

Review

More than what they eat: uncoupled biophysical constraints underlie geographic patterns of herbivory

Joshua S. Lynn, Jason D. Fridley and Vigdis Vandvik

J. S. Lynn (<https://orcid.org/0000-0002-7190-7991>) ✉ (Joshua.Lynn@uib.no) and V. Vandvik (<https://orcid.org/0000-0003-4651-4798>), Dept of Biological Sciences and Bjerkenes Centre for Climate Research, Univ. of Bergen, Bergen, Norway. – J. D. Fridley (<https://orcid.org/0000-0002-0581-376X>), Dept of Biology, Syracuse Univ., Syracuse, NY, USA.

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Herbivory rates have classically been hypothesized to decrease from the tropics towards higher latitudes because the more benign abiotic conditions in tropical systems foster greater ecosystem complexity including greater intensity of biotic interactions. However, attempts to quantify latitudinal patterns of herbivory often fail to support this hypothesis. While biases have been offered as explanations for null results, here, we argue that framing the question of latitudinal variation in herbivory around nutrient and energetic constraints of insect herbivores and plants may provide mechanistic explanations of latitudinal herbivory patterns. As a case study, we focused on sodium as an uncoupled nutrient between herbivore and plant communities: sodium is a key limiting micronutrient for herbivore neural and muscular development while present at orders of magnitude lower concentrations in plants. We compared sodium deposition with latitude, mean annual temperature (MAT) and actual evapotranspiration (measure of primary productivity, AET) in their ability to predict consumed percentage leaf area from published datasets. Leaf percent herbivory increased with sodium deposition and MAT and decreased with latitude but was unrelated to AET. Sodium had comparable effect size and predictive ability to either MAT or latitude. Additionally, herbivory was highest in locales with both high sodium deposition and high MAT. Our hypothesis that geographic variation in herbivory is driven by an interaction of unrestrictive temperature environments (high MAT) and limiting nutrient supply to herbivores (high sodium deposition) was strongly supported. We propose that greater generality, predictability and theoretical development on geographic variation in herbivory will arise from a refocus on the biophysical constraints (e.g. productivity, micronutrient availability, leaf mass consumed) that ultimately control consumer interactions rather than latitude *per se*. This refocus is likely to open new hypotheses for the evolution of defense syndromes across plant populations and communities based on the specific geography of limiting nutrients.

Keywords: biogeography, metabolic theory of ecology, nutrient colimitation, plant defense traits, resource availability hypothesis, sodium

'Call for a picnic, a merciful salt lick' – from 'Wonderful' by Cate le Bon



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Introduction

For decades, researchers have proposed that consumption rates of plants by insects increases from high to low latitudes (hereafter, the latitudinal herbivory hypothesis or LHH, Dobzhansky 1950, Coley and Barone 1996, Schemske et al. 2009). But empirical support for the LHH has been equivocal: studies have variably shown increased herbivory from high to low latitude (Pennings and Silliman 2005, Baskett and Schemske 2018), decreased herbivory from high to low latitude (Adams and Zhang 2009, Loughnan and Williams 2019), non-linear relationships (Kim 2014) and null/no latitudinal relationship (Lynn and Fridley 2019). Proposed causes behind the patterns are numerous, with climate (Adams and Zhang 2009, Moreira et al. 2015), variation in herbivore communities (Anstett et al. 2014), top-down predator controls (Björkman et al. 2011) and variation in plant chemical defense (Anstett et al. 2015) and functional traits (Lynn and Fridley 2019) all being invoked to explain the disparate patterns.

The lack of consensus around the LHH has driven concerns over publication and methodological biases that over- or underestimate the strength of the latitudinal gradients of herbivory (Moles 2013, Anstett et al. 2016, Moles and Ollerton 2016, Zvereva and Kozlov 2019, 2021). For example, meta-analyses have found little support for the LHH and latitudinal gradients in plant defenses (Moles et al. 2011a, b). Some have argued that methodological issues, including when sampling occurs, leaf age and latitudinal extent of the survey, may account for lack of support (Anstett et al. 2016, Baskett and Schemske 2018). But many of the studies that reject the LHH are robust to these methodological concerns (Adams and Zhang 2009, Lynn and Fridley 2019). Additionally, if the mechanisms generating the LHH are as strong as hypothesized (Anstett et al. 2016), the pattern should be apparent regardless of leaf age and across spatial gradients associated with high turnover in the hypothesized environmental driver of the LHH (i.e. temperature). On the other hand, Zvereva and Kozlov (2019) found that past work has likely overestimated spatial turnover in herbivory rates because of methodologies prone to cognitive bias that find support for a given hypothesis, suggesting that past studies support the LHH more than is merited by empirical data. If instead the LHH lacks universality because it is context-dependent, then consideration of additional factors may help strengthen the predictive value of LHH theory (Moles and Ollerton 2016).

Few studies have framed the LHH explicitly in terms of energy and nutrient availability for plants and herbivores (Lynn and Fridley 2019), which limits the generality of past studies. Fundamentally, individuals in both plant and herbivore communities are converting assimilated energy in excess of that required for growth and maintenance into production of offspring (Brown et al. 1993, Chown and Gaston 2010, Fridley 2017). If we recast the LHH in terms of available energy for metabolic work, then higher rates of leaf consumption in the tropics are a result of higher available energy for

herbivores produced by plants in the warmer tropics (i.e. net primary productivity or NPP). However, energy availability is only one of several factors that play a role in both plant and animal productivity. For example, plant production is not solely limited by temperature, but varies spatially based on direct and indirect limitations set by energy (temperature/sunlight/ CO_2), water and nutrients (Harpole et al. 2011, Michaletz et al. 2014, 2018, Bracken et al. 2015). Further, herbivore populations and communities are dependent on the amount and nutritional quality of available plant matter for their metabolic requirements (Denno and Douglass 1986, Chown and Gaston 2010, 2016, Karban et al. 2012, Kaspari et al. 2017, Welte et al. 2019). Additionally, factors such as temperature are likely to influence plant (Rudgers et al. 2014, Fridley et al. 2016, Töpfer et al. 2018) and herbivore (Robinet and Roques 2010, Boggs and Inouye 2012, Murray et al. 2013) population production and fitness at different rates and time scales.

