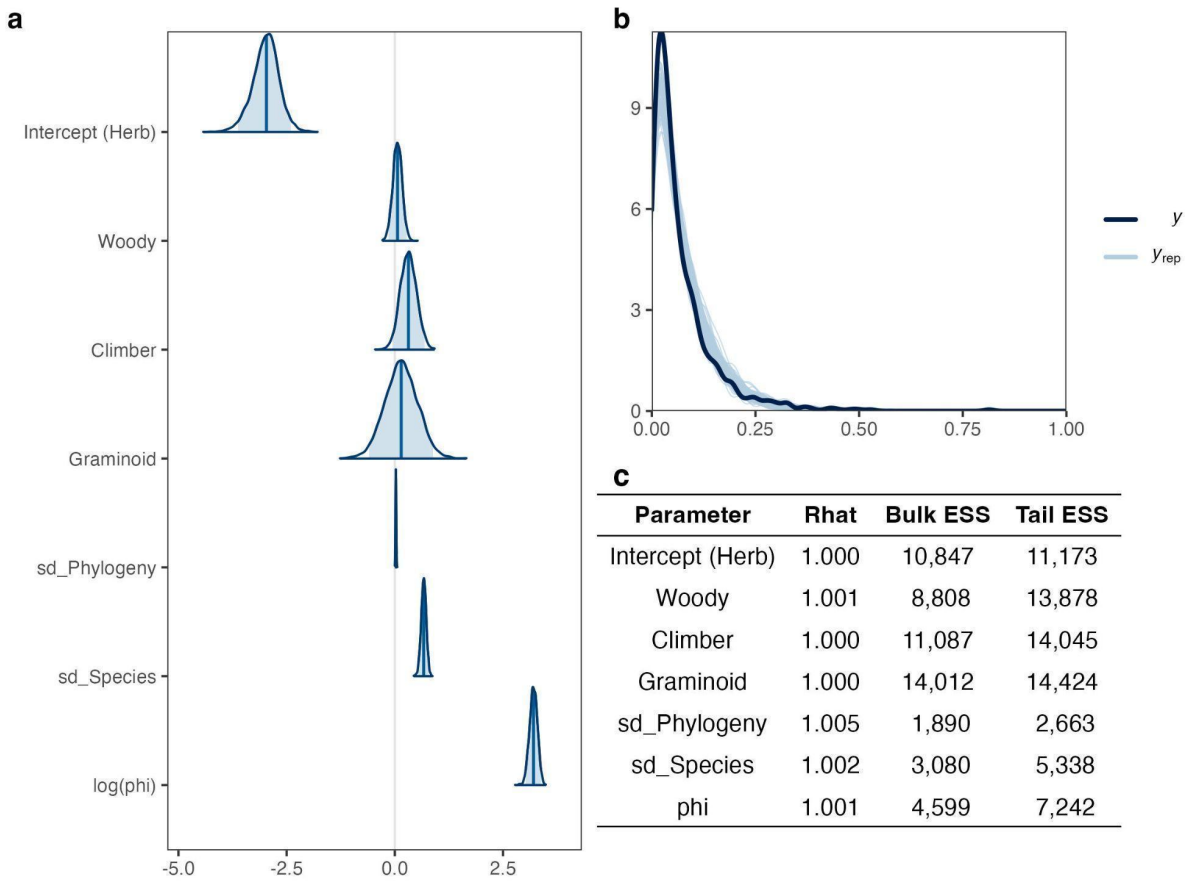
Parameter	Rhat	Bulk ESS	Tail ESS
Intercept	1.000	12,205	11,539
Plant size	1.001	14,462	15,647
sd_Phylogeny	1.012	1,561	2,867
sd_Species	1.009	2,755	5,908
phi	1.004	4,719	7,508

Fig. S8. Summary of the model of the relationship between mean herbivory and plant size. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. Plant size is log transformed plant diameter. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b**) and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 735 surveys of 472 plant species.



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Parameter	Rhat	Bulk ESS	Tail ESS
Intercept (Herb)	1.000	10,847	11,173
Woody	1.001	8,808	13,878
Climber	1.000	11,087	14,045
Graminoid	1.000	14,012	14,424
sd_Phylogeny	1.005	1,890	2,663
sd_Species	1.002	3,080	5,338
phi	1.001	4,599	7,242

Fig. S9. Summary of the model of the relationship between mean herbivory and plant growth form. (**a**) Posterior distributions of parameters from this phylogenetic beta regression. The intercept is the predicted mean for herbs, whereas parameters for other growth forms are differences from herbs. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. Phi is the precision parameter. The shaded regions show the 95% probability mass. (**b**) and (**c**) Posterior predictive check with 100 draws and diagnostics table from the same model. ESS is effective sample size. Sample size is 790 surveys of 503 species.

