

Global Biogeochemical Cycles^{*}

RESEARCH ARTICLE

10.1029/2024GB008367

Key Points:

- Insect herbivores release more nutrients in warmer and drier forests, with temperature effects being stronger than precipitation effects
- Insect herbivory and nutrient flux trends are more variable at local scales, with minor effects of successional stage or soil substrate age
- Changes in insect-mediated nutrient fluxes are primarily driven by foliar biomass production and leaf-level herbivory

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:

Hwang, B. C., Giardina, C. P., Barrios-Garcia, M. N., Diao, H., Duboscq-Carra, V. G., Hemp, A., et al. (2025). Insect herbivory releases more nutrients in warmer and drier forests. *Global Biogeochemical Cycles*, 39, e2024GB008367. <https://doi.org/10.1029/2024GB008367>

Received 19 SEP 2024

Accepted 12 MAR 2025

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Insect Herbivory Releases More Nutrients in Warmer and Drier Forests

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Abstract Climate, forest successional stage, and soil substrate age can alter herbivore communities and their effects on biogeochemical cycling, but the size and spatial variability of these effects are poorly quantified. To address this knowledge gap, we established a globally distributed network of 50 broadleaved old-growth forests across six continents, encompassing well-constrained local-scale gradients in mean annual temperature (MAT), mean annual precipitation (MAP), succession, and soil substrate age. We used this network to investigate how these variables impact insect foliar herbivory and the associated carbon, nitrogen, phosphorus, and silica fluxes in forest ecosystems. Over 1 to 2 years, we measured stand-level foliar biomass production, leaf-level herbivory, and foliar element concentrations. At the global scale, insect herbivores liberated higher amounts of elements from the canopies of warmer and drier sites than those of cooler and wetter sites with patterns for phosphorus being most pronounced. MAT exerted a stronger influence over insect-mediated element fluxes than MAP. Foliar biomass production and leaf-level herbivory responses to MAT and MAP were mainly responsible for the observed changes in insect-mediated element fluxes; we also observed minor effects of foliar phosphorus concentration on phosphorus fluxes. Local-scale trends were mixed and successional stage or soil substrate age did not appear to influence insect herbivore-mediated element fluxes. These results demonstrate that climate effects on plant-herbivore interactions are stronger at large than small scales, at which herbivory rates and nutrient fluxes appear to be more strongly affected by a diversity of non-climate factors.

Plain Language Summary Climate changes and soil development can affect herbivore populations and their influence on nutrient cycles, but the exact size and variability of these effects are unclear. We set up a network of 50 old-growth broadleaved forest sites across six continents to study how temperature, precipitation, succession, and soil substrate age impact insect herbivory and nutrient release, including carbon, nitrogen, phosphorus, and silica. We found that insects released more carbon and nutrients from the canopy in warmer, drier forests, with temperature having a stronger impact than precipitation. At the local scale, the results were more variable, and successional or soil development played a smaller role in carbon and nutrient cycling mediated by insect herbivores. This shows that large-scale climate factors are key drivers, while local factors add complexity to herbivore effects on forest biogeochemical cycling.

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1. Introduction

Insect herbivores mediate an important biogeochemical exchange between plants and soil by (a) consuming foliage and releasing essential nutrients from element-rich green leaves directly to the soil as excreta, cadavers, and unconsumed leaf fragments, and (b) accelerating leaf abscission and leaching (Bardgett & Wardle, 2010; Hartley & Jones, 2008). Insect deposits often contain higher concentrations of labile nutrients than senesced leaf litter, and in some forests, fluxes of nutrients derived from these deposits can rival or surpass fluxes of labile nutrients derived from atmospheric deposition or bedrock weathering (Hartley & Jones, 2008; Hwang et al., 2024b; Metcalfe et al., 2014). In the absence of herbivory, senescence-driven abscission is preceded by efficient resorption of most foliar nutrients (Vergutz et al., 2012). In the presence of herbivores, nutrients from consumed green leaf material are released during and following herbivory before resorption can take place—with nutrients that to some extent would otherwise have remained unavailable to competing plants and the larger soil community (Lovett et al., 2002).

The impacts of insect herbivory on plant-soil element fluxes are influenced by several factors, including the composition of the herbivore community, the rate of herbivory, the plant species affected, and the degree of nutrient limitation to plant productivity (Bardgett & Wardle, 2010; Hartley & Jones, 2008). For instance, boreal forests are often significantly constrained by the availability of nitrogen (N), while tropical forests are particularly limited in phosphorus (P). In these ecosystems, insect herbivory can potentially enhance plant-soil nutrient fluxes, thereby altering the nutrient limitations that regulate plant growth (Johnson & Turner, 2019; Kaukonen et al., 2013; Weintraub, 2011). Interactions with other elements are not as well understood. For instance, the impact of herbivory on silicon (Si) fluxes in natural settings is understudied even though Si is important for plant functioning and defense as well as biogeochemical cycling (Hwang & Metcalfe, 2021).

Climate impacts on forest productivity and nutrient cycling depend on the climate variable of interest as well as biotic and other abiotic conditions at a site (Balzotti & Asner, 2018; Bonan, 2008; Schuur, 2003). A classic meta-analysis of forest warming experiments (Rustad et al., 2001) reported that warming increases N cycling and availability, with more recent work along an elevation gradient showing that variation in temperature sensitivity can be high across elements (Litton et al., 2020). How relationships between physical (e.g., soil, climate) and plant community properties (e.g., productivity, foliar chemistry) drive regional patterns also remain unclear (Anstett et al., 2016; Endara & Coley, 2011). While variation in biotic and abiotic conditions explain biogeochemical heterogeneity at multiple scales, the contributions of herbivory to this heterogeneity are understudied.

Temperature effects on insect herbivores (e.g., abundance, development, activity) are highly variable across plant-herbivore pairs and across ecosystem types, with limited research showing the full range of positive, negative, and no response to warming (Bale et al., 2002; Lemoine et al., 2014; O'Connor, 2009; Warlo & Kautz, 2024). This variation may relate to water availability (Brenes-Arguedas et al., 2009; Hamann et al., 2021) or to deleterious effects of warming for insect species with narrow thermal tolerances as found in the tropics (Bauerfeind & Fischer, 2013; Deutsch et al., 2008). Conversely, a subarctic study showed that warmer and wetter conditions increased herbivory across feeding guilds (Barrio et al., 2017).

Forest successional stage and soil substrate age can also influence herbivory (Davidson, 1993); however, the influence of stage and age on the interactions of insect herbivores and host plants remains understudied. As nutrient availability becomes progressively more limited with successional stage or soil substrate age (Peltzer et al., 2010; Wardle et al., 2004), plant communities tend to shift towards species with a conservative resource use strategy including growing slower and producing leaves with a lower nutrient content and a higher content of defensive compounds—both conferring resistance to herbivory (Cornwell et al., 2008; Santiago, 2007). These foliar changes should lead to a reduction in herbivory, but Metcalfe et al. (2016) found that N and P fluxes mediated by *Deporaus betulae* on *Betula pubescens* increased with time since fire in a boreal successional sequence and despite a decline in plant productivity. This increase was possibly due to higher herbivory rates, physiological changes with increasing canopy, or density of trees in the oldest and middle-aged islands, respectively. Research on other chronosequences is needed to clarify the impact of successional stage and soil substrate age on insect-mediated element fluxes.

We established a globally distributed network of herbivory research sites (Hwang et al., 2024b) to address the knowledge gap caused by the scarcity of multifactorial studies investigating plant-insect herbivore interactions and their effects on biogeochemical processes (Hamann et al., 2021; Jamieson et al., 2012). We designed this

network to explore how mean annual temperature (MAT), mean annual precipitation (MAP), forest successional stage, and soil substrate age influence insect herbivore-mediated carbon (C) and nutrient fluxes. In this study, we expand on previous analyses (Hwang et al., 2024b) to investigate how key environmental variables—MAT, MAP, successional stage, and soil substrate age—affect the gross and net insect-mediated release of elements from the canopy through foliar consumption at both global and local scales. We calculated this release as the product of canopy foliar production, green leaf (henceforth foliar) element concentration for C, N, P and Si, leaf-level herbivory rates (henceforth herbivory), and foliar element resorption. We explore the effects of MAT and MAP on insect-mediated element fluxes at two scales: (a) globally, with sites arrayed along global-scale gradients in MAT and MAP (hereafter Global MAT and Global MAP) and (b) locally, with sites located along elevation and precipitation gradients (hereafter Local MAT and Local MAP). We also assessed the effects of successional stage and soil substrate age on insect-mediated fluxes along successional and age chronosequences. We refer to elements consumed by insect herbivores in the canopy and deposited to the soil as insect-mediated element fluxes, where H_c is the estimated amount (gross) of an element insect herbivores consumed, and H_i is the estimated additional (net) nutrient input from insect herbivores removing green leaf material before resorption of these elements would typically occur prior to leaf drop. We hypothesized that:

1. Increasing environmental stress of colder and drier environments affects herbivores such that lower MAT and MAP drive: (a) decreased foliar biomass production, (b) decreased herbivory rate, (c) decreased foliar element concentrations, (d) increased nutrient resorption efficiency, (e) decreased insect herbivore consumption (H_c), and (f) decreased herbivore-mediated element input (H_i).
2. Herbivore-mediated nutrient fluxes will be lower in older ecosystems than in younger ecosystems.
3. Local and Global gradients should show broadly similar patterns, though Local gradients will show clearer and more consistent climate patterns of herbivory metrics than Global gradients because the latter are less constrained and are thus more variable.

2. Materials and Methods

2.1. Study Sites

We established 50 mature broadleaved forest-dominated sites spanning six continents and encompassing nine elevation gradients, three rainfall gradients, two forest successional age chronosequences, and one soil substrate age gradient in broadleaved-dominated forests on six continents (Table 1). To control for disturbance history, we set up sites in native old-growth forests for which we could not find documented evidence or visible indications of recent human activity (Hwang et al., 2024b). We selected gradients that minimized confounding influences of vegetation composition, other climatic variables, edaphic variables, and land use, while also providing important data points for Global scale analyses (Table S1, Figure 1; Hwang et al., 2024b). Elevation transects (Local MAT gradients) were compact, with sites for one transect extending 58 km, and the other eight transects spanning less than 20 km (Table S1). Precipitation, successional stage, and soil substrate age transects sometimes extended over longer distances, but even so these gradients were highly constrained with respect to MAT and dominant tree species (Hwang et al., 2024b).

