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The association of leaf lifespan and background insect herbivory at the interspecific level

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Abstract. Herbivory is well known to be a major selective pressure that affects plant communities, but the leaf traits that mediate variations in herbivory at the interspecific level remain controversial. We collected published data on background insect herbivory and leaf traits from a wide variety of species to test the hypothesis that species with intermediate leaf lifespans, lower fiber, and higher nutrient contents in leaves should have higher levels of herbivory. We found that at the interspecific level herbivory had a hump-shaped relationship with leaf lifespan and a positive relationship with leaf size. Surprisingly, our data show that nutritional traits have little relationship to herbivory. Our study provides new insights relevant to the recent debate on leaf trait–herbivory relationships. These findings are especially helpful in explaining the general patterns of herbivory detected on the global scale.

Key words: herbivore; leaf lifespan; leaf size; leaf traits; plant defense; plant–herbivore interactions; resistance; specific leaf area.

INTRODUCTION

Herbivory is the most important pathway for energy flow from autotrophic plants to higher trophic levels and, therefore, has profound effects on community structure and ecological functions (Coley and Barone 1996, Agrawal 2007). However, recent studies have triggered contentious debates about the factors that affect herbivory, especially at the interspecific level (Carmona et al. 2011, Agrawal and Weber 2015).

For decades, plants' secondary metabolites have been considered the most important factor affecting herbivory (Agrawal 2007, 2011). Recently, however, a series of interspecific and community-level studies have found a negligible relationship between secondary metabolites and herbivory, suggesting that their effect on herbivory may be overestimated (Carmona et al. 2011, Loranger et al. 2012, Schuldt et al. 2012). This has led to the recent debate on their role in mediating herbivory (Carmona et al. 2011, Agrawal and Weber 2015). Agrawal and Weber (2015) argued that community-level studies may not provide reliable tests of plant-trait–herbivory relationships, because of the clade specificity of secondary metabolites, the correlation of unmeasured traits and extreme phenotypes. They suggested that future studies should focus on the intraspecific level or a narrow phylogenetic scale (e.g., a plant genus).

We agree that community-level studies indeed have pitfalls when testing the effect of secondary metabolites on herbivory (Agrawal and Weber 2015), but they are still a valuable way to explore questions that cannot be answered by intraspecific studies. First, the main theoretical hypotheses about plant defense (e.g., the resource availability hypothesis, the plant apparency hypothesis, and the latitudinal herbivory-defense hypothesis) are community level, but not intraspecific- or clade-level hypotheses. The ultimate purpose of these hypotheses is to explain the strong variation in herbivory among different species (Coley et al. 1985, Lim et al. 2015, Anstett et al. 2016, Hahn and Maron 2016, Zhang et al. 2016). To do so, it is essential to use interspecific or community-level studies to test these hypotheses. Secondly, understanding the community divergence and function of plants' antiherbivore traits is especially important in explaining the patterns of diversity among herbivores at large scales (Becerra 2015). Finally, compared to intraspecific studies, community-level studies may be more important in helping us identify the "common currency" that shapes plant defense and herbivory across a wide variety of plant species.

To understand interspecific variation in herbivory, we must take into account the growth and defense strategies of plants, as well as herbivory's cost to plants (Wright et al. 2004, Lim et al. 2015). Species at opposite ends of the leaf economics spectrum tend to have very different growth and defense strategies (Wright et al. 2004) that can correspondingly influence the level of herbivory (Lim et al. 2015). Species with longer leaf lifespans, lower nutritional quality, and higher leaf dry mass content are assumed to be associated with lower growth rates and higher levels of defense against herbivores, because such leaves are costly to produce (Wright et al. 2004); thus, they should exhibit relatively lower levels of herbivory (Coley et al. 1985, Coley 1987). Recently, however, Pearse and Karban (2013) found that trees with

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intermediate leaf lifespans accumulated the highest abundance of herbivores in 55 oak species. Therefore, to date, the way in which these leaf economic-related traits correlate with herbivory is still far from clear, especially on a broad phylogenetic scale (Lim et al. 2015).

