HERBIVORY

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

The Herbivory Variability Network*†

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.

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 toward 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*), can increase the importance of competition among herbivores (*17*), can maintain diversity by facilitating the evolutionary coexistence of alternative strategies (*18*), and can 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*). 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. In this work, 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 by being a more-consistently important force within plant populations. Second, we hypothesize that herbivory is more variable among small plants compared with large plants. Large

*Corresponding author. Email: william.wetzel@montana.edu
†Herbivory Variability Network authors and affiliations are listed in the supplementary materials.

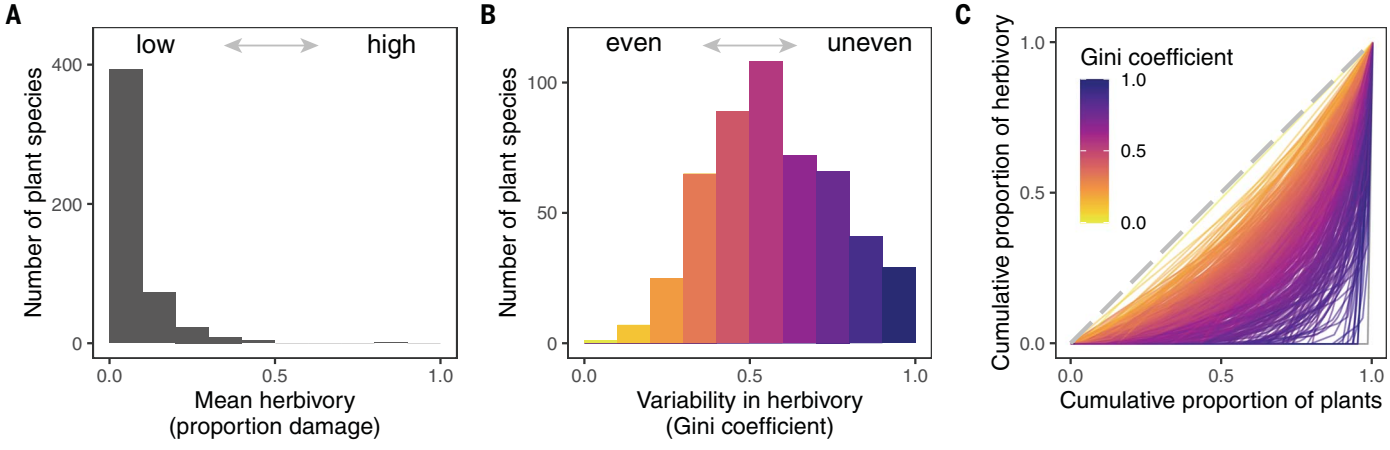

Fig. 1. Mean and variability in plant-herbivore interactions. (**A**) Histogram of the number of plant species with different mean proportion leaf area damaged by herbivores. (**B**) Histogram of the Gini coefficient values for all plant species in our dataset. (**C**) Lorenz curves from all 790 population 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 (B)]. Sample sizes are 790 surveys of 503 plant species.

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plants, which represent a greater sampling area, should average over small-scale random variation in herbivory, resulting in values closer to the population mean, whereas 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