An interesting opportunity to test key predictions of this reframing of the LHH emerges in cases where plants and herbivores have different requirements for the same resource, so that it is limiting for one group, but not for the other. We call this uncoupled resource limitation. For instance, sodium (Na) is a key limiting resource for insect populations (Kaspari et al. 2008, Welte et al. 2019, 2020), but is much less important as a constraint on plant growth. Sodium concentration in plant leaves is often less than 0.1% by mass (Ovington 1956, Botkin et al. 1973, Singh and Singh 1991) and sodium can be toxic to plants at high concentrations by disrupting potassium channels for osmotic regulation (Kronzucker et al. 2013). Insect herbivores can have up to one-thousand times higher sodium content than plants (Cromack et al. 1977) and sodium plays a crucial role in their neural and muscular function (Clausen et al. 1991, Zakon 2012, Snell-Rood et al. 2014). This inequality in demand for sodium suggests that sodium can be a limiting factor for herbivore populations and that insects may dedicate time and energy towards sodium assimilation to maintain normal metabolic function (Kaspari 2020), especially given the relatively high turnover of sodium in animal tissues (Blair-West et al. 1968). Sodium foraging should thus be higher in low-sodium environments where it may limit insect fitness. Empirical support for the central role of sodium in the regulation of insect populations and communities is growing. For example: 1) sodium addition increased invertebrate abundance one standard deviation above that of control plots (Kaspari et al. 2017) and increased the positive effect of food and habitat (plant biomass) on insect abundance (Welte et al. 2019), 2) sodium bait use by ants, indicative of sodium limitation, increased in inland sites where sodium deposition is low (Kaspari et al. 2008), and finally 3) nectarivores are three times more likely to accept sodium solution than frugivores, likely because nectar is low in sodium compared to fruits (Ravenscraft and Boggs 2016). We propose that limiting uncoupled resources like sodium can disrupt the otherwise expected latitudinal trend in herbivory in at least two ways: their availability may be unrelated to latitude and associated

instead with proximity to resource sources like, in the case of sodium, oceans (Kaspari 2012), and their promotion of herbivore function may have little to negative effect on plant function.

Here, we propose and review methodological advancements and theory that refocusing the LHH around energy and nutrient availability will improve prediction of geographic variation in herbivory and resolve conflicting evidence of the existence of the LHH. We start with an empirical case study of how sodium may regulate insect herbivore consumption of plants. We hypothesize that 1) sodium is as a good predictor of geographic variation in herbivory as latitude, and 2) sodium may improve overall model performance and explain discrepancies in past tests of the LHH because of its specific geography (highest near coasts) and its clear benefit for herbivores while not affecting plants (i.e. an uncoupled constraint). We focus on sodium because a) micronutrients like sodium are underrepresented in past work which has focused on the role of macronutrients such as nitrogen and phosphorus in predicting geographic variation in herbivory (Lynn and Fridley 2019, Kent et al. 2020), and b) as an uncoupled constraint on herbivore (Snell-Rood et al. 2014) but not plant metabolism (Kronzucker et al. 2013), sodium has a high potential to explain deviations from LHH predictions. This is because sodium shortfalls may constrain herbivory rates in locales where conditions are otherwise optimal for plant and herbivore performance (e.g. high temperature, high plant production, Kaspari 2020). To test these predictions, we gathered datasets on herbivory from published studies and investigated whether sodium deposition rates across the world predicted herbivory rates compared to latitude, temperature and actual evapotranspiration (which is highly correlated with primary productivity globally). In congruence with the LHH, we expected higher herbivory towards lower latitude as available energy increases, but, given the important role of sodium in the regulation of insect herbivore communities, latitudinal patterns in herbivory are expected to be moderated by the availability of sodium. We focus on insect herbivory, as the LHH has been investigated almost exclusively as a plant-insect problem (Anstett et al. 2016), but note that much of what we apply to insects about sodium limitation applies to vertebrate consumers (Kaspari 2020).

We then discuss new research directions and methodologies that focus on energy availability (Brown et al. 1993) and nutrients (Kaspari and Powers 2016) to explain and predict variation in plant-herbivore interactions across geographic scales. This refocus on the biophysical constraints of herbivory and plant investment strategies generates novel alternative hypotheses for the mechanisms driving higher defense investment in the tropics. We then discuss how focusing on leaf area consumed versus mass consumed estimates of herbivory has hampered cross-species comparisons and theory development. We additionally develop a predictive, metabolic theory (Brown et al. 2004) treatment of the LHH made possible by reframing herbivory as mass and caloric transfer between trophic levels (Box 1).

Case study: Does sodium deposition improve predictions of geographic variation in herbivory?

Latitudinal herbivory data

We gathered data from published studies on latitudinal gradients in herbivory. On 6th July 2021, we performed a Web of Science search with the terms ‘herbiv*’ and ‘latitud*’ which returned 1211 articles to analyze for usable data. To be included, a study had to be peer-reviewed, purposively assessed a latitudinal gradient of within plant species leaf consumption, not part of a common garden study (i.e. natural populations), and express herbivory as percent leaf area damaged by herbivores. We focused on percent leaf area because it is the most used metric of damage in LHH studies. Additionally, we did not include studies that used damage categories (Barrio et al. 2017) where the percent area damaged is placed in categories such as 0, 0.1–1, 1–5, 5–25, 25–50, 50–75 and 75–100%. Studies that use this category system are internally consistent, but difficult to incorporate with data that assess damage continuously from 0 to 100% because: a) as an example, 50% damage in the category system can be represented by either 37.5% or 62.5% by taking the midpoints of each category (Barrio et al. 2017), which adds error and leads to a loss of information compared to continuous damage assessments, and b) categories make damage an ordinal variable rather than a continuous variable (with transformation) and require different statistics (Guisan and Harrell 2000). A detailed overview of selection and data processing from the studies can be found in the Supporting information. We incorporated herbivory data at the site \times species level (averaged across individuals of a species at a sampling location). For studies without published data but with figures and geographic metadata available (i.e. latitude and longitude), we extracted site means of herbivory and latitude using ImageJ and the figure calibration plugin (Schneider et al. 2012). Extracted values were then cross-referenced with geographic metadata of the study to assign proper geocoordinates. In total, 14 studies met our criteria and contained site-level leaf herbivory data for analysis. From each study, we gathered taxonomic data on the study organism (plant family and species names), year of measurement, site names, latitude and longitude (decimal degrees, WGS 84), percentage leaf area removed or affected by herbivory at the site level, and notes about the study or data processing. The final list of studies, making up a total of 301 site by species datapoints, used was: Adams et al. (2009), Salazar and Marquis (2012), Bravo-Monzón et al. (2014), Kim (2014), Lehdal and Ågren (2015), Wang et al. (2016), Feller et al. (2017), Kooyers et al. (2017), Baskett and Schemske (2018), Rivkin et al. (2018), Hahn et al. (2019), Loughnan and Williams (2019), Lynn and Fridley (2019) and Kent et al. (2020).