2.2. Green Leaf and Soil Collections

To characterize green leaf nutrient levels, we sampled and pooled 25 g of fresh, healthy leaves from multiple heights in the canopy and from at least 10 randomly selected trees per site (1 sample per site). We sampled green leaves during the growing season for deciduous and temperate evergreen broadleaved forest sites, and every dry and wet season for evergreen tropical broadleaved forest sites. To characterize soil, we pooled, homogenized, and sieved (2 mm) 10 cores (0–15 cm depth) per site once during the growing season for all sites (1 sample per site). We dried all green leaves and soils at 65–70°C until a constant mass was reached and ground them for chemical analysis.

2.3. Estimates of Leaf-Level Herbivory Rate From Litterfall Collections

Our methodology was specifically designed for broadleaved forests (Hwang et al., 2024b) to help standardize seed types across the globally distributed network. At each site, we installed 10 to 20 litter traps of known area, located 0.3–1.0 m above the surface of the ground, and spaced at 20-m intervals. We collected broadleaved leaf litter for 1 or 2 years (between 2019 and 2021) every 14–31 days. One observer assessed insect damage to collected leaves using

Table 1
Summary of Ecological Characteristics Across All Sites

Location	Gradient	MAT range (°C)	MAP range (mm)	Age range (y)
Argentina	MAP	7.7–7.9	1,245–2,484	–
Chile	MAT	6.6–7.5	2,100–2,254	–
Cooloolool, Australia	CHR	20.3–21.0	1,548	350–40,000
Mt. Lewis, Australia	MAT	17.4–23.1	1,155–3,662	–
Tanzania	MAT	9.7–12.4	1,710–2,520	–
Hawai'i, USA	MAP	15.3–16.1	2,400–5,500	–
Hawai'i, USA	MAT	15.1–17.3	3,101–4,292	–
Hawai'i, USA	CHR	15.6–16.6	2,346–3,433	300–4,100,000
North Carolina, USA	MAT	8.9–11.9	2,100–2,094	–
Georgia	MAP	9.8–10.7	787–1,242	–
Georgia	MAT	5.0–10.6	787–793	–
China	MAT	1.0–4.1	634–863	–
Romania	MAT	6.7–8.7	942–1,084	–
Sweden	CHR	–1.4	750	160–5,330
Finland	MAT	–0.6–0.2	434–445	–

Note. Additional site descriptions can be found in Table S1 and Hwang et al. (2024b).

a classification system described in Allende (1989), scoring insect damage by the amount of leaf area removed (0%–1%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, and >75%). This method is more cost-effective and typically as accurate as digitization-based approaches (Johnson et al., 2016; Kozlov & Zvereva, 2017). These estimates of herbivory rate from abscised leaves integrate insect damage that accumulates over the entire lifespan of leaves and thus provide an unbiased, community-level estimate of background. The method does not capture loss of entire leaves (or branches with leaves) as can happen with the browsing of larger-bodied herbivores. After visual classification, we dried all leaves at 70°C to constant mass, weighed them, and estimated total leaf litterfall biomass ($\text{g m}^{-2} \text{y}^{-1}$). We also pooled a subsample of leaves from each litter trap by site, finely ground the homogenized subsample (1 sample per site), and conducted chemical analyses to estimate the nutrient content of senesced leaves.

2.4. Chemical Analyses

We combusted finely ground and homogenized green leaf, senesced leaf litter, and soil samples in an elemental analyzer (Flash 2000, Thermo Scientific, Bremen, Germany) at Copenhagen University, Denmark to obtain total C and N concentrations (Hwang et al., 2024b). We digested samples in sulfuric acid to prepare samples for high temperature ignition using an autoanalyzer (Seal AA500 Continuous Flow Analyzer, Seal Analytical GmbH, Norderstedt, Germany) at Copenhagen University, Denmark to determine total P (Breuning-Madsen et al., 2008). For Si concentrations, we digested samples in a sodium carbonate solution and analyzed them with a SmartChem® 200 Discrete Analyzer (AMS Alliance, KPM Analytics, Westborough, MA, USA) at Lund University, Sweden (Zahajská, 2021).

2.5. Estimates of Foliar Biomass Production and Insect Herbivore-Mediated Element Fluxes

We estimated annual leaf biomass production based on 1 or 2 years of litterfall biomass collections and used these estimates to calculate nutrient fluxes resulting from insect defoliation (Metcalf et al., 2014). The first step was to measure the total dry mass of leaf litter accumulated over the year (L_H) and divide grams of dried leaves by the known trap area to yield $\text{g m}^{-2} \text{y}^{-1}$ estimates. We then converted the total dry mass of leaf litter accumulated over the year (L_H) to annual foliar biomass production (FP, $\text{g m}^{-2} \text{y}^{-1}$) calculated as $L_H/(1 - H)$, where H is the proportion of leaf litter area removed by insect herbivores (% area removed $\text{m}^{-2} \text{y}^{-1}$). We converted FP to element production with green leaf element concentration (F_E) data, where subscript E is either element C, N, P, or Si. F_E was then multiplied by H, yielding total leaf elements consumed by insect herbivores (H_C , $\text{g m}^{-2} \text{y}^{-1}$). To

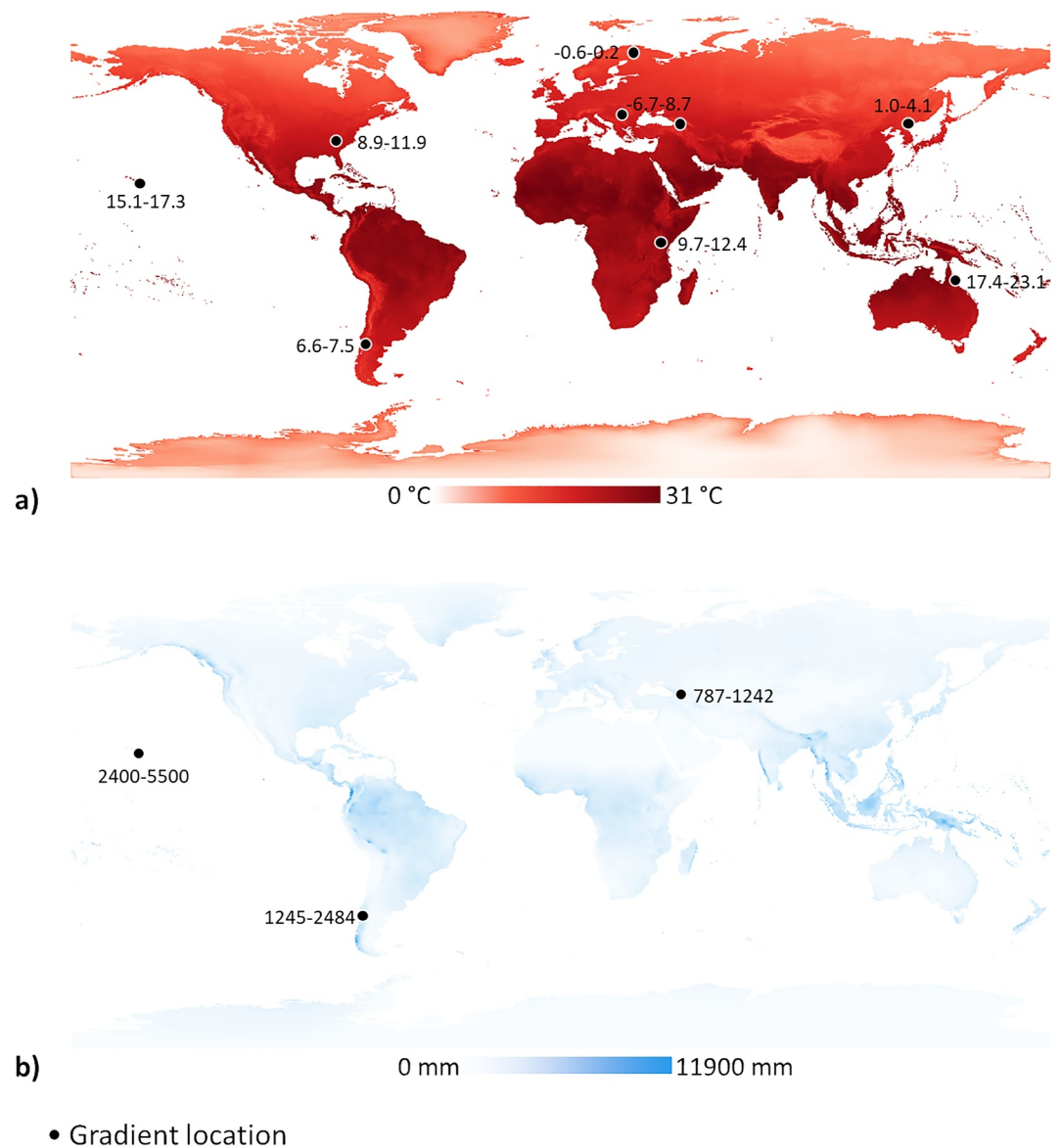


Figure 1. Map of climate gradients. Black circles and values represent locations and ranges of (a) mean annual temperature (°C) and (b) mean annual precipitation (mm) gradients. Base map climate data (means from 1970 to 2000) were derived from [Worldclim.com](https://worldclim.org/) (Fick & Hijmans, 2017).

account for differences in site characteristics, we further divided H_c by FP at each site to obtain the relative proportion of each element removed by insect herbivores.