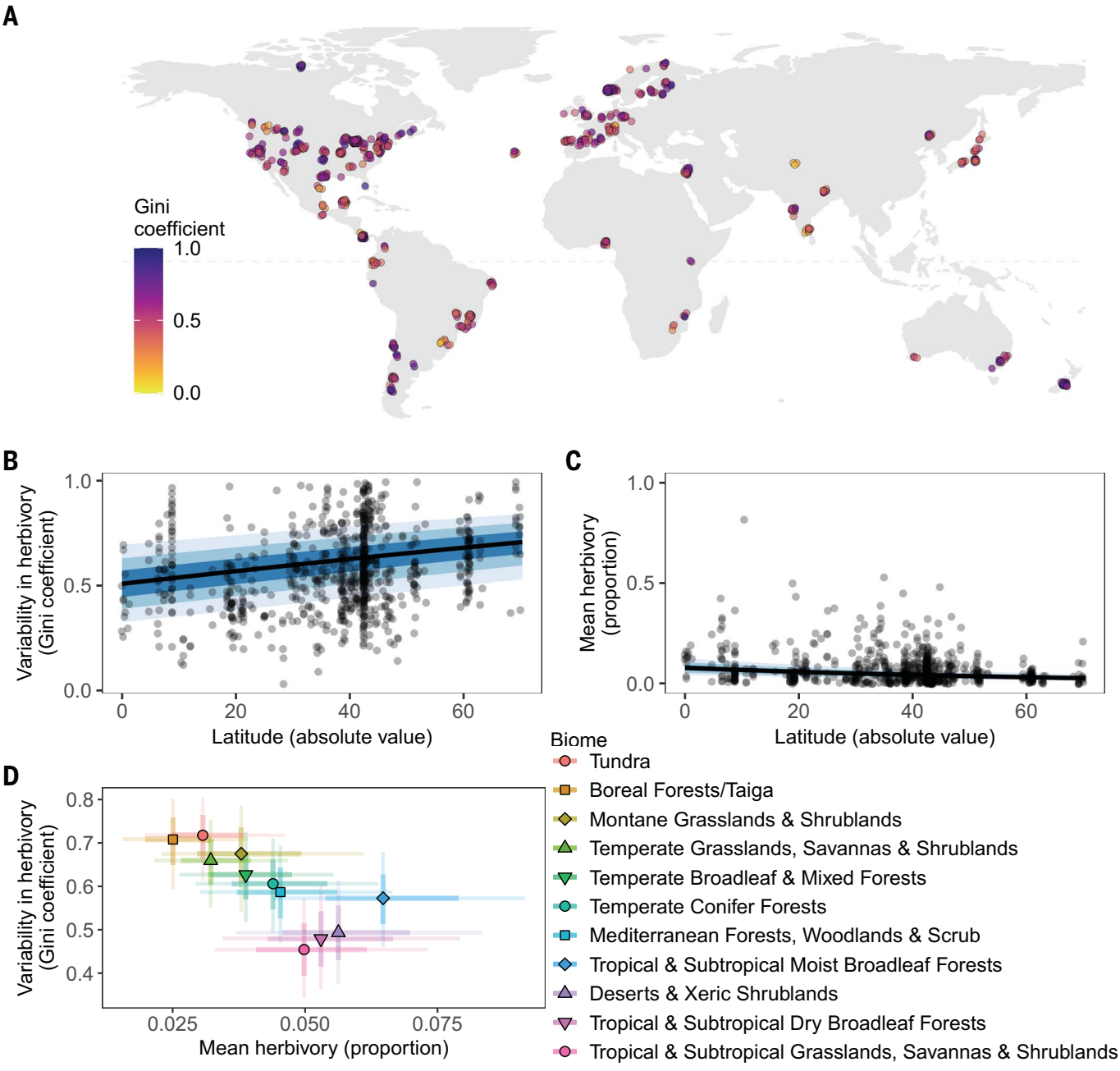

Fig. 2. Global patterns of variability in herbivory within plant populations. (**A**) The geographic distribution of our sampling sites, colored by variability in herbivory among individuals within populations (Gini coefficient). Points are slightly jittered for visibility. (**B** and **C**) Variability in herbivory increased (B) and mean herbivory decreased (C) 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 [ρ = −0.67 (−0.94 to −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.

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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*). By contrast, we sampled 60 individuals per population, which allowed 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 to 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% confidence interval: 0.40 to 0.78)] (Fig. 1). On average, the most-damaged individual in each plant population lost 34.2% (32.4 to 36.0%) of its leaf area to herbivory, whereas 27.9% (25.9 to 29.9%) of individuals completely or essentially escaped herbivory (<0.5% damage). Half of the damage in each population was concentrated on 11.3% (10.7 to 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. 1, B and C). Even though the Gini coefficient normalizes by the mean, it can nevertheless be correlated with it. 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 ($\rho = -0.46$) (fig. S1).