Based on data collected from published papers and data sets, we attempted to identify the leaf traits associated with herbivory across a wide variety of plant species. Compared to previous studies that have focused primarily on mechanical and chemical defense traits, we focused here on leaf traits related to the leaf economic spectrum and nutritional quality. According to a recently developed conceptual diagram (Pearse and Karban 2013), we hypothesized that species with intermediate leaf lifespans should have the highest level of herbivory, because of the trade-off between the palatability of leaves and the feeding period of herbivores. We also hypothesized that species with higher fiber but lower nutrient contents in leaves should exhibit lower levels of herbivory.

Methods

Collection of herbivory data

To make the data more comparable, we included as the measure of herbivory only studies that used the total percentage of leaf area damaged by insect herbivores (including chewing and mining damage), which is the method used most commonly to measure herbivory (Andrew et al. 2012). Leaf damage by galling, phloem- and xylem-feeding insects was not included (Turcotte et al. 2014*b*). We collected data on leaf herbivory from published data sets (Kozlov et al. 2014, 2015*b*, Turcotte et al. 2014*b*) and other literature. For one data set, we used only the herbivory data collected from published papers to obtain the authors' permission (Kozlov et al. 2015*b*). In addition, we used "herbivory," "leaf area loss," "leaf damage," "defoliation," "folivory," and "plant–herbivore interaction" as keywords in searches of the Web of Sciences and Google Scholar. We collected data on herbivory and species information from each suitable literature source according to several criteria: (1) only data capable of representing most of the damage a leaf suffers in its lifetime were included, while daily herbivory rates were excluded, (2) for experimental studies, only the control data were included, (3) in the same study site, if herbivory was measured as a time series, the mean value of the various time samples was used, (4) only observations conducted in the field were considered, while those conducted in greenhouses or labs were excluded, and (5) studies conducted during outbreaks of some herbivores were excluded. Thus, we included data only on "background herbivory" (Kozlov et al. 2015*b*). The levels of herbivory presented in texts, tables, or figures were extracted with the UTHSCSA Image Tool (University of Texas, San Antonio, Texas, USA), and the mean levels were used in data analysis.

For each study, we recorded the coordinates of the study site. We also collected such climatic factors as mean annual temperature (MAT) from the original literature or information about the study sites found through web searches. Precipitation was not included as an explanatory variable because a previous study found it showed no correlation with herbivory on a global scale (Zhang et al. 2016). If this information was not available, temperature data were extracted from the CRU CL 2.0 data set, a set of global climate grids with 10 min spatial resolution.

Collection of leaf trait data

Based on the species list that included data on herbivory, we searched the data on the leaf traits of each species in an open access database (Kattge et al. 2011) and other published literature (Coley 1983, Escudero et al. 1992, Reich et al. 1998, Wright et al. 2004, Tian 2007, Chen et al. 2012, Li 2014, Kozlov et al. 2015*a*, Li et al. 2016). We focused on traits intimately related to plants' growth and defense strategies: leaf lifespan, specific leaf area (SLA), and nitrogen and phosphorus content (Wright et al. 2004). Leaf lifespan refers to the average duration of the life of leaves on the plant. Longer life spans require higher constructive costs for plants. Specific leaf area is the leaf area of one side divided by its oven-dry mass. SLA is a mechanical trait that affects leaves' palatability to herbivores. In addition to the leaf traits listed, we also included two morphological leaf traits, leaf dry mass content (LDMC, the oven-dry mass of a leaf divided by its water-saturated fresh mass) and size, as well as five nutritional traits: carbon content, leaf phosphorus/nitrogen content per area, and the C:N and N:P in leaves. All of these traits are assumed to have considerable effects on herbivory at the interspecific level (Kurokawa et al. 2010, Garibaldi et al. 2011, Pearse 2011, Joern et al. 2012, Loranger et al. 2012, Schuldt et al. 2012, Heard and Sax 2013, Metcalfe et al. 2014), but rarely have they been tested across a broad array of plant species (but see Kozlov et al. 2015*a*).