Sodium deposition and temperature data extraction

We used sodium deposition data from the World Data Center for Precipitation Chemistry (WDCPC, <<http://wdcpc.org>>)

detailed in Vet et al. (2014). Data were derived from the 2001 Hemispheric Transport of Air Pollution ensemble mean model results for total wet and dry deposition of sea salt in kg/hectare/year (hereafter, sodium deposition). We used sodium deposition because it likely better represents sodium availability in the system over soil sodium content, given soil sodium can be unavailable in rock or immobile in drier regions. Additionally, other global estimates of soil sodium are in percent estimates of available cation exchange capacity rather than direct estimates of sodium on a g/area basis that may be usable by consumers (Batjes 2016). We used the *raster* package (Hijmans 2021) to create a grid of sodium deposition with a 1° resolution in R (<www.r-project.org>) and used the geographic coordinates of the herbivory study sites to sample sodium deposition. We gathered temperature data averaged over 1970–2000 from the WorldClim Bioclimatic variable dataset (Fick and Hijmans 2017). We used data on mean annual temperature (MAT, bioclim1) at a 10-minute resolution and similarly extracted herbivory site specific values. Finally, we took climate normal actual evapotranspiration data (AET, mm summed over the year) from the TerraClimate project (Abatzoglou et al. 2018). AET is highly positively to plant productivity (Fisher et al. 2011) and, therefore, potential productivity available to consumers.

Analyses

Prior to analysis we logit transformed herbivory data, given it is expressed as a percentage/proportion of leaf area which violates normality assumptions (Warton and Hui 2011). Herbivory data were adjusted by 0.01 prior to analysis to avoid 0s and 1s becoming negative and positive infinity, respectively. We also standardized predictor variables (latitude, sodium deposition, MAT and AET) to a mean of zero and standard deviation of 0.5 to allow comparison of their coefficients as effect sizes. Prior to standardization, we took the absolute value of latitude (avoids negative values from southern hemisphere) and natural log of sodium deposition.

We compared the predictive ability of latitude to 1) temperature (MAT) as the underlying abiotic gradient hypothesized to be driving much of the geographical variation in herbivory, 2) plant productivity (represented by AET) as an estimate of available energy for herbivores to consume and 3) sodium deposition as our novel hypothesis that increased sodium deposition releases herbivore communities from sodium limitation and increases herbivore damage. We constructed hierarchical Bayesian models (Hobbs and Hooten 2015) accounting for phylogenetic signal (Villemereuil et al. 2012, Frank et al. 2017) that linearly predict site herbivory as:

$$\text{herbivory}_i \sim N(\mu_i, \sigma^2)$$

$$\mu_i = \beta_0 + \beta_1 x_i + N(0, \sigma^2_{\text{species}}, \Sigma) + N(0, \sigma^2_{\text{study}})$$

where herbivory of a site, i , is a normally distributed random variable with mean, μ_i and variance, σ^2 . Each of the x_i predictor variables (latitude, sodium deposition, MAT, AET) were used in separate models to predict herbivory linearly (intercept β_0 , slope β_1). The remaining terms are group-level random-variance terms for plant species ($\sigma^2_{\text{species}}, \Sigma$, $n = 20$) and the study (σ^2_{study} , $n = 14$) from which the data were gathered. The species random-variance term incorporated phylogenetic relatedness with a variance–covariance matrix (Σ) of shared branch lengths between species (Villemereuil et al. 2012). We used the ALLMB phylogeny from Smith and Brown (2018), shown in the Supporting information. We estimated Pagel's lambda (λ), where values close to zero indicate phylogenetic independence and values close to one indicate Brownian evolution (Table 1).

All priors were vague/uninformative with normal priors for slope and intercept terms ($N(0, 1E-6)$), a multivariate normal prior for the species random effect, gamma priors for variance terms ($\Gamma(0.001, 0.001)$) and uniform Pagel's λ priors ($U(0, 1)$). Additionally, we investigated a model of the interactive effects of sodium deposition and MAT following the specification above but with additional slope terms for the added linear terms. Finally, we fit an intercept-only model to test if the above models improved prediction over the simplest model possible.

Models were parameterized with JAGS (Plummer 2003) in the 'R2jags' package (Su and Yajima 2021) using R (<www.r-project.org>). All models were run on three chains for at least 100 000 iterations with a 50 000 burn-in or until the Gelman–Rubin statistic was close to one ($\hat{R} < 1.01$; Gelman and Rubin 1992). Unique parameter estimation and good mixing were inspected with traceplots. We investigated two posterior predictive checks. First, we plotted the residual sums of squares (SSQ) for the observed data against the SSQ of data simulated by the models. Good fitting models have points falling on a 1:1 line, suggesting that the data simulated by the model has a similar error structure to the observed data. Second, we calculated Bayesian 'p-values', which assess the proportion of model runs with SSQ of the observed data greater than SSQ of the simulated data (Gelman et al. 1996). Values around 0.5 indicate adequate model fit (Table 1). We compared models based on Watanabe–Akaike information criterion (WAIC) and leave-one-out cross-validation (LOOCV), which are appropriate for hierarchical models (Hooten and Hobbs 2015). We used the 'loo' package (Vehtari et al. 2020) to calculate the criterion. We additionally report 'Bayesian R^2 ' values (Gelman et al. 2019). Code for the analyses can be found on GitHub (<<https://github.com/jslynn33/Biophysical-Constraints-Herbivory-Review>>).