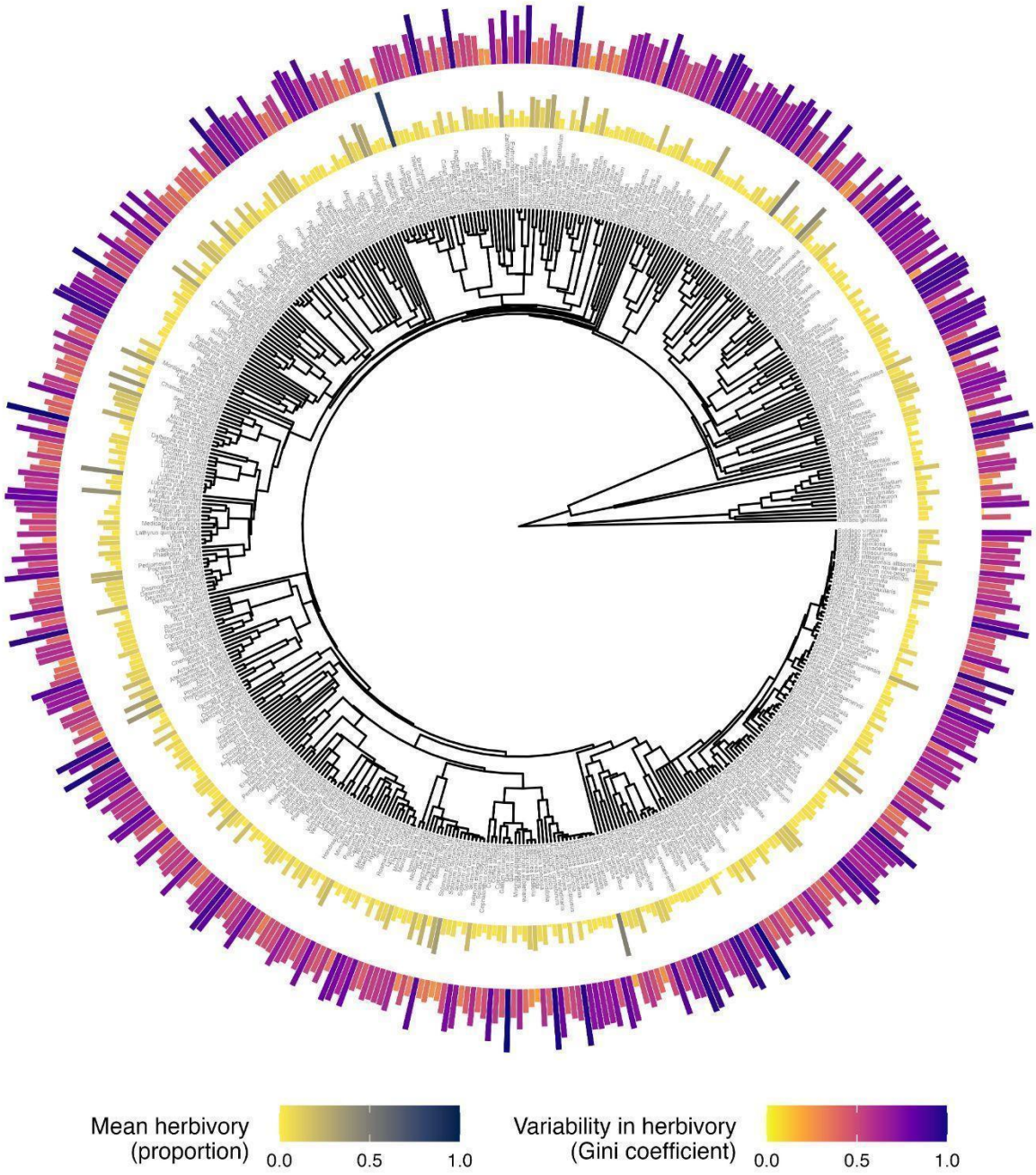

Fig. S10. The phylogeny of all 503 species in the dataset. Levels of variation in herbivory among plants within populations (Gini coefficient) show greater phylogenetic signal ($\lambda = 0.51$ [0.45–0.51], $p < 0.001$) than mean herbivory levels ($\lambda_{Mean} = 0.07$ [0.06–0.08], $p > 0.1$). This figure is as Fig. 4 in the main text except with all species shown, whereas Fig. 4 omits less well represented families for clarity.