In the absence of herbivory, nutrients in green leaves are resorbed during senescence, with a portion remaining in senesced leaves transferred to the soil as litterfall biomass. Herbivory disrupts this process because insects consume leaves before nutrient resorption can take place and thus divert nutrients into insect biomass and frass. This reduces the efficiency of plant internal nutrient recycling by diverting some fraction of the total stock available for resorption during senescence. To evaluate the importance of this herbivory-mediated diversion and the resulting flux, we estimated foliar nutrient resorption—the percentage reduction in element mass per unit dry mass in senesced leaves relative to green leaves—of C, N, and P. To account for the transition from green leaves to litter, we utilized mass loss correction factors of 0.780 and 0.784 for predominantly evergreen and predominantly deciduous angiosperm forests, respectively (based on Vergutz et al. (2012)). We assumed: (a) minimal nutrient leaching from litterfall traps between collections and (b) that herbivores consume only green leaves with

Table 2

Acronyms and Equations Used for Herbivory-Related Calculations Following Metcalfe et al. (2014)

Description	Acronym	Unit	Equation
Element C, N, P, or Si	E	NA	NA
Green leaf concentration of E	F_E	Proportion	NA
Leaf litter concentration of E	B_E	Proportion	NA
Foliar biomass production	FP	$\text{g m}^{-2} \text{y}^{-1}$	$L_H/(1 + H)$
Herbivory as proportion of leaf litter area removed	H	Proportion	NA
E consumed by insect herbivores (gross input of E by insect herbivores)	H_cE	$\text{g m}^{-2} \text{y}^{-1}$	$FP \times F_E \times H$
Relative intensity of elemental mass consumed by insect herbivores	H_cE/FP	Proportion	H_cE/FP
Additional E input from insect herbivores folivores due to green leaf consumption before resorption (net input of E by insect herbivores)	H_iE	$\text{g m}^{-2} \text{y}^{-1}$	$L_{EH} + H_cE - L_E$
Foliar input of E to soil without H (litter-mediated input of E)	L_E	$\text{g m}^{-2} \text{y}^{-1}$	$(FP \times F_E) \times (1 - RE_E)$
Foliar input of E to soil with H	L_{EH}	$\text{g m}^{-2} \text{y}^{-1}$	$L_H \times L_E \times (1 - RE_E)$
Annual broadleaved litterfall with H	L_H	$\text{g m}^{-2} \text{y}^{-1}$	Total annual dry weight of leaf litter/area of trap
Global mass correction factor due to leaf senescence (Vergutz et al., 2012)	Q	Proportion	0.780 for evergreen angiosperm forests; 0.784 for deciduous angiosperm forests
Resorption efficiency of E	RE_E	Proportion	$1 - (B_E/F_E \times Q)$

consumption being completed prior to the initiation of resorption. By combining H_c with resorption estimates for C, N and P for our research sites, we were able to estimate this “herbivore-mediated element input” (H_i , $\text{g m}^{-2} \text{y}^{-1}$), defined as the additional flux of C, N or P from plants to soil caused by herbivores removing green leaf material before resorption of these elements, which would usually occur before leaf drop. That is, H_i is the difference in total (litter + herbivore-mediated) nutrient input for a site with herbivores and that same site without herbivores (see Table 2 for all acronyms and equations). This analysis does not provide insights into the C use efficiency of herbivores as it does not distinguish between C allocated to herbivore biomass versus respiration. Such calculations would be highly uncertain since these allocations are poorly constrained for most locations and herbivore groups (Wiegert & Petersen, 1983). Instead, we report gross (H_c) and net (H_i) C removed from the foliage by herbivory.

2.6. Estimates of MAT, MAP, and Successional Stage or Soil Substrate Age

To obtain air temperature estimates, we installed TMS-4 dataloggers (Tomst S.R.O, Czech Republic) at each site during the collection period. Where we encountered data gaps (6 sites), we supplemented our data set with other local measurements (e.g., meteorological stations, site data from existing literature) to finalize MAT estimates. We used a combination of local weather station data and published values to establish a MAP estimate for all sites (Table S1, Hwang et al., 2024b). We used existing literature to determine successional and soil substrate ages for chronosequence sites (Thompson, 1981; Vitousek, 2004; Wardle et al., 2004).

2.7. Data Analysis

We used mixed linear regression analyses to assess successional stage and soil substrate age as well as Global and Local MAT and MAP patterns in insect herbivore-mediated fluxes across gradients using the R 4.2.1 statistical environment. We built mixed linear models in the lme4 package (Bates et al., 2015) where each transect was considered a random effect to account for site-specific geographic and floristic characteristics. For Global and Local MAT gradient data sets, adding elevation or MAP as a factor to models either raised the Akaike Information Criteria (AIC) or did not lower them by more than 2 (Burnham et al., 2011), meaning that removing elevation and MAP as factors did not substantially reduce the performance of the models. Likewise, for the Global and Local MAP gradients, adding elevation or MAT as a factor did not improve the AIC by more than 2 for models. Subsequently, we analyzed the Global and Local MAT gradient data sets using MAT as the fixed factor, the Global and Local MAP gradient data sets using MAP as the fixed factor, and the successional and soil gradient data sets using age as the fixed factor. We considered site to be a random factor in all models. For more robust estimates of foliar biomass production, herbivory rate, H_c , and H_i , we averaged litter trap values within each site,

resulting in 29 observations for the Global MAT gradient and 10 observations for the Global MAP gradient. We also averaged litter biomass per trap values within each of the 13 successional or soil substrate age sites.

Prior to running regressions, we produced standardized regression coefficient (β) values for the global-scale analysis by converting all variables to z scores across each data set ($n = 29$ for the Global MAT gradient, $n = 10$ for the Global MAP gradient) after log- or logit-transforming variables, as necessary. To evaluate the effects of climate along local gradients, we generated β values by converting all variables to z scores across each individual transect after any necessary log or logit transformations. To constrain 95% confidence intervals (CI) of the effect sizes, we performed 1,000 parametric bootstrap simulations. Fitted residuals from the linear mixed-effects model (using the lmer function) were resampled and added to the predicted values to generate new data sets. Each data set was refitted using the same model structure to estimate effect sizes. The 95% CIs were calculated as the 2.5th and 97.5th percentiles of the bootstrap distribution. This approach provided a conservative estimate of significance without relying on assumptions about degrees of freedom (Luke, 2017). Effects were deemed significant when the 95% CI did not overlap zero.

To quantify the strength of the contribution of individual precursor variables (herbivory rate, foliar biomass production, foliar element concentration, resorption) to element fluxes from H_c and H_i , we calculated the root mean square error between the z -score standardized precursor variables and z -score standardized H_c and H_i for each element along each natural gradient (Figure 2). Smaller values indicate where the gradient trend between the precursor variable and elemental flux (H_c and H_i) were more similar.

To depict the variation of insect-mediated element flux responses along Local gradients among individual transects, we plotted H_c against MAT, MAP, and succession or soil substrate age class for each transect as a figure panel (Figure 3). To visually but not statistically represent the overall outcome of the variation at the local level, we also plotted mean H_c against mean Local MAT, that is, the mean MAT z score for all cooler sites, the mean MAT z score of middle sites, and the mean MAT z score of the warmer sites from all MAT transects (Figure 4). We generated similar plots to depict mean Local $H_c \times$ MAP and $H_c \times$ age class to visualize the overall pattern of local MAP and successional stage and soil substrate age effects on H_c , respectively. These plots are for visualization purposes only, however, and we refer to results of the linear mixed models for effect sizes and evaluations of significance.

3. Data

All data from this study are available in a repository (Hwang et al., 2024a).

4. Results

4.1. Foliar Biomass Production and Leaf-Level Herbivory Rate

Mean foliar biomass production across the all sites ($n = 50$) was $310.0 \pm 28.5 \text{ g m}^{-2} \text{ y}^{-1}$ and mean herbivory was $3.3 \pm 0.4\%$ (Table 3). We estimated a mean of $41.5 \pm 2.8\%$ of leaves across all sites that exhibited some level of defoliation. The mean foliar biomass production and herbivory rate for wet, warm sites was significantly higher than the mean foliar biomass production for dry, cool sites across the globally distributed network (Figure 5, Table 4). Foliar biomass production (CI = 0.73, 1.00, where CI = the lower and upper bounds of a 95% confidence interval) and herbivory rate (CI = 0.15, 0.80) significantly increased with rising MAT along the Global MAT gradient (Table 4; Hwang et al., 2024b). In contrast, foliar biomass production ($25.2 \text{ g m}^{-2} \text{ yr}^{-1}$ to $117.4 \text{ g m}^{-2} \text{ yr}^{-1}$) and herbivory rate (0.63%–10.54%) along Local MAT gradients were highly variable (Table 4). Neither foliar biomass production nor herbivory rate positively correlated with MAP, successional stage, or soil substrate age along Global or Local gradients (Table 4).

4.2. Green Leaf Element Concentrations and Resorption

Of the foliar element concentrations (Table 4), foliar P concentration significantly decreased with increasing Global MAT (CI = -0.90 , -0.07) and Local MAT (CI = -0.75 , -0.002). Foliar N resorption significantly increased with Local MAT (CI = 0.22, 0.87) but did not significantly change with Global MAT. Neither Global nor Local MAP gradients were significantly related to foliar elemental concentrations or resorption of any element in this study. Successional stage and soil substrate age had inconsistent effects on foliar element concentrations and resorption, negatively affecting foliar Si concentration (CI = -1.10 , -0.14) and C resorption (CI = -1.03 , 0.02) with age.