Results

Leaf herbivory decreased towards higher latitudes and increased with higher sodium deposition and MAT, but was unrelated to AET (Fig. 1), supporting all except our AET hypotheses. Additionally, models of the interactive effects of MAT and sodium deposition suggest that both limit the

Table 1. Model selection results comparing predictors of variation in herbivory. Lower WAIC or LOOCV values indicate lower within sample predictive error. Δ WAIC and Δ LOOCV are the differences in information criterion between a given and best model. 'Bayesian p-values', assess if data generated from the model have similar residual error to the observed data. Bayesian p-values close to 0.5 represent a properly fitting model. Pagel's λ quantifies phylogenetic signal in herbivory across species with uncertainty (standard deviation) in parentheses. 'Bayesian R^2 ' is a Bayesian approximation to the coefficient of determination (not estimated for the intercept-only model).

Model	WAIC	Δ WAIC	LOOCV	Δ LOOCV	Bayesian p-value	Pagel's λ	Bayesian R^2
MAT \times Na	729.0	0.0	729.3	0.0	0.498	0.491 (\pm 0.260)	0.116
Latitude	733.2	4.2	733.4	4.1	0.498	0.611 (\pm 0.293)	0.094
MAT	734.2	5.2	734.4	5.1	0.498	0.572 (\pm 0.298)	0.077
Na	735.0	6	735.2	5.9	0.498	0.504 (\pm 0.288)	0.066
Intercept only	744.9	15.9	745.1	15.8	0.501	0.627 (\pm 0.300)	
AET	746.5	17.5	746.7	17.4	0.500	0.601 (\pm 0.303)	0.006

amount of herbivory observed across the globe, and that herbivory increases with MAT are limited unless there is also an increase in sodium deposition and vice versa (Fig. 2). Model selection suggested herbivory is best predicted by the interactive effects of MAT and sodium, with very little difference (< 2 WAIC or LOOCV) in predictive ability between latitude, MAT and sodium deposition (Table 1). All predictors were an improvement over an intercept-only model except AET (Table 1). Finally, Pagel's λ varied between 0.49 and 0.63 depending on the model, suggesting there was moderate phylogenetic signal in leaf area consumed across species, but there was high uncertainty associated with these estimates (SD = 0.3, Table 1).

These results point to a few conclusions: 1) latitude and temperature as representations of energy availability are necessary but insufficient for explanations of geographic variation in herbivory, and 2) factors that limit one side of the trophic interaction (e.g. sodium) can be as important in limiting herbivory as factors that promote productivity for both consumers and producers (e.g. MAT), as reflected by the interaction model. Most surprising is that sodium aerosol deposition alone predicted variation in herbivory when we were unable to consider bioavailable sodium in the soils and no study considered sodium availability or deposition a priori in their sampling design. Three alternative hypotheses for the predictive ability of sodium deposition would be that: 1) it

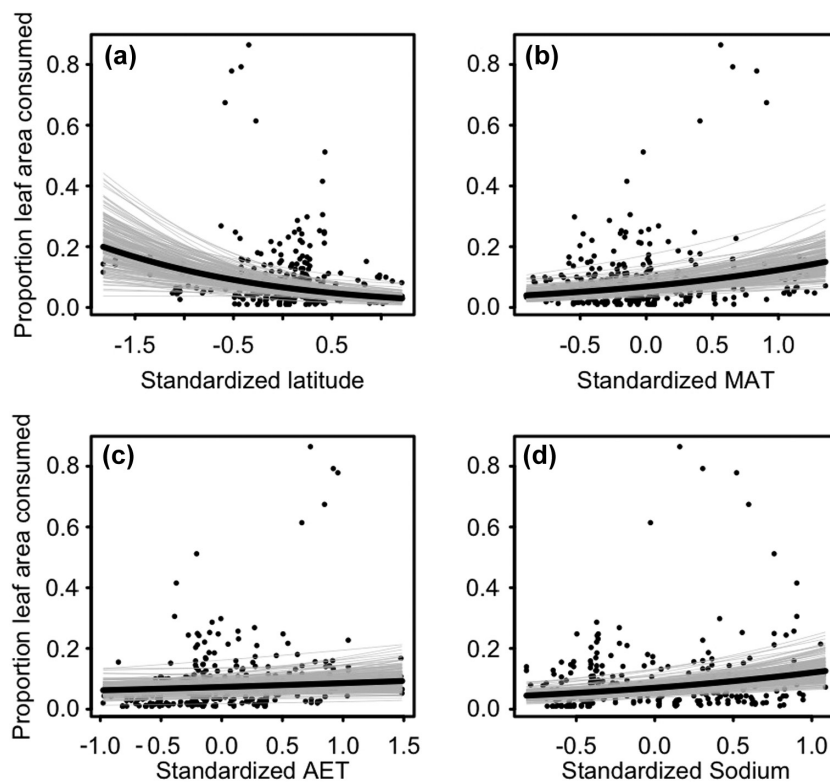


Figure 1. Patterns of herbivory with latitude (a), mean annual temperature (MAT, b), actual evapotranspiration (AET, c) and sodium (Na) deposition (d) with data for proportion leaf damage averaged for a site ($n = 301$). Solid lines represent the mean of the posterior with gray lines as 200 independent draws of slope and intercept terms from the posterior distribution. All predictor variables were standardized for the analyses. Lines appear to have curvature from logit back-transformations.