Geographic patterns of variability

We found strong support for the latitudinal variability gradient hypothesis (Fig. 2, A and B). Variation was lowest at the equator [Gini = 0.51 (0.33 to 0.69)] and increased toward 70°N and 70°S (70°N/S) [Gini = 0.70 (0.54 to 0.84); Bayesian coefficient of determination (R^2) = 5%; posterior probability (p_p) = 1.0; Bayes factor (BF) = 2.0×10^4]. Mean herbivory, by contrast, declined with latitude, from 8.0% (4.1 to 12.3%) at the equator to 2.9% (1.4 to 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 = 2.9×10^4) (Fig. 2C, figs. S2 and S3, and tables S1 to 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 it was lower in magnitude, with a 20% (6 to 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 and fig. S5). Whereas there was a negative correlation between the mean and Gini coefficient among biomes [$\rho = -0.68$ (-0.95 to -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. 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*), which means that variability at high latitudes, where mean herbivory is low, should erode selection through nonlinear averaging (*14*), all else being equal. Our finding is also consistent with the hypothesis that inducible defenses are more common among temperate compared with tropical plants (*29*, *30*) because 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 to 2.05 m, encompassing ~90% of our populations) resulted in a 32.7% (20.6 to 44.7%) decrease in the Gini coefficient [from 0.70 (0.54 to 0.85) to 0.47 (0.29 to 0.66); R^2 = 13.3%; p_p = 1.0; BF = 4.6×10^7] (Fig. 3A and fig. 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 to 100% cover in our dataset) (tables S4 and S5) (*32*). Woody species, which averaged 4.1 times as large as herbs in our dataset, had 10.9% (2.9 to 19.1%) lower Gini coefficients compared with herbaceous species [0.56 (0.37 to 0.76) versus 0.63 (0.44 to 0.81); BF = 4.25]. However, the overall variance explained by growth form, including climber and graminoid categories, was low (R^2 = 2.8%) (Fig. 3B and fig. S7), which suggests that mean size is a more-important determinant of herbivory patterns than growth form. Mean herbivory, by contrast,

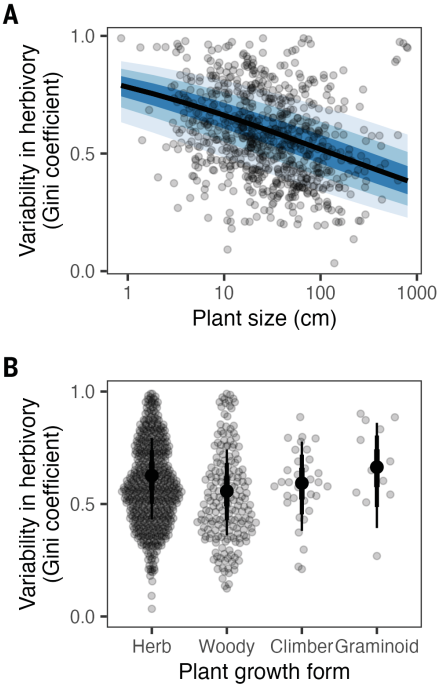

Fig. 3. Plant size shapes variability in herbivory. (**A**) Variability in herbivory among individuals within populations declines with the average size (height or canopy diameter for prostrate species) of plants in the population (R^2 = 13.3%; p_p = 1.0; BF = 4.6×10^7; 735 surveys of 472 species). (**B**) Variability in herbivory, however, is only weakly related to plant growth form (R^2 = 2.8%), with woody plants having 10.9% (2.9 to 19.1%) lower Gini coefficients compared with 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 gray point is one survey.