GRAD	SCALE	SITE	H _c C				H _c N				H _c P				H _c Si				H _i C				H _i N				H _i P			
			FP	H	F _c	FP	H	N _f	FP	H	P _f	FP	H	Si _f	FP	H	C _f	RE _c	FP	H	N _f	RE _N	FP	H	P _f	RE _P	FP	H	P _f	RE _P
MAT	GLOBAL	AUST	0.1	0.3	1.6	0.1	0.3	1.2	0.0	0.2	1.9	0.2	0.4	0.8	0.1	0.1	1.5	1.3	0.0	0.2	1.1	1.9	0.0	0.2	1.8	1.0	0.0	0.2	1.8	1.0
MAT	GLOBAL	CHIL	0.2	0.2	0.1	0.4	0.0	0.7	0.3	0.1	0.2	0.0	0.4	0.2	0.6	0.2	0.3	0.1	0.2	0.2	0.8	0.8	0.6	0.2	0.1	1.1	0.6	0.2	0.1	1.1
MAT	GLOBAL	CHIN	0.2	0.1	0.7	0.3	0.0	0.3	0.4	0.0	0.3	0.6	0.2	0.3	0.4	0.0	0.8	0.3	0.3	0.0	0.3	0.3	0.3	0.1	0.4	0.4	0.3	0.1	0.4	0.4
MAT	GLOBAL	FINL	0.2	0.2	0.1	0.3	0.2	0.4	0.4	0.0	0.8	0.8	0.3	0.7	1.6	1.1	1.4	0.6	0.3	0.8	1.0	0.7	1.6	1.1	0.4	1.6	1.6	1.1	0.4	1.6
MAT	GLOBAL	GEOR	0.6	0.4	0.5	0.5	0.5	0.9	0.7	0.3	0.4	0.2	0.8	0.7	0.4	0.6	0.3	0.9	0.5	0.5	0.8	1.2	0.6	0.4	0.3	0.8	0.6	0.4	0.3	0.8
MAT	GLOBAL	HAWA	0.0	0.2	1.2	0.1	0.1	0.3	0.2	0.1	0.6	0.4	0.1	0.4	0.2	0.1	1.3	0.4	0.1	0.3	0.6	0.4	0.2	0.1	0.6	0.3	0.2	0.1	0.6	0.3
MAT	GLOBAL	NOCA	0.6	0.3	0.1	0.6	0.4	0.4	0.6	0.3	0.4	0.4	0.6	0.6	0.5	0.4	0.0	0.2	0.6	0.3	0.5	0.7	0.5	0.4	0.3	0.8	0.5	0.4	0.3	0.8
MAT	GLOBAL	ROMA	0.3	0.1	0.8	0.3	0.1	0.7	0.3	0.1	1.2	0.2	0.2	0.7	0.3	0.1	0.8	0.8	0.3	0.1	0.7	0.8	0.2	0.2	1.1	0.5	0.2	0.2	1.1	0.5
MAT	GLOBAL	TANZ	0.2	0.1	0.9	0.4	0.1	0.2	0.3	0.0	0.3	0.1	0.2	0.4	0.4	0.1	1.0	1.4	0.0	0.2	0.5	0.0	0.3	0.0	0.3	0.1	0.3	0.0	0.3	0.1
MAT	GLOBAL	MEAN	0.3	0.2	0.7	0.3	0.2	0.6	0.4	0.1	0.7	0.3	0.4	0.5	0.5	0.3	0.8	0.7	0.3	0.3	0.7	0.8	0.5	0.3	0.6	0.7	0.5	0.3	0.6	0.7
MAP	GLOBAL	ARGE	0.1	0.0	0.3	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.2	0.4	0.2	0.3	0.5	0.5	0.2	0.3	0.3	0.5	0.2	0.3	0.3	0.5
MAP	GLOBAL	GEOR	0.7	0.5	0.7	1.3	0.1	0.3	1.3	0.1	0.4	1.2	0.1	0.2	0.0	1.2	1.0	0.1	1.1	0.0	1.1	0.1	1.1	0.1	0.1	0.8	1.1	0.1	0.1	0.8
MAP	GLOBAL	HAWA	0.1	0.7	1.0	0.8	0.0	1.2	0.9	0.1	0.9	1.1	0.4	0.5	0.0	0.8	1.9	0.9	1.3	0.5	0.2	0.9	1.2	0.5	0.5	0.6	1.2	0.5	0.5	0.6
MAP	GLOBAL	MEAN	0.3	0.4	0.6	0.7	0.1	0.5	0.7	0.1	0.4	0.8	0.2	0.2	0.0	0.7	1.0	0.5	0.9	0.3	0.6	0.5	0.8	0.3	0.3	0.6	0.8	0.3	0.3	0.6
MAT	LOCAL	AUST	1.0	0.3	1.0	1.1	0.2	0.7	1.0	0.3	0.9	1.2	0.0	0.9	1.2	0.1	1.1	0.7	0.7	0.5	0.3	0.0	1.0	0.2	1.0	0.2	1.0	0.2	1.0	0.2
MAT	LOCAL	CHIL	0.4	0.0	0.5	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.3	0.1	0.1	0.4	0.1	0.8	0.4	0.0	0.4	0.5	0.2	0.2	0.2	0.9	0.2	0.2	0.2	0.9
MAT	LOCAL	CHIN	0.1	0.6	1.1	0.1	0.5	0.5	0.1	0.6	0.2	0.2	0.7	0.1	0.0	0.5	1.0	0.7	0.2	0.8	0.8	0.0	0.1	0.4	0.0	0.8	0.1	0.4	0.0	0.8
MAT	LOCAL	FINL	0.0	1.2	1.3	0.1	1.1	0.2	1.2	0.1	0.0	1.0	0.2	0.1	1.3	0.1	0.1	1.1	0.0	1.2	0.4	0.4	1.3	0.1	0.1	1.3	1.3	0.1	0.1	1.3
MAT	LOCAL	GEOR	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.3	0.6	0.2	0.2	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.0	0.2	0.2	0.7	0.4	0.2	0.2	0.7	0.4
MAT	LOCAL	HAWA	0.5	0.1	1.1	0.3	0.1	0.9	0.3	0.1	0.0	0.6	0.2	0.1	1.0	0.6	0.6	0.4	1.0	0.6	0.2	0.1	0.3	0.1	0.0	0.4	0.3	0.1	0.0	0.4
MAT	LOCAL	NOCA	0.7	0.1	0.7	0.7	0.0	1.2	0.7	0.1	1.0	0.8	0.1	1.1	0.6	0.0	0.6	0.4	0.7	0.1	1.2	0.4	0.8	0.1	1.1	0.3	0.8	0.1	1.1	0.3
MAT	LOCAL	ROMA	0.3	0.7	0.2	0.5	0.5	0.3	0.5	0.5	0.1	0.5	0.5	0.2	0.6	0.4	0.4	0.1	0.4	0.6	0.4	0.6	0.5	0.5	0.1	0.2	0.5	0.5	0.1	0.2
MAT	LOCAL	TANZ	0.2	0.1	0.8	0.2	0.0	0.1	0.3	0.1	0.2	0.1	0.1	0.2	0.3	0.0	0.9	0.6	0.0	0.2	0.3	0.5	0.4	0.2	0.3	0.1	0.4	0.2	0.3	0.1
MAT	LOCAL	MEAN	0.4	0.3	0.7	0.4	0.3	0.5	0.5	0.3	0.4	0.5	0.3	0.3	0.6	0.2	0.5	0.5	0.4	0.5	0.5	0.3	0.5	0.2	0.4	0.5	0.5	0.2	0.4	0.5
MAP	LOCAL	ARGE	0.3	0.2	0.1	0.3	0.2	0.3	0.1	0.4	0.8	0.4	1.0	0.0	0.7	0.1	0.7	0.7	0.4	0.2	0.2	0.2	0.1	0.5	0.8	0.1	0.1	0.5	0.8	0.1
MAP	LOCAL	GEOR	0.0	0.1	0.4	0.1	0.0	1.0	0.1	0.0	1.0	0.2	0.1	0.1	0.5	0.4	0.5	0.0	0.4	0.3	0.0	0.5	0.9	0.8	0.2	0.8	0.9	0.8	0.2	0.8
MAP	LOCAL	HAWA	0.0	0.0	0.9	0.2	0.1	0.9	0.0	0.1	0.9	0.9	0.8	0.2	0.1	0.0	1.1	0.5	0.3	0.2	0.7	0.3	0.0	0.1	1.0	0.7	0.0	0.1	1.0	0.7
MAP	LOCAL	MEAN	0.1	0.1	0.5	0.2	0.1	0.8	0.1	0.2	0.9	0.5	0.7	0.1	0.4	0.2	0.8	0.4	0.4	0.2	0.3	0.3	0.3	0.4	0.7	0.5	0.3	0.4	0.7	0.5
CHR	LOCAL	AUST	1.3	0.5	0.8	1.3	0.5	1.1	1.4	0.5	0.2	1.1	0.2	0.1	1.2	0.3	1.0	0.2	1.3	0.5	0.8	0.3	2.8	1.0	0.4	2.0	2.8	1.0	0.4	2.0
CHR	LOCAL	HAWA	0.6	0.3	0.2	0.6	0.3	0.8	0.6	0.3	0.5	0.6	0.3	0.4	0.6	0.3	0.8	0.5	0.6	0.3	0.2	0.5	0.9	1.5	1.1	0.7	0.9	1.5	1.1	0.7
CHR	LOCAL	SWED	0.2	0.3	0.4	0.4	0.1	0.4	0.7	0.2	0.3	0.2	0.3	0.5	0.4	0.1	0.4	0.4	0.6	0.1	0.9	0.5	0.3	0.8	0.6	0.5	0.3	0.8	0.6	0.5
CHR	LOCAL	MEAN	0.2	0.3	0.4	0.4	0.1	0.4	0.7	0.2	0.3	0.2	0.3	0.5	0.4	0.1	0.4	0.4	0.6	0.1	0.9	0.5	0.3	0.8	0.6	0.5	0.3	0.8	0.6	0.5

Figure 2. Precursor contributions to insect-mediated element fluxes along climate gradients. Relative contributions of precursors to insect-mediated element fluxes along global mean annual temperature (MAT) and mean annual precipitation (MAP) gradients and local MAT and MAP gradients. Values show root mean square error calculated between the transformed and z-score standardized precursor variables and transformed and z-score standardized gross insect-mediated flux (H_c) and net insect-mediated flux (H_i) for each element (carbon, nitrogen, phosphorus, and silicon) along each gradient. Smaller values (red) indicate where the gradient trend between the precursor variable and elemental flux (H_c and H_i) were more similar, and thus the precursor variable exerted greater control over the elemental flux. By contrast, greater values (blue) show where the elemental flux gradient trends diverged more strongly from the precursor gradient trend, so the precursor exerted less control over the elemental flux.