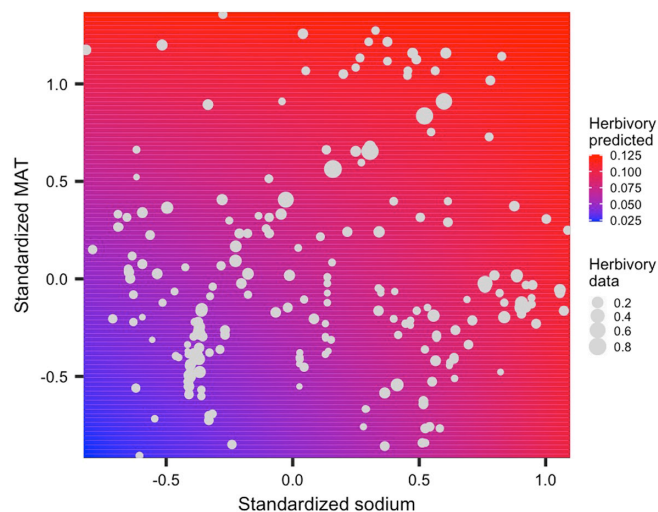


Figure 2. Heatmap plots of how mean annual temperature (MAT) interacts with sodium (Na) deposition to predict amount of herbivory damage averaged for a site ($n = 301$). Warm colors (red) indicate higher predicted herbivory while cooler colors (blue) indicate less predicted herbivory. Gray points represent the mean of observed site herbivory by varying in size. All predictor variables were standardized for the analyses.

also represents climate stability along coasts over continental, low sodium deposition areas, 2) sodium deposition represents higher annual precipitation, and 3) which applies to all the variables investigated here, this correlational approach may capture the influence of other drivers (e.g. calcium) of geographic variation in herbivory that happen to be correlated with the drivers used in these analyses. Explanations (1) and (2) seem unlikely given that we found weak evidence that sodium deposition was correlated with either diurnal temperature range ($r > -0.54$) or isothermality ($r < 0.11$), which are measures of climate stability, or annual precipitation ($r < 0.29$). For the third explanation, this is a possibility with all correlative studies, but our approach of strong a priori hypotheses challenged with data should engender confidence in the results. We note that controlled experiments are required to formally test the hypotheses supported by this analysis. Additionally, we had no data on sodium concentrations in soil or leaf tissue, where past work suggests plants' leaf sodium concentrations increase with soil sodium (Doughty et al. 2016) and high sodium leaves have greater herbivory (Welti and Kaspari 2021). We expand on these results below and point to other methodological improvements and theory (Box 1) that may improve predictability of geographic variation in herbivory.

Temperature and uncoupled resources determine geographic variation in herbivory

The underlying mechanism hypothesized behind geographic variation in herbivory is that the abiotic environment, mainly

temperature, acts as less of a selective force on plant and herbivory populations in the tropics than in higher latitude systems (Dobzhansky 1950, MacArthur 1972). That higher temperatures increase metabolic rates and are more conducive to biological activity in the tropics is uncontroversial (Brown 2014), but temperature alone does not limit biological activity. Context-dependency in plant–herbivore interactions is a rule (Chamberlain et al. 2014, Lynn et al. 2019) and applies to the LHH as much as it applies within communities or landscapes. It takes at least 25 different elements to build an organism and any one may be scarce enough to limit biological activity (Kaspari 2012, Kaspari and Powers 2016). The LHH should be reframed conditionally: consumption rates of plants by insects increases from high to low latitudes if temperature is limiting rates of consumption (Box 1). Temperature is critically important for controlling biological rates and so the conditional LHH often holds (Coley and Barone 1996, Moreira et al. 2015, Baskett and Schemske 2018). But a conditional LHH also suggests that studies rejecting the LHH are to be expected and are not methodologically flawed (Anstett et al. 2016) – they have identified systems where temperature is not limiting consumption rates (Moles et al. 2011a). This conclusion is supported by our result that herbivory is limited by both temperature and sodium deposition in concert.

Resource limitation can be uncoupled between plant and herbivore communities. We hypothesized that sodium would limit herbivory globally, which was supported. Specifically, in high temperature areas where the LHH predicts higher herbivory, we found evidence that sodium deposition limited the amount of herbivory. Given that sodium is often toxic to plants (Maathuis 2014) but critical for insect development (Snell-Rood et al. 2014, Kaspari 2020), this result is evidence that uncoupled nutrient requirements between plants and their herbivores can influence global patterns of herbivory. The LHH will not hold where uncoupled resources dominate and limit one side of the trophic interaction. Experimental work in a temperate grassland community demonstrates the uncoupled limitations of plants and their insect herbivores: adding nitrogen and phosphorus greatly increased plant biomass but had no effect on orthopteran abundance unless paired with sodium addition, which almost doubled orthopteran abundance (Prather et al. 2018). This aligns with our result that AET, as an estimate of plant productivity, was unrelated to herbivory while higher sodium deposition related to higher herbivory, suggesting insects are generally mineral nutrient and not carbohydrate limited. Additionally, there is evidence that macronutrient addition (NPK) across grasslands globally leads mammal herbivores to preferentially prey upon plants with higher leaf sodium (Borer et al. 2019). Early evidence further suggests sodium addition across four grasslands increases consumption by herbivores and fungal pathogen damage over controls (Welti and Kaspari 2021). However, a globally distributed experiment with sodium addition across natural sodium gradients is required to fully assess the role of sodium limitation in driving patterns of plant consumption by insects.

Box 1. Room for more theory?

Theory development around the LHH has been lagging, likely because of the disagreement around the existence of the pattern and lack of communication across fields. However, there are several theoretical developments that could be applied to the hypothesis. For instance, O'Connor et al. (2011) developed models that apply Arrhenius temperature dependence to predator-prey abundance models and Gilbert et al. (2014) developed a temperature dependent version of the classical Rosenzweig and MacArthur (1963) consumer–resource models. However, these models rely on estimates of parameters such as carrying capacity (K), which are difficult to estimate in the field (Sayre 2008). Additionally, the models ignore the mass-dependence of metabolic rates, where the underlying body size distributions of the interacting plant and herbivore communities can alter predictions (Osmond et al. 2017).