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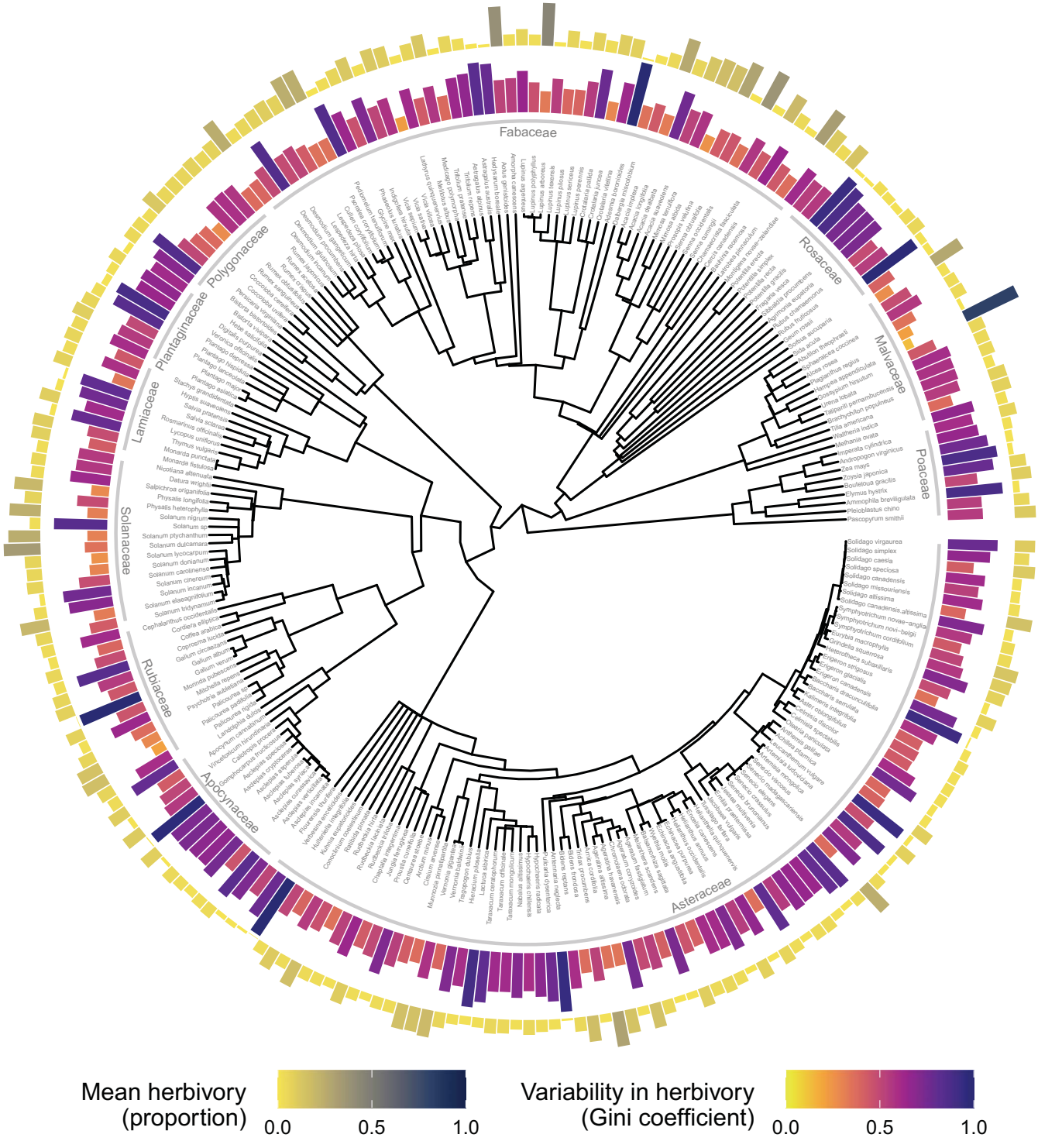

Fig. 4. Phylogenetic patterns of mean and variability in herbivory. Variability in herbivory among plants within populations (Gini coefficient) show greater phylogenetic signal [Pagel's λ = 0.51 (0.45 to 0.52); $P < 0.001$] compared with mean herbivory levels [Pagel's λ = 0.07 (0.06 to 0.08); $P > 0.1$].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

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 says 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, by contrast, are more likely to escape herbivory entirely or be severely damaged by a few events, which results in high variability. A key implication of this phenomenon is that

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larger species (and larger stages within species) should experience greater selection for high concentrations of constitutive defenses or tolerance. Smaller species (and stages), by 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 that 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 to 0.52); $P < 0.001$], indicating that more-closely related species display more-similar variability levels (Fig. 4 and fig. S10). Mean herbivory, by contrast, did not show meaningful phylogenetic signal [$\lambda = 0.07$ (0.06 to 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. 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 versus temperate systems and woody versus herbaceous growth forms (tables S6 and S7), which indicates that the evolution of variability in herbivory seems to be driven by conserved plant traits and is therefore a biologically informative feature rather than random noise.

Conclusions

The assumption that plant-herbivore interactions are highly variable has long dominated ecology and evolution, with foundational works on so-called 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. Although 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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SUPPLEMENTARY MATERIALS

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Herbivory Variability Network Authors
Materials and Methods
Supplementary Text
Figs. S1 to S10
Tables S1 to S7
References (*37*–*58*)
MDAR Reproducibility Checklist