Data analyses

To account for the effects of phylogenetic relationships among species, we used both ordinary least square (OLS) and phylogenetic least square (PGLS) regressions to evaluate the trait–herbivory relationship (Lim et al. 2015). Considering the nature of the data and the possible effects of other factors (plant growth form, latitude, temperature) on the trait–herbivory relationship, we analyzed the data in two steps: (1) species-level analyses and (2) random resampling tests, which take into account the effect of intraspecific variation in herbivory.

Species-level analyses

To make a one-to-one correspondence between leaf traits and herbivory possible, and to fulfill the requirement of the PGLS analyses, the data for a given species derived from different populations were averaged before data analysis, as in previous studies (Turcotte et al. 2014*a*, Kozlov et al. 2015*a*, Lim et al. 2015, Díaz et al. 2016). Although both herbivory and leaf traits can vary with numerous factors within a species, in general, intraspecific variation is smaller than is interspecific variation (Schuldt et al. 2012, Auger and Shipley 2013, Hulshof et al. 2013, Krober et al. 2015, Siefert et al. 2015). Based on data available currently, making population-level matches between leaf traits and herbivory is nearly impossible on a global scale (Kozlov et al. 2015*b*, Lim et al. 2015). Nevertheless, we also conducted random resampling tests to account for the intraspecific variation in herbivory. However, for leaf traits, we used the averaged value of each species over all the analyses, the method used commonly in recent global analyses of leaf traits (Kozlov et al. 2015*a*, Díaz et al. 2016).

Because most species included data only on a few of the leaf traits collected, we could not analyze the combined effects on herbivory of all the leaf traits in a full model; therefore, the relationship between herbivory and each leaf trait was analyzed separately. The combined effects of different leaf traits on herbivory were analyzed whenever possible. First, we used OLS regression to fit the relationship between leaf traits and herbivory and compared linear and quadratic regressions using the Akaike information criterion (AIC). Then, we conducted a PGLS regression to account for the possible effects on our analyses of evolutionary relationships among species. In all these analyses, the plant growth form (woody or non-woody) was used as a covariate, because of its strong effect on herbivory (Turcotte et al. 2014*a*, Kozlov et al. 2015*a*, *b*, Zhang et al. 2016). Species-level phylogeny was generated from a super tree using Phylomatic (v.3.0, stored tree "20120829", Webb and Donoghue 2005). We calculated divergence times in the trees with the BLADJ algorithm in Phylocom (Webb et al. 2008). The PGLS analyses were performed using the phylolm package in R (Ho and Ané 2014) under several models for the error term: the Pagel's Lambda, Brownian motion (BM), and Ornstein–Uhlenbeck models (OUfixedRoot and OUrandomRoot). Model selection was based on the AIC values (Ho and Ané 2014).

Resampling tests

For a given species, herbivory data can be collected from more than one site. This intraspecific variation can affect the conclusions derived from the species-level analyses above. To take into account the intraspecific variation in herbivory and the influences of other factors, we used a random resampling test to reevaluate the trait–herbivory relationship.

For a given species, in each resampling, we selected just one study site randomly, and the data associated with this site were used in the analyses. The latitude, MAT of the study site, growth form of the species, and leaf traits were used as explanatory variables of herbivory in a full model. Latitude and MAT were chosen because of their effects in shaping global patterns of herbivory (Kozlov et al. 2015*b*, Lim et al. 2015, Zhang et al. 2016). This resampling process was iterated 1000 times and, each time, both OLS and PGLS regressions were used to evaluate the effects of different factors on herbivory, the same method we used in the species level analyses. The resamplings were conducted with the SURVEYSELECT Procedure in SAS 9.3 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Herbivory and leaf trait values were collected for 698 plant species. The herbivory data were collected from 1,651 data points from 293 publications (see Data S1 for the data set and list of literature). The mean herbivory level for all these species was 8.37% (SE = 0.24%, $n = 1{,}651$). These data were collected from 1959 to 2014, and herbivory showed no trends with the years of data collection ($r = -0.024$, $P = 0.3411$, Pearson correlation, Appendix S1: Fig. S1).