An intuitive next step could apply the metabolic theory of ecology (MTE, Brown et al. 2004, Sibly et al. 2012) to how temperature and body mass of plants and herbivores interact to determine rates of transfer between trophic levels (Burnside et al. 2014). Here, we see the advantage of switching to a mass-based assessment of herbivory for theory development, where rates of consumption expressed as mass with caloric value can be predicted by body size and temperature. Past work overwhelming supports the necessity of both MTE and stoichiometric theory for predicting herbivory in various ecosystems (Hillebrand et al. 2009, Moorthi et al. 2016). As a first step for applying prior MTE advances (Brown et al. 2004, Sibly et al. 2012, Schramski et al. 2015) to the LHH, energy flux (consumption rate) is given by:

$$C = C_0 M^0 e^{-E/kT} [R]$$

where mass-specific consumption rate (C, in g year⁻¹) scales with a normalization constant (C₀), insect community biomass (M) and Arrhenius temperature dependence (e^{-E/kT}) in a given locale. This portion of the equation is an MTE formulation of the LHH: consumption rates increase with temperature and therefore from the poles to the tropics, given equivalent mass of insect communities. However, consumption is also dependent on [R], or resources supply rate (reviewed by Cross et al. 2015), which can include plant productivity and sodium. [R] can additionally be expanded to handle colimitation of resources by assessing the shape of response surfaces across natural gradients of hypothesized limiting resources (Sperfeld et al. 2016). This is the conditionally reformulated LHH: consumption rates are moderated by the nutrient availability in the system. Additionally, the normalization constant (intercept on a log–log scale) can vary in predictable and biologically meaningful ways (Niklas and Hammond 2019), such as the taxonomic and trait make-up of the interacting communities (e.g. defense traits, feeding guilds). This is a surface-level treatment of MTE to the LHH, but a more thorough and empirically tested application could be invaluable in generalizing and predicting variation in herbivory across space.

What about defense?

Assessments of the geography of nutrient limitation may also help to resolve controversies around latitudinal variation in plant defense. Investment in defense is not entirely determined by interactions with herbivores: it is also dependent on resource availability (Coley et al. 1985). The resource availability hypothesis (RAH) states that species from high resource environments have low defense investment and high growth rates to compensate for resources lost to herbivory, while species from low resource environments invest in defense to protect limiting resources from herbivory and other forms of tissue loss, leading to lower growth rates (Coley et al. 1985, Endara and Coley 2011). The RAH is widely supported (Endara and Coley 2011), though its application to intraspecific variation in defense requires further investigation (Hahn and Maron 2016). Applying the RAH to the LHH generates several new insights.

First, temperature is not a resource, but a measure of kinetic energy. When a plant is eaten, it does not lose temperature, it loses resources such as sugars, water and proteins.

Though temperature generally increases plant growth rates (Körner 2015) which is associated with compensatory growth strategies, it is unintuitive how natural selection would drive trait evolution that limits the loss of temperature from plants to herbivores. If temperature per se is an unlikely driver of plant investment in defense strategy, the RAH predicts that differences among species and communities across latitudes are driven by differences in limiting mineral nutrients, precipitation or resources related to plant growth other than temperature. Therefore, assumptions that lower latitudes and elevations, geographical gradients generally associated with temperature, are higher resource environments may not be valid (Hahn and Maron 2016).

Considering the RAH with respect to latitudinal defense patterns necessitates a reassessment of the causal mechanisms of latitudinal and geographic defense gradients. Dobzhansky (1950) suggested that, given a more stable temperature environment in the tropics, organisms are under greater selective pressure from diverse natural enemies in the tropics compared to temperate regions where a harsh climatic environment poses the greatest selective pressure (note, the tropics

do experience seasonal precipitation). However, Dobzhansky (1950) also discussed how the tropics have been geologically stable compared to temperate regions during the last glacial maximum. This geological stability means tropical soils have experienced less mechanical weathering and are phosphorus-poor compared to temperate regions (Wardle 2004, Huston 2012, Augusto et al. 2017). Applying the RAH suggests that latitudinal gradients of increased defense towards the tropics could be caused not by a more stable temperature environment, but by high selective pressure for greater plant defense investment against losing phosphorus and water/leaf desiccation during the dry season. Though broad generalizations of nutrient availability of temperate versus tropical environments are valid, spatial patterns of nutrient availability are highly variable on multiple spatial scales (Kaspari and Powers 2016). This variation makes it difficult pick a resource gradient to sample a priori and assess the role of nutrient variability in prior studies of latitudinal defense gradients. The two hypotheses for what may cause latitudinal trends in defense traits are not mutually exclusive, but little attention has been paid to the resource availability alternative that may be driving patterns attributed to a more climatically benign environment in the tropics and explain deviations from the expected latitudinal defense pattern (Box 1).

There is some support of the RAH from studies of intraspecific variation in defense traits across latitudes. For instance, Pratt et al. (2014) found that leaf terpene concentrations in plants grown in a common garden decreased from low to high precipitation of the populations' origin, suggesting populations from low-stress environments tolerated herbivory better compared to populations from high-stress environments. Along the same lines, Moreira et al. (2018) found that leaf tannins in *Quercus robur* decreased with higher precipitation across latitudes. Though not latitudinally explicit, prior work within tropical (Fine et al. 2006) and sub-tropical (Cunningham et al. 1999) systems suggests that species from more nutrient-poor habitats invest more in defense. More data on how consumable limiting resources, especially phosphorus, influence latitudinal intraspecific variation in defense are needed, especially if they are paired with plant growth rates to fully assess the RAH (Coley et al. 1985, Hahn and Maron 2016).

Sodium will influence patterns in plant defense as well. Deviations from RAH predictions (intra- and interspecific) are predicted where conditions for plant growth are optimal but uncoupled from sodium limitations on consumers. As a hypothetical example, take an environment that is optimal for plant growth where the RAH predicts plants would tolerate herbivory, but there is also high sodium availability effectively supplying herbivores with unlimited food (biomass production) and resources. Selective forces of herbivores on plants may switch to favor resistance strategies in such environments. However, sodium stress or toxicity for plants may drive more resource conservative leaf strategies (Wright et al. 2004), which is another sodium-based mechanism for resistant strategies in plants. Sodium may also directly influence plant defense (Kaspari 2020). For instance, plants that are

less salty than their neighbors may experience limited herbivory (Freeland et al. 1985). Sodium-mediated plant–herbivore interactions and how they drive patterns in defense investment is a promising area for future research.