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The Herbivory Variability Network*, M. L. Robinson, P. G. Hahn, B. D. Inouye, N. Underwood, S. R. Whitehead, K. C. Abbott, E. M. Bruna, N. I. Cacho, L. A. Dyer, L. Abdala-Roberts, W. J. Allen, J. F. Andrade, D. F. Angulo, D. Anjos, D. N. Anstett, R. Bagchi, S. Bagchi, M. Barbosa, S. Barrett, C. A. Baskett, E. Ben-Simchon, K. J. Bloodworth, J. L. Bronstein, Y. M. Buckley, K. T. Burghardt, C. Bustos-Segura, E. S. Calixto, R. L. Carvalho, B. Castagneyrol, M. C. Chiuffo, D. Cino#lu, E. Cinto Mejía, M. C. Cock, R. Cogni, O. L. Cope, T. Cornelissen, D. R. Cortez, D. W. Crowder, C. Dallstream, W. Dáttilo, J. K. Davis, R. D. Dimarco, H. E. Dole, I. N. Egbon, M. Eisenring, A. Ejomah, B. D. Elderd, M.-J. Endara, M. D. Eubanks, S. E. Everingham, K. N. Farah, R. P. Farias, A. P. Fernandes, G. W. Fernandes, M. Ferrante, A. Finn, G. A. Florjancic, M. L. Forister, Q. N. Fox, E. Frago, F. M. França, A. S. Getman-Pickering, Z. Getman-Pickering, E. Gianoli, B. Gooden, M. M. Gossner, K. A. Greig, S. Gripenberg, R. Groenteman, P. Grof-Tisza, N. Haack, L. Hahn, S. M. Haq, A. M. Helms, J. Hennecke, S. L. Hermann, L. M. Holeski, S. Holm, M. C. Hutchinson, E. E. Jackson, S. Kagiya, A. Kalske, M. Kalwajtys, R. Karban, R. Kariyat, T. Keasar, M. F. Kersch-Becker, H. M. Kharouba, T. N. Kim, D. M. Kimuyu, J. Kluse, S. E. Koerner, K. J. Komatsu, S. Krishnan, M. Laihonen, L. Lamelas-López, M. C. LaScaleia, N. Lecomte, C. R. Lehn, X. Li, R. L. Lindroth, E. F. LoPresti, M. Losada, A. M. Louthan, V. J. Luizzi, S. C. Lynch, J. S. Lynn, N. J. Lyon, L. F. Maia, R. A. Maia, T. L. Mannall, B. S. Martin, T. J. Massad, A. C. McCall, K. McGurrin, A. C. Merwin, Z. Mijango-Ramos, C. H. Mills, A. T. Moles, C. M. Moore, X. Moreira, C. R. Morrison, M. C. Moshobane, A. Muola, R. Nakadai, K. Nakajima, S. Novais, C. O. Ogbebor, H. Ohsaki, V. S. Pan, N. A. Pardikes, M. Pareja, N. Parthasarathy, R. R. Pawar, Q. Paynter, I. S. Pearse, R. M. Penczykowski, A. A. Pepi, C. C. Pereira, S. S. Phartyal, F. I. Piper, K. Poveda, E. G. Pringle, J. Puy, T. Quijano, C. Quintero, S. Rasmann, C. Rosche, L. Y. Rosenheim, J. A. Rosenheim, J. B. Runyon, A. Sadeh, Y. Sakata, D. M. Salcido, C. Salgado-Luarte, B. A. Santos, Y. Sapir, Y. Sasal, Y. Sato, M. Sawant, H. Schroeder, I. Schumann, M. Segoli, H. Segre, O. Shelef, N. Shinohara, R. P. Singh, D. S. Smith, M. Sobral, G. C. Stotz, A. J. M. Tack, M. Tayal, J. F. Tooker, D. Torrico-Bazoberry, K. Tougeron, A. M. Trowbridge, S. Utsumi, O. Uyi, J. L. Vaca-Uribe, A. Valtonen, L. J. A. van Dijk, V. Vandvik, J. Villellas, L. P. Waller, M. G. Weber, A. Yamawo, S. Yim, P. L. Zarnetske, L. N. Zehr, Z. Zhong, and W. C. Wetzel

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Editor's summary

Herbivory is a major selection pressure on plants, which have evolved many different physical and chemical adaptations to prevent animals from eating their tissues. However, herbivory pressure can be highly variable, even between plants in the same population. The Herbivory Variability Network consortium used standardized surveys to compare herbivory variability within populations at 790 sites across five continents. They found that the weak increase in mean herbivory at lower latitudes was accompanied by lower variation between individuals. Smaller plant species had higher herbivory variability, which also showed a phylogenetic signal. These findings highlight how variation in species interactions can influence eco-evolutionary outcomes. —Bianca Lopez

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