Species-level analyses

At the species level, we found a quadratic relationship between leaf lifespan and herbivory both with OLS and PGLS regression (Table 1: the Lambda model was preferred in all PGLS analyses). Woody species had a 1.4 times higher level of herbivory than did non-woody species ($F_{1,696} = 51.6$, $P < 0.0001$, Appendix S1: Fig. S2). However, when combined with leaf lifespan, the effect of growth form on herbivory became nonsignificant (Table 1). Further analysis showed that woody species had significantly longer leaf lifespans ($F_{1,237} = 149.31$, $P < 0.0001$, Appendix S1: Fig. S2) than did non-woody species. Species in the Southern Hemisphere also had longer leaf lifespans and higher levels of herbivory than did species in the Northern Hemisphere (Appendix S1: Fig. S3).

When plant growth form was eliminated from the full model, the hump-shaped relationship between leaf lifespan and herbivory became clearer (Table 1), and showed that species with intermediate leaf lifespans had the highest levels of herbivory (Fig. 1). The quadratic regression fit the leaf lifespan–herbivory relationship

TABLE 1. The relationship of leaf lifespan (LL) and plant growth form with herbivory at the interspecific level based on ordinary least square (OLS) regression and phylogenetic generalized least square regression (PGLS).

Variable	Slope estimated	*t*	*P*
OLS			
LL	3.3878	4.62	<0.0001
LL × LL	−1.7305	−5.33	<0.0001
Growth form	0.2778	1.21	0.2270
PGLS			
LL	1.7651	2.28	0.0237
LL × LL	−0.8213	−2.29	0.0231
Growth form	0.3278	1.30	0.1963

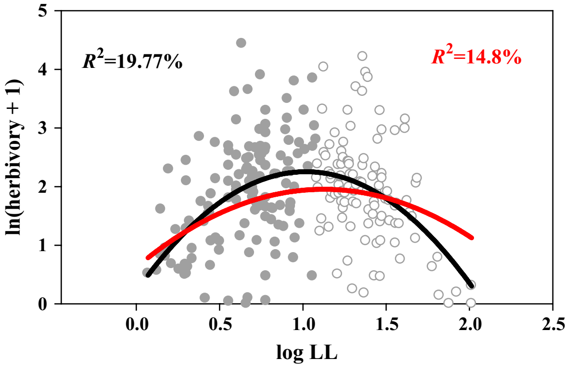

FIG. 1. The relationships between herbivory and leaf lifespan (LL; measured in months) at the interspecific level, with each dot representing a species. The black and red lines were fitted by the ordinary least square regression (for LL, slope = 4.0042, t = 7.58, P < 0.0001; for LL × LL, slope = −1.9670, t = −7.57, P < 0.0001) and phylogenetic least square regression (for LL, slope = 2.3618, t = 3.74, P = 0.0002; for LL × LL, slope = −1.0496, t = −3.31, P = 0.0011) respectively. Solid dots represent deciduous species with leaf lifespans less than 1 yr, open dots represent evergreen species with leaf lifespans greater than 1 yr. [Color figure can be viewed at wileyonlinelibrary.com]

much better than did a linear regression model (ΔAIC = 50.7 for OLS regression and ΔAIC = 7.4 for PGLS). Leaf lifespan explained 19.77% and 14.80% of the interspecific variation in herbivory based on the OLS and PGLS regression models, respectively. For deciduous species (with leaf lifespans shorter than 1 yr), herbivory tended to increase with leaf lifespan. However, for evergreen species (with leaf lifespans longer than 1 yr), herbivory tended to decrease with leaf lifespan (Fig. 1).

Both OLS regression (t = 4.40, P < 0.0001) and PGLS (t = 3.14, P = 0.002) detected a significant positive relationship between leaf size and herbivory (Fig. 2). In the data set, 126 species included trait values of both leaf lifespan and leaf size. For these species, the two variables were analyzed in combination to predict herbivory. A hump-shaped relationship between leaf lifespan and herbivory and a positive relationship between leaf size and herbivory were also detected (Fig. 3). The OLS regression showed that, in combination, leaf lifespan and size explained 31.2% of the variation in herbivory ($F_{3,122}$ = 18.7, P < 0.0001, Fig. 3). The PGLS analyses showed a similar pattern ($F_{3,122}$ = 13.56, P < 0.0001, R^2 = 25.0%, Fig. 3).