4.3. Insect Herbivore-Mediated Element Fluxes (H_c and H_i)

Warmer and drier sites supported the largest H_cN and H_cP fluxes, though specific biotic factors influenced these fluxes somewhat differently across Global and Local gradients. The effects of Global MAT on all insect-mediated element fluxes (Table 4) were strongly positive although effect sizes were variable between elements (H_cC β = 0.80, H_cN β = 0.80, H_cP β = 0.75, H_cSi β = 0.75). The effects of Global MAT on these fluxes after normalizing by site foliar biomass production (H_c/FP) were positive but less than absolute amounts of H_c (H_cC/FP β = 0.51, H_cN/FP β = 0.42, H_cP/FP β = 0.32, H_cSi/FP β = 0.50), although the effect of Global MAT was not significant for P (Table 4). Global MAT exerted stronger influences on foliar biomass production, herbivory rate, and so insect-mediated element fluxes than on foliar element concentrations (Tables 1 and 4). By comparison, the

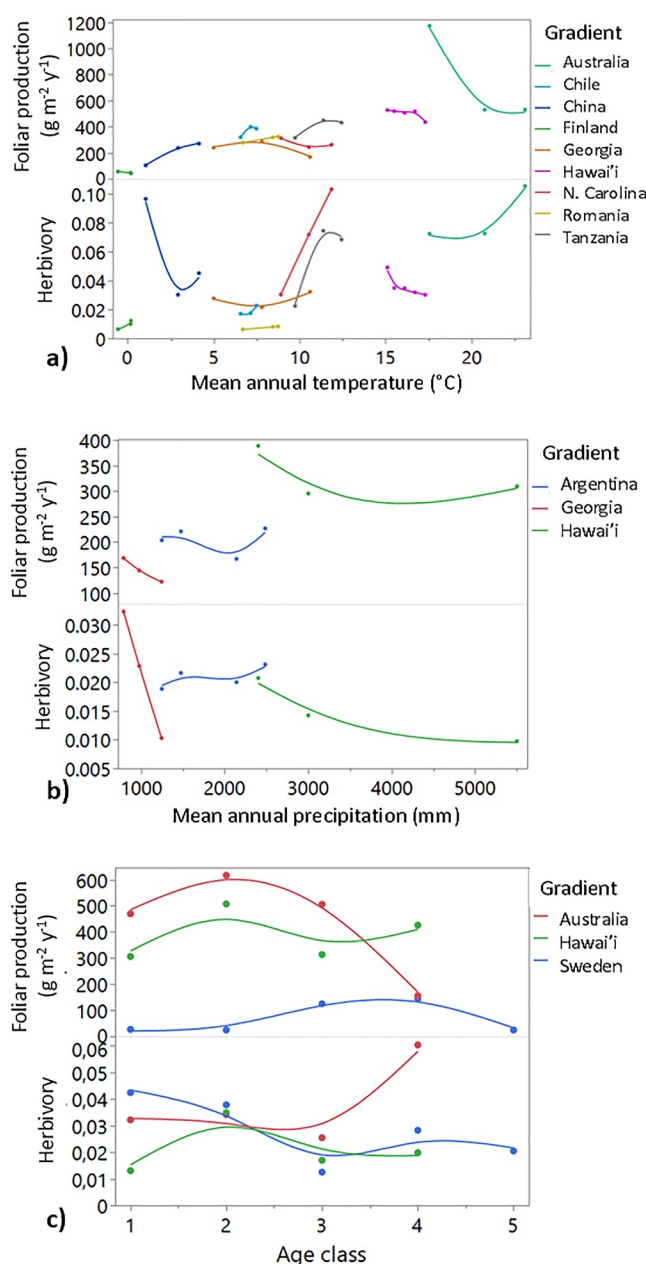


Figure 3. Foliar biomass production and herbivory rate along environmental gradients. Foliar biomass production ($\text{g m}^{-2} \text{y}^{-1}$) and herbivory (proportion leaf area removed) along (a) mean annual temperature ($^{\circ}\text{C}$), (b) mean annual precipitation (mm), and (c) successional stage or soil substrate age (age 1 youngest) gradients at each site (circles). Circles depict means within a site (3–25 traps per site) and lines represent best-fitted lines.

effects of Global MAP on insect-mediated element fluxes and other variables were weaker and more variable, with notable negative trends for H_cP ($\text{CI} = -0.81, -0.11$), H_iN ($\text{CI} = -1.17, -0.39$), and H_iP ($-1.16, -0.32$) (Table 4; Figures 4 and 5). Relative to each site's foliar biomass production, $\text{H}_c\text{N}/\text{FP}$ ($\beta = -0.68$) and $\text{H}_c\text{P}/\text{FP}$ ($\beta = -0.74$) were both strongly and negatively linked to Global MAT but not to Global MAP or successional stage and soil substrate age (Table 4). There was considerable variation in all insect-mediated element fluxes in absolute amounts (H_c) along the Local MAT, Local MAP, and successional stage or soil substrate age gradients (Figure 6). When normalized by site foliar biomass production (H_c/FP), however, relative amounts of C

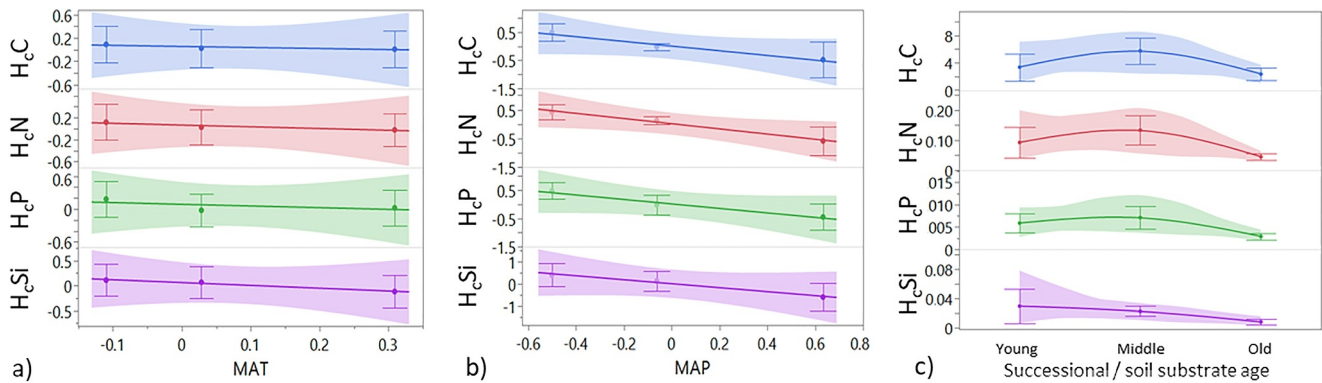


Figure 4. Mean gradient response of H_c ($\text{g m}^{-2} \text{y}^{-1}$) to (a) mean Local mean annual temperature (MAT) ($n = 29$), (b) mean Local mean annual precipitation ($n = 10$), and (c) mean Local successional or substrate age ($n = 13$). Data were log-transformed and z -standardized at three levels (e.g., the mean MAT z score for all cooler sites, the mean MAT z score of middle sites, and the mean MAT z score of the warmer sites from all MAT transects). Lines are best-fit through site means, bars represent ± 1 SE, and shaded bands surrounding lines represent the bootstrap confidence region for each fit.

(CI = 0.08, 0.30), N (CI = 0.04, 0.25), and P (CI = 0.01, 0.17) positively correlated with Local MAT (Table 4). Nevertheless, these correlations were significantly weaker for Local MAT compared to Global MAT (Table 4).

5. Discussion

5.1. Global and Local Effects of MAT, MAP, Successional Stage, and Soil Substrate Age on Foliar Biomass Production and Leaf-Level Herbivory Rate

In support of our first hypothesis, warmer sites supported higher foliar biomass production and insect herbivory rates at the Global scale (Table 4). Local gradients did not fully support our first or third hypotheses, however, showing variable effects of MAT and MAP on rates of foliar biomass production and herbivory (Table 4). While variation in foliar biomass production along environmental gradients can stem from co-varying conditions of vegetation, bedrock type and age, soil type, or land-use (Raich et al., 1997; Sundqvist et al., 2011), we took considerable measures in site selection to minimize confounding effects of other environmental variables (Hwang et al., 2024b). Contrary to our third hypothesis, our results highlight that the effects of MAT or MAP can be much weaker at the Local level than at the Global level. Applying results from the Global MAT gradient that spanned 23.7°C , for example, could conceal changes happening along Local MAT gradients, which spanned from 0.8°C (Finland) to 5.7°C (Hawai'i). Within certain Local gradients, we identified factors that might have obscured the effects of local variation in MAT. For example, the warmest site on the subarctic gradient was the least productive yet supported the greatest herbivory (Figure 3), perhaps because of the effects of night-time cold air drainage on plant physiology (Pepin et al., 2022). The fact that the lowest site still experienced the highest herbivory rate suggests that the effects of the temperature inversion were within the tolerance of local insect herbivores. For the Australian MAT transect, cyclone damage to lower elevation (warmer) coastal sites might account for higher foliar biomass production observed at the higher elevation (colder) sites (Figure 3). Similarly, applying changes observed over local gradients may miss important additional processes and confounding factors operating at the global level (e.g., shifts in species composition). The positive relationship between herbivory and global MAT may be influenced by the growing season, as MAT and growing season length are positively correlated. Warmer temperatures can extend feeding periods, increase herbivore abundance, and, in some cases, allow for an additional generation (Bale et al., 2002). Additionally, the longer lifespan of broadleaves in warmer climates may provide extended access to herbivores (Kikuzawa et al., 2013). However, temperature effects on herbivory are likely to vary among different plant-herbivore pairs as well as regions (Lemoine et al., 2014).

In line with our first hypothesis, foliar biomass production increased with rising Global MAP (Table 4). However, herbivory rate did not vary significantly with Global MAP. Our results underscore the high level of variance in herbivory-related measures at the Global level, in line with our third hypothesis. It is possible that the drier end of our Global MAP gradient was not dry enough to detect MAP trends in herbivory specific to more arid ecosystem types, and our focus on closed canopy, mature/old growth broadleaved forests might have limited selection of drier and more open canopied sites. Local MAP did not significantly explain either foliar biomass production, herbivory

Table 3

Abiotic Characteristics for Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP) Gradient, and Chronosequence (CHR) Sites