Table S1. Summary of the model of the relationship between the Gini coefficient of herbivory and latitude and its interaction with hemisphere. As described in the methods, we started our latitudinal analyses by fitting models that allowed for different latitudinal slopes in the Northern Hemisphere (652 surveys) and Southern Hemisphere (138 surveys). The model is a phylogenetic beta regression. Latitude is absolute value and scaled. Hemi. interxn (S) is the interaction parameter describing the difference in slope between the N and S Hemispheres. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. L95CI and U95CI are the lower and upper bounds of the 95% credible interval. ESS is effective sample size. Sample size is 790 surveys of 503 species. The 95% credible interval for the interaction parameter overlapped zero and had a Bayes factor of 0.23, suggesting support for the hypothesis of similar latidudinal slopes between hemispheres. We therefore focused our analyses on models with one latitudinal gradient slope (with the absolute value of latitude) and presented those models in the main text.

Parameter	Estimate	SE	L95CI	U95CI	Rhat	Bulk ESS	Tail ESS
Intercept	0.53	0.38	-0.20	1.30	1.000	10,502	12,057
Latitude (N)	0.15	0.04	0.07	0.22	1.000	14,276	15,467
Hemi. interxn (S)	0.14	0.08	-0.01	0.30	1.000	14,577	15,595
sd_Phylogeny	0.04	0.01	0.02	0.05	1.002	3,031	5,680
sd_Species	0.48	0.06	0.36	0.58	1.001	2,841	4,656
phi	10.90	0.88	9.26	12.66	1.000	5,075	8,998

Table S2. Summary of the model of the relationship between mean herbivory and latitude and its interaction with hemisphere. The model is a phylogenetic beta regression. Latitude is absolute value and scaled. Hemi. interxn (S) is the interaction parameter describing the difference in slope between the N and S Hemispheres. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. L95CI and U95CI are the lower and upper bounds of the 95% credible interval. ESS is effective sample size. Sample size is 790 surveys of 503 species. The 95% credible interval for the interaction parameter overlapped zero, and we therefore focused our analyses on models with one latitudinal gradient slope (with the absolute value of latitude) and presented those models in the main text.

Parameter	Estimate	SE	L95CI	U95CI	Rhat	Bulk ESS	Tail ESS
Intercept	-3.02	0.28	-3.61	-2.50	1.000	9,765	10,399
Latitude (N)	-0.23	0.04	-0.31	-0.15	1.000	12,823	13,802
Hemi. interxn (S)	0.01	0.08	-0.16	0.18	1.000	13,668	14,650
sd_Phylogeny	0.02	0.01	0.01	0.04	1.002	2,207	3,823
sd_Species	0.64	0.06	0.52	0.75	1.001	3,517	6,230
phi	25.16	2.32	20.66	29.76	1.001	4,611	8,233

Table S3. Summary of the model of the Gini coefficient as a function of latitude and focal plant abundance. We tested the potential for differences in plant abundances to influence the observed latitudinal gradient in herbivory variability by re-fitting our Gini coefficient latitudinal gradient model (Fig. 2 and Fig. S2) with focal plant abundance (percent cover) as a covariate, thus estimating the marginal effect of latitude conditional on plant abundance. The parameter for latitude in this model was still strongly positive (p_p = 1.0, BF = 1.9e2). This suggests that the association between latitude and herbivory variability is not explained by differences in plant abundance. Latitude is absolute value and scaled. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. L95CI and U95CI are the lower and upper bounds of the 95% credible interval. ESS is effective sample size. Sample size is 643 surveys of 410 species.

Parameter	Estimate	SE	L95CI	U95CI	Rhat	Bulk ESS	Tail ESS
Intercept	1.06	0.38	0.36	1.83	1.000	29,684	25,802
Latitude	0.15	0.03	0.09	0.22	1.000	47,968	33,646
Plant abundance	-0.01	0.00	-0.01	-0.01	1.000	51,968	35,503
sd_Phylogeny	0.03	0.01	0.02	0.04	1.002	5,504	10,570
sd_Species	0.49	0.06	0.37	0.61	1.003	6,638	12,927
phi	11.13	1.00	9.26	13.18	1.002	11,126	19,847