A positive relationship between LDMC and herbivory (t = 2.89, P = 0.004) was detected by OLS regression; however, when the phylogenetic relationships among species were taken into account, the relationship became non-significant (P > 0.05). None of the other leaf traits showed significant relationships with herbivory (P > 0.05 in all analyses).

Random resampling tests

First, a full model with the latitude, MAT of the study site, and the growth form and leaf lifespan of the species as explanatory variables of herbivory was conducted in each of the 1,000 resamplings. The results showed that plant growth form and latitude had little relationship with herbivory, both in OLS and PGLS regressions (Table 2). Therefore, the two variables were dropped in a simplified model. In this model, in nearly all cases (>98%), leaf lifespan showed a significant quadratic relationship with herbivory (Table 2, Fig. 4). MAT also showed a significant positive relationship with herbivory in most cases (>90%; Table 2).

Taking variations in MAT, latitude of the study site, and plant growth form into account did not change the positive relationship between leaf size and herbivory. In most cases, herbivory showed a significant positive correlation with leaf size (100% in OLS and 95.4% in PGLS regression). In more than 90% of cases, herbivory varied significantly with the growth form of plants (Appendix S1: Table S1).

DISCUSSION

In examining data collected on a wide variety of plant species, we found that leaf lifespan and size were key traits that correlated with herbivory at the interspecific level, and these main findings are unlikely to change when the effects of intraspecific variation in herbivory, plant growth form, latitude, temperature, and the phylogenetic relationship between species were taken into account. This study provides new insights relevant to the recent debate on the relationships between leaf traits and herbivory (Carmona et al. 2011, Agrawal and Weber 2015). These findings are especially helpful in explaining patterns in herbivory detected recently at the global level.

We found a solid hump-shaped relationship between herbivory and leaf lifespan. This finding is quite important in understanding the trait–herbivory relationship in natural communities. The relationships between leaf lifespan and plant growth and defense strategies was noted approximately three decades ago (Coley et al. 1985, Coley 1987), but the way in which herbivory varies with leaf lifespan has rarely been tested explicitly (Pearse and Karban 2013). Previous studies have found positive (Loranger et al. 2012), negative (Silva et al. 2015), and no relationships (Kozlov et al. 2015*a*) between leaf lifespan and herbivory. However, to predict herbivory, all of these studies used leaf lifespan categories (e.g., deciduous and evergreen) rather than the value of the leaf lifespan for each species. We suggest that dividing species into two or three classes by their leaf lifespans in data analyses can lead to contradictory conclusions, because of the nonlinear relationship between the two variables that we show here. Our findings are consistent with a previous study in which the abundance of leaf miners in 55 oak species was greatest in those with intermediate leaf lifespans (Pearse and Karban 2013). Leaves with longer lifespans are often heavily sclerotized and highly defended by secondary chemical metabolites, because they are costly to produce (Coley 1987, Wright et al. 2004);