Variable	Unit	Mean	Minimum	Maximum
Foliar biomass production (FP)	$\text{g m}^{-2} \text{ y}^{-1}$	310.02 ± 28.48	25.23	1174.04
Herbivory rate (H)	% leaf area removed per year	3.34 ± 0.36	0.63	10.54
Soil C (S_C)	% dry weight	10.21 ± 1.12	0.83	39.05
Soil N (S_N)	% dry weight	0.71 ± 0.08	0.04	1.82
Soil P (S_P)	% dry weight	0.09 ± 0.01	0.01	0.28
Soil Si (S_{Si})	% dry weight	1.49 ± 0.14	0.15	4.41
Green leaf C (F_C)	% dry weight	48.22 ± 0.37	42.58	54.70
Green leaf N (F_N)	% dry weight	1.79 ± 0.08	0.61	3.06
Green leaf P (F_P)	% dry weight	0.13 ± 0.01	0.02	0.25
Green leaf Si (F_{Si})	% dry weight	0.42 ± 0.06	0.09	1.44
Litter C (L_C)	% dry weight	49.70 ± 0.32	41.71	55.38
Litter N (L_N)	% dry weight	0.98 ± 0.05	0.10	1.75
Litter P (L_P)	% dry weight	0.06 ± 0.01	0.01	0.20
Litter Si (L_{Si})	% dry weight	0.61 ± 0.08	0.11	2.58
C resorption (RE_C)	%	19.62 ± 0.57	9.33	32.50
N resorption (RE_N)	%	53.80 ± 1.79	15.69	72.93
P resorption (RE_P)	%	62.73 ± 1.74	23.71	81.67
H_c of C (H_C)	$\text{g m}^{-2} \text{ y}^{-1}$	5.77 ± 1.06	0.19	41.83
H_c of N (H_N)	$\text{g m}^{-2} \text{ y}^{-1}$	0.22 ± 0.05	0.01	1.64
H_c of P (H_P)	$\text{g m}^{-2} \text{ y}^{-1}$	0.014 ± 0.003	0.001	0.102
H_c of Si (H_{Si})	$\text{g m}^{-2} \text{ y}^{-1}$	0.046 ± 0.009	0.001	0.325
H_i of C (H_iC)	$\text{g m}^{-2} \text{ y}^{-1}$	1.10 ± 0.21	0.03	8.76
H_i of N (H_iN)	$\text{g m}^{-2} \text{ y}^{-1}$	0.15 ± 0.04	0.01	0.77
H_i of P (H_iP)	$\text{g m}^{-2} \text{ y}^{-1}$	0.0142 ± 0.0042	0.0004	0.0587
H_C/FP	%	1.56 ± 0.17	0.28	5.07
H_N/FP	%	0.06 ± 0.01	0.01	0.30
H_P/FP	%	0.004 ± 0.001	0.001	0.018
H_{Si}/FP	%	0.013 ± 0.002	0.001	0.048

Note. Means, minimums, and maximums of ecological characteristics across all sites and gradients with standard errors ($n = 50$).

rate, or any other insect herbivore-related variable, suggesting a higher level of variance in herbivory-related measures at the Local level. An increase in MAP at warmer and wetter tropical sites did not stimulate foliar biomass production as it did for the drier temperate sites (Figure 3), in line with prior MAP analyses (Luyssaert et al., 2007). That is, additional water in a system not limited by water may not enhance productivity (Sundqvist et al., 2013), and in some cases, may reduce it (Lyu et al., 2021). Consistent with other studies along temperate and tropical MAP transects, but in contrast to our first and third hypotheses, we did not observe a significant change in herbivory rate with increasing Local MAP (Leckey et al., 2014; Moreira et al., 2015). Previous studies have shown contrasting responses of herbivory rate to MAP: a positive relationship between herbivory rate and increasing MAP in regions of limited rainfall (Shure et al., 1998; Vasconcellos et al., 2010) and a negative relationship between herbivory rate and increasing MAP in wet regions (Weissflog et al., 2018). This and other studies highlight both the lack of a Global MAP trend and the variability of site-specific effects of Local MAP on herbivory rate. Taken together, these findings suggest that MAP likely does not exert a consistent or strong effect on insect herbivores.

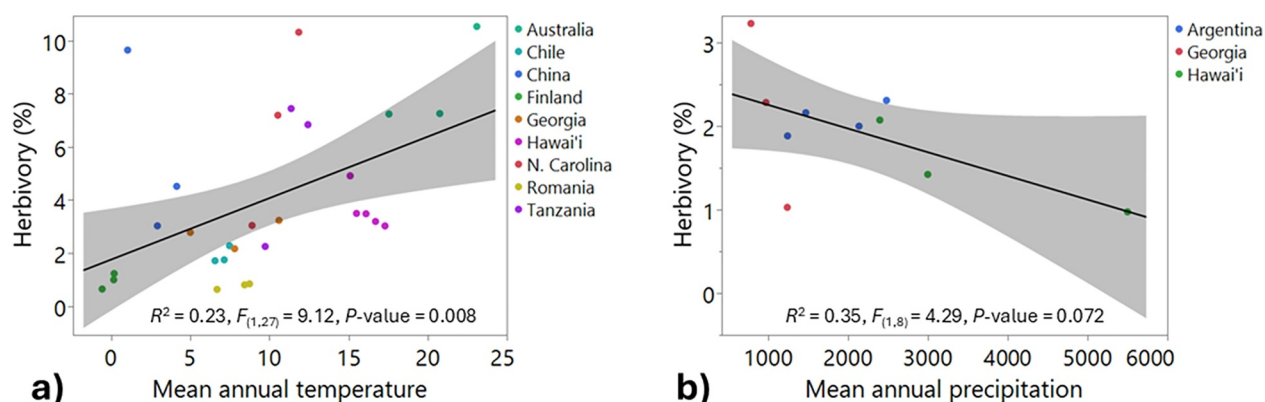


Figure 5. Herbivory (% leaf area removed) along (a) mean annual temperature (°C) and (b) mean annual precipitation (mm) gradients. Circles depict means within a site (12–25 traps per site), lines represent best-fitted lines, and bands are 95% CIs. F-statistics, degrees of freedom, *P*-values, and R^2 values are reported for each simple regression.

In accordance with established theories about plant resource use strategies and ecosystem development (Cornwell et al., 2008; Peltzer et al., 2010; Santiago, 2007; Wardle et al., 2004; but see Metcalfe et al., 2016), the limited number of chronosequences sampled, combined with the significant variability among them, resulted in a weak overall relationship between successional stage or soil substrate age and the various herbivory-related measures recorded. Comparing chronosequences with similar disturbance types and recovery conditions could help reduce variability and clarify how successional stage or soil substrate age influences insect-mediated effects on biogeochemical processes.

While MAT, MAP, successional stage, and soil substrate age gradients have provided powerful models for examining how ecosystems respond to environmental change, we recognize several limitations of the Local MAT, MAP, successional stage, and soil substrate age gradients used in this study. We took steps during site selection to minimize variation in potentially confounding variables that could impact herbivory and related metrics (Hwang et al., 2024b), but it may not be possible to eliminate all sources of confounding variation. In Hawai'i, for example, we used soil substrate age (Vitousek, 2004) and MAT (Litton et al., 2020) gradients, developed for testing fundamental questions about the response of terrestrial element cycling to environmental variation, where potentially confounding factors such as vegetation composition, other climate variables, disturbance history, and geology are largely constant. In some of our other gradients, however, the microclimate or inter- and intra-specific variation in plant and animal traits may lead to different species compositions and interactions (e.g., Australia; Moreira et al., 2018).

Our approach of measuring insect herbivory at the community level provides a valuable integrated overview, capturing broad-scale patterns which are impossible to derive from traditional approaches targeting individual plants and/or leaves. As such, the approach lacks the resolution to identify specific mechanisms and processes, or isolate the relative significance of individual components of the plant and herbivore community. However, these topics have long been, and should continue to be, best probed with widely accepted and applied methods (e.g., Barrio et al., 2017; Brenes-Arguedas et al., 2009; Lemoine et al., 2014; Moreira et al., 2015). Combining such approaches with our broader community-level perspective could provide complementary insights into how environmental gradients shape insect-mediated nutrient fluxes.

An expanded sampling of a wider range of climatic conditions would be needed to elaborate the nature of MAT and MAP controls over herbivory. Future studies could also examine how biomass production and herbivory rates vary intra- and inter-annually as these finer scale temporal patterns can provide insights into ecosystem responses to climate variation (Leckey et al., 2014; Lyu et al., 2021; Shure et al., 1998). Long-term experimental manipulation of water availability (e.g., Nepstad et al., 2007) could also be used to explore herbivory responses to reduced rainfall within a replicated statistical design.

Table 4

The Impact of Mean Annual Temperature, Mean Annual Precipitation, Successional Stage and Soil Substrate Age Along Global and Local Gradients on Herbivory-Related Characteristics