Table S4. Summary of the model of the Gini coefficient as a function of plant size and latitude. Our finding that the Gini coefficient increases with plant size could be explained by the decline in plant size with increasing latitude (ρ = -0.35 in our dataset) and the negative relationship between latitude and the Gini coefficient. In other words, latitude could conceivably have been the driver of the negative Gini coefficient–plant size association we found. We accounted for this association by fitting a phylogenetic beta regression model of the Gini coefficient with both plant size and latitude as predictors, thus estimating the marginal effect of each predictor conditional on the other predictor. The parameter for plant size in this model was still strongly negative (p_p = 1.0, BF = 2.7e6). This suggests that the association between plant size and herbivory variability is not explained by the negative effect of latitude on plant size and is consistent with the plant size hypothesis. Likewise, the parameter for latitude was still positive with plant size in the model (p_p = 1.0, BF = 3.9). Plant size is log transformed plant diameter. Latitude is absolute value and scaled. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. L95CI and U95CI are the lower and upper bounds of the 95% credible interval. ESS is effective sample size. Sample size is 735 surveys of 472 species.

Parameter	Estimate	SE	L95CI	U95CI	Rhat	Bulk ESS	Tail ESS
Intercept	1.18	0.36	0.47	1.90	1.000	29,091	26,788
Plant size	-0.24	0.03	-0.30	-0.18	1.000	36,299	31,797
Latitude	0.10	0.03	0.04	0.16	1.000	38,588	33,626
sd_Phylogeny	0.03	0.01	0.02	0.04	1.000	6,305	11,931
sd_Species	0.47	0.05	0.37	0.57	1.001	6,534	11,734
phi	12.70	1.03	10.76	14.83	1.001	11,679	19,389

Table S5. Summary of the model of the Gini coefficient as a function of plant size and focal plant abundance. We tested the potential for differences in plant abundances to influence the observed relationship between plant size and herbivory variability by re-fitting our plant size model (Fig. 3A and Fig. S6) with focal plant abundance (percent cover) as a covariate, thus estimating the marginal effect of plant size conditional on plant abundance. The parameter for plant size in this model was still strongly negative (p_p = 1.0, BF = 1.8e6). This suggests that the association between plant size and herbivory variability is not explained by differences in plant abundance. Plant size is on a log scale. Plant abundance is percent cover of the focal plant species. sd_Phylogeny is the standard deviation of the phylogenetic random effect. sd_Species is the standard deviation of the random effect grouping surveys (populations) by species. L95CI and U95CI are the lower and upper bounds of the 95% credible interval. ESS is effective sample size. Sample size is 621 surveys of 397 species.

Parameter	Estimate	SE	L95CI	U95CI	Rhat	Bulk ESS	Tail ESS
Intercept	1.66	0.38	0.96	2.45	1.000	59,406	51,306
Plant size	-0.25	0.03	-0.31	-0.18	1.000	84,664	67,984
Plant abundance	-0.01	0.00	-0.01	0.00	1.000	92,280	70,625
sd_Phylogeny	0.02	0.01	0.01	0.04	1.001	9,658	14,592
sd_Species	0.45	0.06	0.33	0.57	1.001	11,438	20,234
phi	11.30	1.01	9.41	13.37	1.001	20,917	35,989

Table S6. Parameter estimates of models of evolution of variability in herbivory (Gini coefficient) and mean herbivory (logit-transformed) as a function of plant growth form. Means and standard deviations of parameter estimates across 100 phylogenetic trees are provided. Models considered herbivory evolving under Brownian Motion where the rate of evolution (σ^2) was shared across trait states (BM1 model) or allowed to vary depending on the trait (herbaceous vs. woody) (BMS). We also examined Ornstein-Uhlenbeck models (OU1) that considered herbivory evolving under a regime with a single evolutionary optimum θ while keeping rate (σ^2) and strength of pull towards an evolutionary optimum (α) constant, and OUM models, which allow for herbivory to evolve towards different optima, depending on the trait (herbaceous vs. woody). Stochastic maps of trait evolution were generated with *make.simmap* in 'phytools'. Models were fit using the 'OUwie' package in R. To compare models, we used the average BIC across 100 trees. Variability in herbivory across herbaceous and woody taxa (Gini) is best modeled as evolving with constant rate and strength of selection towards different optima (OUM model ΔBIC = 4.5 lower than OU1) so that the optimum is higher in herbaceous taxa (θ= 0.6) compared to woody ones (θ= 0.52). In contrast, the best model for mean herbivory suggests that herbaceous and woody taxa are evolving under a selection regime with a constant rate and strength of selection towards a single optimum (OU1).