Is herbivory being appropriately quantified to test the LHH?

Leaf damage is mostly measured as percent leaf area lost or damaged by herbivores in studies assessing the LHH. This captures one negative impact of herbivory to plants—loss of leaf area for light capture and carbon assimilation. However, a focus on percentage leaf area removed ignores the mass of tissue and nutrients lost by the plant and gained by the herbivore. Given the LHH is predicated on higher temperature and energy availability in the tropics (Dobzhansky 1950), then the more direct measure of caloric energy transfer between plant and herbivore is mass. Percent leaf area consumed can be used to estimate mass consumed (Těšitel et al. 2021) by also measuring specific leaf area (SLA, Pérez-Harguindeguy et al. 2013). SLA relates leaf area for light capture to dry mass investment (leaf area in m²/leaf dry mass in g). By sampling damaged leaves and calculating their SLA, one can back calculate the mass consumed by herbivores with:

$$M_c = (A_c \times M_s) / A_s$$

where M_c is the mass consumed (c) by herbivores and M_s is the mass of the sampled (s) leaf used for SLA measurements (both in g). A_c is the estimated area of the leaf consumed from reconstruction with image analysis or by applying visual estimates of percent leaf area consumed to the measured remaining area, and A_s is the area of the sampled leaf for SLA measurements (both in m²).

To demonstrate this point (Fig. 3), we used SLA and leaf damage estimate data from a previously published article (Lynn and Fridley 2019) that assessed latitudinal variation in herbivory on *Solidago altissima*. The study sampled 20 populations spanning over 10° of latitude. We assessed variation between populations in how estimates of percent leaf area damage translated to total leaf area consumed (Fig. 3a), leaf mass consumed (Fig. 3b) and the relation of leaf mass versus leaf area consumed (Fig. 3c). When we consider intraspecific variation in leaf investment, an estimate of 20% herbivory can translate to ~0.5–2.5 cm² of leaf area consumed (Fig. 3a), ~0.005–0.020 g of leaf mass consumed (Fig. 3b) and a given estimate of leaf area consumed can translate to variation of over 2-times the leaf mass consumed across populations (Fig. 3c). Using percent leaf area to test the LHH is intuitive because it relativizes consumption to the amount of leaf area present to be consumed, but it clearly obscures important variation in what is lost by the plant and gained by the herbivore.

There are several considerations when using this method to estimate consumed mass. First, herbivores (specifically

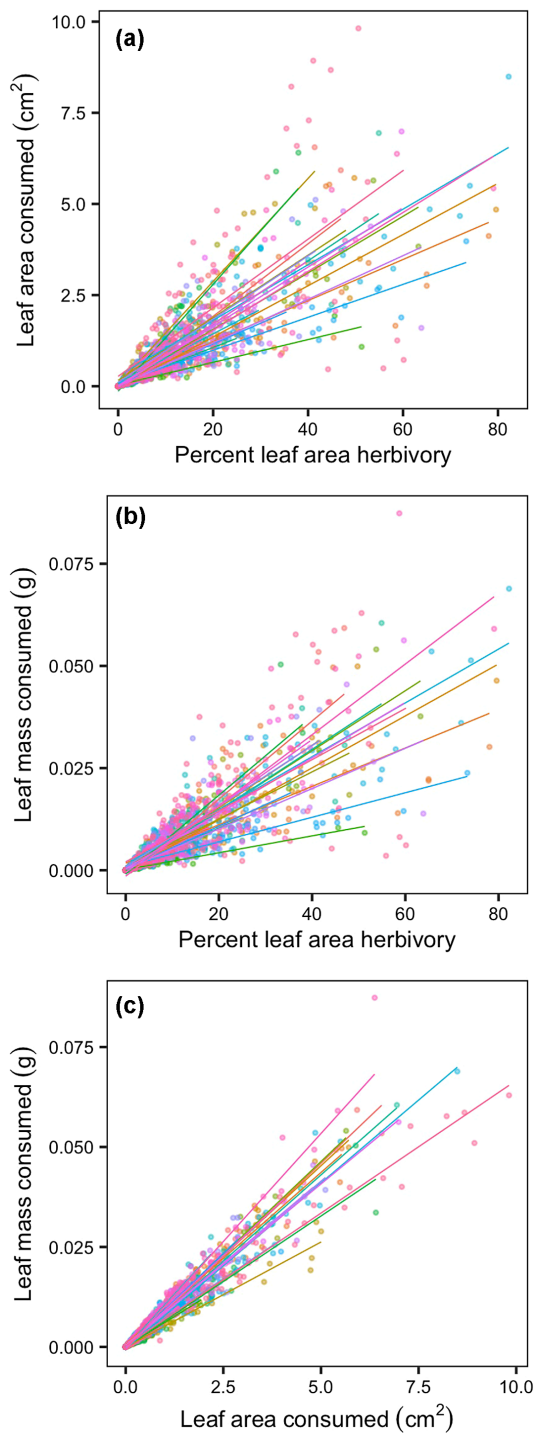


Figure 3. Percent leaf herbivory translates to different area and mass consumed depending on the leaf area to dry mass ratio (specific leaf area or SLA). Each color represents one of the 20 populations of *Solidago altissima* sampled in a latitudinal survey of herbivory described in Lynn and Fridley (2019). Lines were fit with least squares regression. (a) Shows variation among populations in how percent area translates to total leaf area consumed, (b) shows variation in how percent leaf area herbivory translates to leaf mass consumed and (c) shows how variation in leaf mass investment per unit leaf area may lead to different cross species interpretations of the costs of herbivory.