Global gradient					Local gradient		
MAT x	Units	COEF	CI, LO	CI, UP	COEF	CI, LO	CI, UP
Foliar production	$\text{g m}^{-2} \text{y}^{-1}$	0.87	0.73	1.00	−0.04	−0.25	0.16
Leaf-level herbivory	% area removed	0.48	0.15	0.80	0.15	−0.11	0.39
Green leaf C	% dry weight	0.06	−0.43	0.57	−0.03	−0.42	0.39
Green leaf N	% dry weight	−0.15	−0.69	0.36	0.02	−0.37	0.40
Green leaf P	% dry weight	−0.46	−0.90	−0.07	−0.35	−0.75	−0.00
Green leaf Si	% dry weight	0.33	−0.21	0.88	−0.06	−0.31	0.45
H_c of C (H_cC)	$\text{g m}^{-2} \text{y}^{-1}$	0.80	0.60	0.99	0.06	−0.14	0.26
H_c of N (H_cN)	$\text{g m}^{-2} \text{y}^{-1}$	0.80	0.53	0.97	0.07	−0.15	0.29
H_c of P (H_cP)	$\text{g m}^{-2} \text{y}^{-1}$	0.75	0.50	0.99	0.05	−0.21	0.32
H_c of Si (H_cSi)	$\text{g m}^{-2} \text{y}^{-1}$	0.75	0.51	0.97	0.06	−0.26	0.36
H_cC/FP	Proportion	0.51	0.20	0.80	0.19	0.08	0.30
H_cN/FP	Proportion	0.42	0.09	0.75	0.14	0.04	0.25
H_cP/FP	Proportion	0.32	−0.04	0.65	0.08	0.01	0.17
H_cSi/FP	Proportion	0.50	0.13	0.83	0.01	−0.15	0.17
C resorption	%	−0.03	−0.50	0.45	0.08	−0.32	0.47
N resorption	%	−0.32	−0.79	0.15	0.54	0.22	0.87
P resorption	%	−0.14	−0.69	0.40	−0.15	−0.55	0.23
H_i of C (H_iC)	$\text{g m}^{-2} \text{y}^{-1}$	0.76	0.57	0.98	−0.08	−0.37	0.23
H_i of N (H_iN)	$\text{g m}^{-2} \text{y}^{-1}$	0.65	0.38	0.91	0.21	−0.12	0.53
H_i of P (H_iP)	$\text{g m}^{-2} \text{y}^{-1}$	0.71	0.47	0.94	0.12	−0.23	0.48
MAP x	Units	COEF	CI, LO	CI, UP	COEF	CI, LO	CI, UP
Foliar production	$\text{g m}^{-2} \text{y}^{-1}$	0.54	0.20	0.90	−0.27	−0.68	0.15
Leaf-level herbivory	% area removed	−0.35	−0.74	0.02	−0.19	−0.46	0.10
Green leaf C	% dry weight	0.33	0.50	1.26	0.28	−0.37	0.95
Green leaf N	% dry weight	−0.15	−0.67	0.36	−0.11	−0.77	0.58
Green leaf P	% dry weight	0.06	−0.14	0.27	−0.02	−0.71	0.68
Green leaf Si	% dry weight	−0.35	−0.12	0.40	−0.16	−0.84	0.48
H_c of C (H_cC)	$\text{g m}^{-2} \text{y}^{-1}$	0.11	−0.31	0.57	−0.21	−1.34	0.82
H_c of N (H_cN)	$\text{g m}^{-2} \text{y}^{-1}$	−0.31	−0.70	0.05	−0.26	−1.48	0.98
H_c of P (H_cP)	$\text{g m}^{-2} \text{y}^{-1}$	−0.46	−0.81	−0.11	−0.33	−1.48	0.84
H_c of Si (H_cSi)	$\text{g m}^{-2} \text{y}^{-1}$	−0.21	−0.81	0.37	−0.46	−1.78	0.79
H_cC/FP	Proportion	−0.32	−0.69	0.09	−0.19	−0.55	0.12
H_cN/FP	Proportion	−0.68	−0.96	−0.39	−0.06	−0.37	0.25
H_cP/FP	Proportion	−0.74	−1.02	−0.49	0.03	−0.33	0.38
H_cSi/FP	Proportion	−0.47	−0.96	0.09	−0.03	−0.58	0.51
C resorption	%	0.04	−0.83	0.89	0.28	−0.37	0.95
N resorption	%	−0.30	−1.26	0.72	−0.52	−1.12	0.05
P resorption	%	0.43	−0.35	1.30	0.05	−0.70	0.71
H_i of C (H_iC)	$\text{g m}^{-2} \text{y}^{-1}$	0.12	−0.31	0.55	−0.06	−1.07	0.92
H_i of N (H_iN)	$\text{g m}^{-2} \text{y}^{-1}$	−0.78	−1.17	−0.39	−0.02	−1.40	1.27
H_i of P (H_iP)	$\text{g m}^{-2} \text{y}^{-1}$	−0.76	−1.16	−0.32	−0.15	−1.31	1.03

Table 4
Continued

Successional or substrate age x	Units	COEF	CI, LO	CI, UP	COEF	CI, LO	CI, UP
Foliar production	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.20	-0.61	0.22
Leaf-level herbivory	% area removed	NA	NA	NA	0.08	-0.22	0.40
Green leaf C	% dry weight	NA	NA	NA	0.18	-0.52	0.52
Green leaf N	% dry weight	NA	NA	NA	-0.18	-0.74	0.38
Green leaf P	% dry weight	NA	NA	NA	-0.05	-0.62	0.55
Green leaf Si	% dry weight	NA	NA	NA	-0.62	-1.06	-0.17
H_c of C (H_cC)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.16	-0.62	0.32
H_c of N (H_cN)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.22	-0.68	0.28
H_c of P (H_cP)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.26	-0.73	0.23
H_c of Si (H_cSi)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.36	-0.92	0.21
H_cC/FP	Proportion	NA	NA	NA	0.13	-0.41	0.70
H_cN/FP	Proportion	NA	NA	NA	-0.01	-0.55	0.58
H_cP/FP	Proportion	NA	NA	NA	-0.08	-0.61	0.48
H_cSi/FP	Proportion	NA	NA	NA	-0.22	-0.83	0.36
C resorption	%	NA	NA	NA	-0.58	-1.05	-0.09
N resorption	%	NA	NA	NA	-0.03	-0.64	0.58
P resorption	%	NA	NA	NA	0.24	-0.36	0.76
H_i of C (H_iC)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.02	-0.57	0.47
H_i of N (H_iN)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.19	-0.76	0.43
H_i of P (H_iP)	$\text{g m}^{-2} \text{y}^{-1}$	NA	NA	NA	-0.27	-0.80	0.28

Note. Linear mixed-effect modeling results are based on log and logit transformations of variables as appropriate, followed by z standardization. Standardized coefficients (COEF) indicate direction of change with increasing MAT, MAP, or successional age, and the lower (CI, LO) and upper (CI, UP) ends of the confidence intervals describe the uncertainty surrounding the estimates. Variables significantly related to the explanatory variable in question after 1,000 bootstrapping simulations (95% CIs do not overlap with zero) are in bold print.

5.2. Global and Local Effects of MAT, MAP, Successional Stage, and Soil Substrate Age on Foliar Characteristics

We found limited support for our first hypothesis that higher MAT and MAP would positively influence foliar element concentrations and negatively influence nutrient resorption (Table 4). Among foliar element concentrations, only P decreased significantly with Global and Local increases in MAT. Unlike N, which often becomes more available in mineral forms in the soil with warming and can be replenished from external sources (e.g., deposition, fixation), P is replenished to a more limited extent in most ecosystems. While warming may slightly accelerate the rate of mineral P weathering (Goll et al., 2014), these modest changes are expected to be most significant in high-latitude ecosystems, where P limitation seldom dominates (Vitousek et al., 2010). In most tropical and older soils, on the other hand, P is tightly bound to minerals or occluded in forms that are not easily available to plants (Vitousek et al., 2010). Therefore, temperature increases do not directly enhance the release of P in these conditions, leading to limited P availability even in warmer climates (Litton et al., 2020). Additionally, foliar N resorption did not significantly explain variation along Global MAT. Increasing MAT can more strongly influence plant biomass growth than soil N mineralization, resulting in N dilution of green leaves (Aerts et al., 2007). Furthermore, climate shifts (e.g., winter snow addition, spring/summer warming) on senescent leaf N appear to be limited, highlighting the potential for divergent effects of climate on green and senesced leaf nutrient concentrations, and thus resorption (Aerts et al., 2007). That foliar N resorption significantly increased with increasing Local MAT could suggest more severe N than P limitation differences within individual transects and brings to light contrasting resorption responses to changing MAT at different spatial scales (but see Litton et al., 2020). Different irradiance levels along Local MAT gradients could also generate variation in

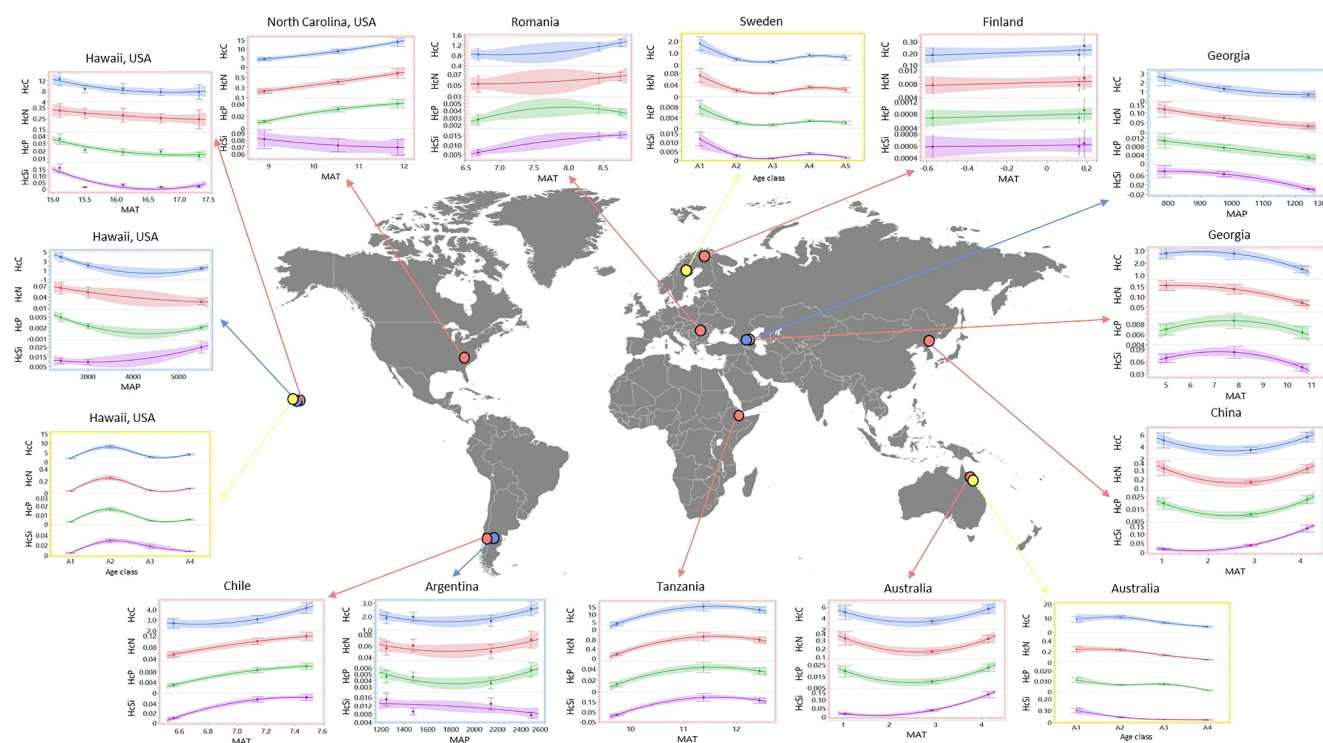


Figure 6. Locations of 9 (red circles) Local mean annual temperature (MAT, °C), 3 (blue circles) mean annual precipitation (MAP, mm), and 3 (yellow circles) successional stage or soil substrate age (age class, A1 is youngest) gradients in central map; and associated responses of the mass of carbon, nitrogen, phosphorus, and silica consumed by insect herbivores H_c ($\text{g m}^{-2} \text{y}^{-1}$) to environmental changes for each location in panels surrounding the map. Graphs with red, blue, and yellow borders represent MAT, MAP, and successional stage or soil substrate age treatments, respectively. Circles in graphs depict mean values from individual sites, lines are smooth curves fit through site means, bars depict ± 1 SE, and shaded bands surrounding lines represent 95% bootstrap confidence region for each fit. The base map was downloaded from [freemaps.com](https://www.freemaps.com).

photosynthetic capacities, growth rates, and plant N economy (Battisti et al., 2013; Yasumura et al., 2006, but see Litton et al., 2020; Lyu et al., 2021).