			Herbaceous						Woody					
Response	**model**	**BIC**	**α**	**α_{SD}**	**σ^2**	**σ^2_{SD}**	**θ**	**θ_{SE}**	**α**	**α_{SD}**	**σ^2**	**σ^2_{SD}**	**θ**	**θ_{SE}**
Variability in herbivory (Gini)	OUM	-105.0	0.91	0.00	0.09	0.01	0.60	0.01	0.91	0.00	0.09	0.01	0.52	0.02
	OU1	-97.0	0.91	0.00	0.09	0.01	0.57	0.01	0.91	0.00	0.09	0.01	0.57	0.01
	BMS	959.4	NA	NA	0.03	0.02	0.63	1.19	NA	NA	0.01	0.01	0.63	1.19
	BM1	1021.1	NA	NA	0.02	0.01	0.61	1.37	NA	NA	0.02	0.01	0.61	1.37
Mean herbivory (logit)	OU1	1797.8	0.91	0.0003	5.34	1.18	-3.20	0.08	0.91	0.0003	5.34	1.18	-3.20	0.08
	OUM	1802.3	0.91	0.0003	5.32	1.18	-3.27	0.10	0.91	0.0003	5.32	1.18	-3.06	0.14
	BMS	2980.7	NA	NA	2.42	1.46	-3.86	10.63	NA	NA	0.35	0.06	-3.86	10.63
	BM1	3089.2	NA	NA	1.98	1.20	-3.80	12.76	NA	NA	1.98	1.20	-3.80	12.76

Table S7. Parameter estimates of models of evolution of variability in herbivory (Gini coefficient) and mean herbivory (logit-transformed) as a function of plant biome affinity. Temperate: ≤23° latitude; tropical: >23° latitude. Means and standard deviation of parameter estimates across 100 phylogenetic trees are provided. Models considered herbivory evolving under Brownian Motion where the rate of evolution (σ^2) was shared across trait states (BM1 model) or allowed to vary depending on the state of the trait (temperate vs. tropical) being examined (BMS). We also examined Ornstein-Uhlenbeck models (OU1) that considered herbivory evolving under a regime with a single evolutionary optimum θ while keeping rate (σ^2) and strength of pull towards an evolutionary optimum (α) constant, and OUM models, which allow for herbivory to evolve towards different optima, depending on the state of the trait (i.e, temperate vs. tropical). Stochastic maps of trait evolution were generated with the *make.simmap* function in the 'phytools' R package. All models were implemented using the 'OUwie' package in R. To compare models, we used the average BIC across the 100 trees described above. Both mean and variability in herbivory evolve under regimes with constant rates and strength of selection towards slightly different evolutionary optima (OUM). Temperate species had a higher optimum for variability (θ=0.6) compared to tropical species (θ=0.5), whereas for mean proportion of herbivory temperate species had a lower optimum (θ=0.036 back-transformed) than tropical species (θ=0.060 back-transformed).

			Temperate						Tropical					
Response	**model**	**BIC**	**α**	**α_{SD}**	**σ^2**	**σ^2_{SD}**	**θ**	**θ_{SE}**	**α**	**α_{SD}**	**σ^2**	**σ^2_{SD}**	**θ**	**θ_{SE}**
Variability in herbivory (Gini)	OUM	-118.0	0.91	0.00	0.09	0.02	0.60	0.01	0.91	0.00	0.09	0.02	0.50	0.02
	OU1	-106.1	0.91	0.00	0.09	0.02	0.57	0.01	0.91	0.00	0.09	0.02	0.57	0.01
	BMS	1037.4	NA	NA	0.03	0.02	0.60	1.07	NA	NA	0.00	0.00	0.60	1.07
	BS1	1130.9	NA	NA	0.02	0.02	0.61	1.39	NA	NA	0.02	0.02	0.61	1.39
Mean herbivory (logit)	OUM	1945.3	0.91	0.0003	5.21	1.85	-3.30	0.09	0.91	0.0003	5.21	1.85	-2.76	0.16
	OU1	1948.3	0.91	0.0003	5.29	1.84	-3.17	0.08	0.91	0.0003	5.29	1.84	-3.17	0.08
	BMS	3240.2	NA	NA	2.25	2.14	-3.85	9.47	NA	NA	0.12	0.04	-3.85	9.47
	BS1	3370.4	NA	NA	2.02	1.97	-3.80	12.73	NA	NA	2.02	1.97	-3.80	12.73