insects) may avoid leaf veins and consume the fleshier leaf lamina (Malishev and Sanson 2015). If this is the case for a set of leaves, one can calculate SLA on a hole punch of the leaf lamina that will more accurately reflect the mass consumed. Second, this same logic should apply to damage by leaf miners (Sinclair and Hughes 2010) and sucking herbivores (Bernays 1998), given the leftover parts of the leaf are accounted for in the mass-loss estimation. Third, plants may have induced responses to herbivory, where the chemical and physical properties of leaves change in response to herbivore damage (Karban and Myers 1989, Agrawal 1998, Barton 2016). This may imply that the SLA of a leaf after damage does not reflect the SLA of the leaf when first damaged. Another option is to use the SLA of an undamaged leaf as the reference to calculate mass consumed. Finally, SLA tends to be positively associated with leaf digestibility (Cornelissen et al. 2004, Pontes et al. 2007), such that the same consumed mass of a low SLA leaf will be less digestible (e.g. more lignin, less soluble sugars) than a high SLA leaf. This ultimately needs to be measured for a full understanding of how mass and area translate to nutritional quality for herbivores.

The use of a mass-based rather than percentage area-based assessment of herbivory has several advantages for assessing the LHH. First, interspecific variation in leaf area spans tends to increase towards lower latitudes (Wright et al. 2017), which can complicate cross-species latitudinal patterns where the same percentage area consumed does not translate to the same mass or area of herbivory. Second, intraspecific variation in SLA appears to be greater than intraspecific variation in leaf area both within and across communities (Siefert et al. 2015), suggesting that the same leaf area percentage across individuals and locations will not represent the same mass consumed by the herbivores (Fig. 3c). Third, young and expanding leaves have higher percentage herbivory than mature leaves, possibly because they are less dense and defended (Coley and Barone 1996, Baskett and Schemske 2018). But herbivory on a mass basis between mature versus expanding leaves may be similar because a larger area of the less dense expanding leaf is required to obtain the same resources as a mature leaf. Fourth, robust comparisons of rates of herbivory across biomes have been impeded by questions around leaf-lifespan (Zhang et al. 2017), where standing damage in tropical and boreal systems may represent years of accumulated damage versus seasonally deciduous temperate systems (Coley and Barone 1996, Lim et al. 2015). Given that SLA is strongly negatively correlated with leaf-lifespan (Wright et al. 2004) at global scales (Messier et al. 2017), incorporating mass investment per area loss may assist the interpretation of cross-biome comparisons when tracking herbivory over time is not possible. The HerbVar Network (<<http://herbvar.org/>>) has developed protocols that mark a clear improvement in accounting for leaf number and plant size and can easily be adapted to estimate leaf mass consumption by additionally sampling leaves for SLA and can aid in cross-species and cross-system comparisons.

The above suggests there is error in herbivory measurements based on percentages, and given the controversy

around the LHH (Anstett et al. 2016, Moles and Ollerton 2016, Zvereva and Kozlov 2019), more thought on what is measured and its meaning is warranted. As many researchers have noted, the optimal test of the LHH would require an assessment of herbivory on whole plant communities rather than focusing on particular species (Coley and Barone 1996, Lim et al. 2015, Anstett et al. 2016, Baskett and Schemske 2018, Rheubottom et al. 2019, Zvereva et al. 2020). The arguments above suggest simply calculating community damage by percentage leaf area lost will misrepresent the amount of herbivory across and within communities by not considering variation in leaf investment. This is especially important from the herbivores' perspective, where mass and quality (i.e. proteins, nutrients) of plant tissue consumed determine herbivore performance (De Bruyn et al. 2002, Wetzal et al. 2016). Additionally, a mass-based estimate of herbivory roots the problem in measurements that can be integrated into theory. For instance, the metabolic theory of ecology would predict rates of biomass consumption increase with temperature and biomass of the herbivore community, but consumption is also dependent on limiting resource supply (Box 1).

Conclusions

We advanced several intersecting avenues of future research that can move the study of geographic patterns of herbivory beyond the recent controversy (Anstett et al. 2016, Moles and Ollerton 2016, Zvereva and Kozlov 2019) by refocusing on the biophysical constraints of plant–herbivore interactions. Though methodology and cognitive bias may lead to false-negative or false-positive support for the existence of latitudinal gradients of herbivory, a conditional reframing of the hypothesis can put disparate results into context: rates of herbivory increase towards the tropics with warmer temperatures given other constraints are weak. Sodium may be a key limiting resource for herbivore communities that has little or negative effects on plants, and sodium deposition, especially in combination with temperature, is an equal and possibly better predictor of geographic patterns of herbivory than latitude. The importance of sodium may lie in its uncoupled effects between trophic levels because sites where all other constraints (e.g. temperature, nitrogen, etc.) are favorable for both plant and insect communities may lack enough sodium for insects to maximize consumption rates. Refocusing on constraints outside of temperature has important ramifications for the study of latitudinal defense gradients as well, suggesting that higher defense in the tropics is driven by chronic phosphorus limitation on weathered tropical soils. Additionally, focusing on percent leaf area rather than biomass consumed can confound interpretation of geographic patterns. Future work can overcome this issue by measuring the specific leaf area of partially consumed leaves and back calculating the amount of leaf mass consumed. This will open opportunities for theory development around geographic variation in herbivory based on first principles, such as the metabolic theory of ecology (Box 1).

How rates of plant consumption by herbivores vary over geographic space is still a fascinating question. The lack of consensus around the hypothesis should not be met with discouragement. Given the complexity of different plants with different defenses interacting with different insect communities across different sites with different resource limitations, support in any given study for the latitudinal herbivory hypothesis is surprising and serves as a testament to how strongly temperature regulates biological rates. We propose that this 'zombie idea' (Moles and Ollerton 2016) can be cured by a conditional reformulation and embracing the complexity that comes with procuring the right mixture of elements to build organisms (Kaspari and Powers 2016).

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Author contributions

Joshua S. Lynn: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jason D. Fridley:** Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Vigdis Vandvik.** Conceptualization (supporting); Funding acquisition (supporting); Supervision (supporting); Writing – review and editing (supporting).

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Supporting information

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

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