In contrast to our second hypothesis, lower foliar Si concentration with older successional stage or soil substrate age did not correspond to significantly reduced herbivory rate, indicating the limited importance of Si in herbivore defense. While Si can be utilized by plants for processes that increase structural integrity or for reducing other stressors such as drought or toxicity (Cooke & Leishman, 2011), our results suggest that Si plays a relatively minor role in herbivore defense in mature broadleaved-dominated forests (Hwang et al., 2024b). Si utilization in tree defense can vary strongly across species (Klotz et al., 2023). Trees in this study may have preferentially used other defenses (e.g., lignin, secondary metabolites, volatile compounds) and strategies (e.g., growth over-compensation) rather than Si-based compounds to reduce herbivory.

These results corroborate previous work showing that the size and even direction of foliar element concentration responses to climate changes depend on climate variable, element, region, plant species composition, and seasonality (Litton et al., 2020; Reich & Oleksyn, 2004; Townsend et al., 2008). Lower foliar element concentrations do not necessarily result in lower herbivory rates because foliar element concentrations are often influenced by chemical defense strategies of plants including investments against herbivores. For example, interactions between nutrient concentrations exceeding demand and high levels of toxic compounds can negatively affect consumer performance (Tao et al., 2014). Additionally, insects perform best with a specific blend of nutrient amounts and ratios rather than universal increases in nutrients (Joern et al., 2012, and references therein). In our study, herbivory rate increased with rising Global MAT despite stable foliar N concentrations, which might suggest that trees invested more in foliar biomass production than defense compounds (e.g., N-based secondary metabolites) in response to increases in herbivory along the Global MAT gradient (e.g., to grow or defend; Herms & Mattson, 1992). Stable or even decreasing (in the case of P) foliar element concentrations with increasing MAT could indicate that the combination of increased herbivory rates and increased foliar biomass production might better

explain greater insect-mediated element fluxes along the Global MAT gradient than foliar element concentrations alone. That is, insects may have simply compensated for lower nutritional value on a leaf-level basis by consuming more leaf biomass.

5.3. Effects of Global and Local MAT, MAP, Successional Stage, and Soil Substrate Age on Insect-Mediated Element Fluxes

In partial agreement with our first hypothesis, Global MAT had a larger impact on insect-mediated element fluxes than Global MAP, with both H_c and H_i for all elements increasing with rising Global MAT (Table 4). In contrast, only H_cN decreased with rising Global MAP (Table 4). Foliar biomass production and herbivory rate were the strongest drivers for the impact of Global MAT on insect-mediated element fluxes, while foliar P concentration may have played an additional minor role in the impact of Global MAP on insect-mediated P fluxes (Table 4). In contrast to our third hypothesis, the effects of MAT and MAP on absolute amounts (H_c) of insect-mediated element fluxes were not clearly intensified at the Local level. However, the relative importance of insects in mediating element cycling (H_c/FP) increased with Local MAT (Table 4), suggesting that insects play a greater role in element cycling relative to the overall ecosystem productivity in locally warmer forests. Absolute fluxes might not be significantly linked to Local MAT because foliar biomass production also increases with Local MAT, potentially offsetting changes in insect activity. In contrast, the proportional contribution of insects to element fluxes may increase because processes linked to insect herbivore activity are inherently more temperature-sensitive at the local level. Future studies could include local gradients over wider ranges of MAT or MAP to help clarify potential differences at that scale. Furthermore, we conclude that inferences from climatic gradients beyond the spatial scope of measurement should be interpreted cautiously.

Since we observed the largest insect-mediated element fluxes on the warmer and drier ends of our globally distributed network, we would expect future warming and drying to be associated with an increase in the amount of C and nutrients liberated from the canopy by insect herbivory. Global climate projections linked to ecosystem models project that boreal and subarctic forests will become more productive with future warming (Reyer, 2015). Our study would indicate that these climate-driven increases in foliar biomass production would be paired with increases in herbivory rate and insect-mediated element fluxes in these high latitude ecosystems. We might also expect insect-mediated element fluxes to increase because climate change is predicted to increase the frequency, duration, and severity of insect outbreaks in cooler ecosystems (Harvey et al., 2020; Jepsen et al., 2013). At the other climate extreme, additional warming in already warm ecosystems could lead to declines of insect populations (Harvey et al., 2020), thereby reducing insect-mediated element fluxes. Further, increasing the C available to plants as a result of rising atmospheric $[CO_2]$ and warming-driven increases in total C uptake could also support increased plant level investments into chemical protection against herbivory. Adding to this complexity, any increases in drought frequency, duration, and severity would likely exert large effects on plant-insect herbivore interactions, with variations in effect size and even direction depending on feeding guild (Gely et al., 2020; Warlo & Kautz, 2024), and drought-related weakening of plant defenses (Anderegg et al., 2015). For example, the overall performance of insect herbivores has been shown to decline overall with drought (Huberty & Denno, 2004; Jactel et al., 2012), but sap-sucker performance has been predicted to vary with the severity of drought, increasing under mild drought but decreasing under severe drought (Gely et al., 2020). The exact direction and magnitude of change in insect-mediated element fluxes including all insect feeding guilds, therefore, will likely depend on the tolerance and general response of plant and insect species to the type of climate shift and local features of the plant and insect communities (Bale et al., 2002; Jamieson et al., 2012; Netherer & Schopf, 2010).

Unlike our second hypothesis, we found that insect-mediated nutrient fluxes declined only slightly with increasing successional stage or soil substrate age, with individual chronosequences being highly variable (Figures 3 and 6). As nutrient limitations intensify during the rare later stages of ecosystem retrogression, plants may produce longer-lived, nutrient-poor leaves with stronger defenses against herbivores, resulting in a prevalence of species with these characteristics (Ordoñez et al., 2009; Peltzer et al., 2010; Wardle et al., 2004). Because herbivory usually increases in environments that support fast-growing, nutrient-rich plants, it might be expected that the transfer of nutrients from plants to soil by herbivores will diminish over time since ecosystem disturbance (McNaughton et al., 1989). This may have been the case for the successional sequence in Australia but patterns were less clear for the soil substrate age chronosequence in Hawai'i and the successional sequence in Sweden, and opposite to findings in Metcalfe et al. (2016), which recorded increasing rates of damage over time after ecosystem disturbance. Metcalfe et al. (2016) focused on a single herbivore species (*D. betulae*) with a specialized

physiology adapted to metabolizing high levels of leaf tannins (Haukioja, 2003), occurring particularly toward the older end of the chronosequence. By contrast, our herbivory estimates reflect the contributions of the entire herbivore community, which likely pursue a diverse range of strategies to cope with the shifts in foliar traits across the chronosequence. These variable strategies could explain the different patterns observed across the Swedish chronosequence in this study. In addition to assessing effects of succession or soil development on different insect herbivore feeding guilds on biogeochemical cycling (Gely et al., 2020), future studies could compare specialists and generalists to further disentangle potential differences in element fluxes between plant-herbivore groupings.

6. Summary and Conclusions

Our results provide insights into how changing MAT, MAP, succession, and soil substrate age influence insect herbivore contributions to biogeochemical cycling in forests at both local and much larger spatial scales. Overall, insect herbivores removed more elements from forest canopies in warmer and drier sites than in cooler and wetter sites, with MAT exerting more influence over insect-mediated element fluxes than MAP. Successional stage and soil substrate age did not significantly influence insect herbivore contributions to biogeochemical cycling, and observed local patterns did not always match larger-scale patterns across the entire globally distributed network. Thus, broad inferences of climate effects from natural gradients should be drawn with great caution.

As Applicable—Inclusion in Global Research Statement

Please see Hwang et al. (2024b) for reports on ethical and scientific standards including disclosure of permits, authorizations, and permissions related to this study.

Data Availability Statement

The data on which this article is based are available in Hwang et al. (2024a).

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Acknowledgments

This project was supported by funding from the European Commission under the European Union's Horizon 2020 research and innovation programme (ECOHERB and INTERACT; Grants 682707, 730938, and 871120, respectively). Additional funding for work in Chile was supported by Proyecto Fondecyt 1130898. The USDA Forest Service, Pacific Southwest Research Station provided additional financial and logistical support for work in Hawai'i. We thank Creighton Litton at the University of Hawai'i at Manoa, Jonathan Price at the University of Hawai'i at Hilo, and Peter Vitousek at Stanford University, USA. Thanks to Kaianui Andaya, Alealani Evangelista, Chantilly Keliihoomalu, Chloe Martins-Keliihoomalu, Rebekah Ohara, Cody Pacheco, Kirie Santos, Naneaikeaula Thomas, Kauilamakahikina Thomas, Tyler Uehara, from the USDA Institute of Pacific Islands Forestry, the Akaka Foundation for Tropical Forests, and the Kupu Conservation Leadership Development Program in Hawai'i, USA. We also thank Guanhua Dai, Xiuxiu Wang, and Hao Xu at the Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences, as well as Prof. Dr. Jiabing Wu at the Institute of Applied Ecology, Chinese Academy of Sciences. We also thank Erick Materu, Brayan Materu, and Mgeta Kaswamila from the KiLi Group in Tanzania. We thank Oso Suominen at the Kevo Research Station in Finland. Thanks to Vasile Sebastian Stătescu from Transylvania University in Romania, and thanks to James Costa, Carson Ellis, Morgan Gaglianese-Woody, Thomas Hennesy, Jason Love, Brent Martin, and Angela Faye Martin at the Highlands Biological Station and Western Carolina University in North Carolina, USA. Thanks to Michelle Schiffer and the support staff at the Daintree Rainforest Observatory as well as Lucas Cernusak, Michael Liddell and Susan Laurance at James Cook University Cairns in Australia. We are grateful to Lindy Corwin, Kevin Jackson, and the Cooloola CoastCare team in Queensland, Australia. We thank David Wardle and Johan Eckdahl at Umeå University in Sweden. Thanks to Per Lennart Ambus and his team at the University of Copenhagen, Denmark, as well as Daniel Conley and Isa Doverbratt at Lund University, Sweden.

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