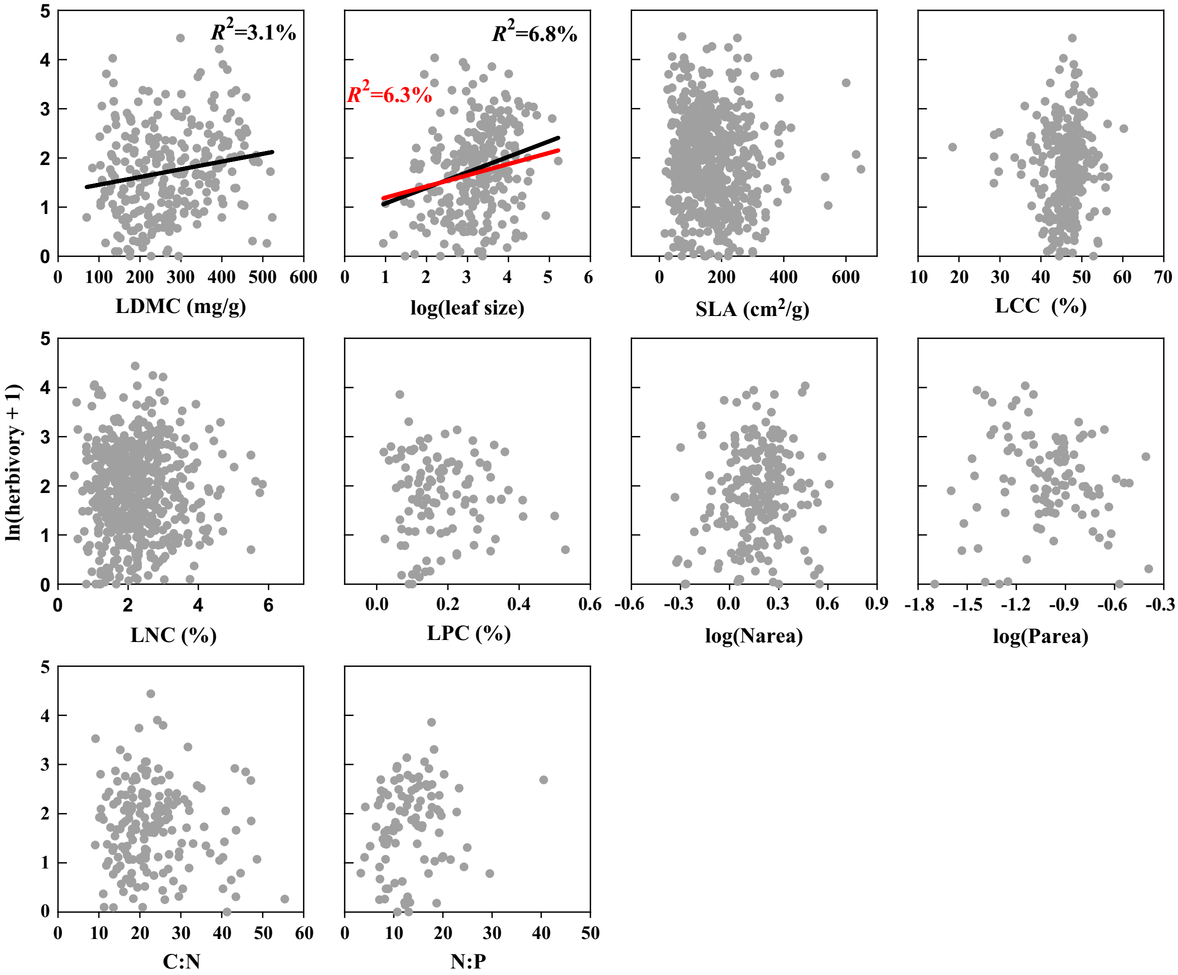

FIG. 2. The relationships between herbivory and other leaf traits at the interspecific level, with each dot representing a species. The black and red lines were fitted by the ordinary least square regression and phylogenetic least square regression respectively. Abbreviations are LDMC, leaf dry mass content; SLA, specific leaf area; LCC, leaf carbon content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; Parea, phosphorus content per area (g/cm^2); Narea, nitrogen content per area (g/cm^2); C:N, carbon:nitrogen ratio in leaves; N:P, nitrogen:phosphorus ratio in leaves. Leaf size mas measured in mm^2. [Color figure can be viewed at wileyonlinelibrary.com]

therefore, these leaves may not be favored by herbivores (Pearse and Karban 2013). Among more deciduous species, herbivores feed on their leaves for limited periods and leaf dropping is considered an avoidance strategy against herbivory (Karban 2007, 2008). Thus, the trade-off between palatability and feeding period can lead to the hump-shaped relationship between leaf lifespan and herbivory (Pearse and Karban 2013). Leaf lifespan is related negatively to the growth rate of plants (Coley 1987, Poorter and Bongers 2006), and, in general, deciduous species grow faster than evergreens species do, and may adopt tolerance strategies to herbivory (Herms and Mattson 1992). In this case, herbivory will be related positively to leaf lifespan in deciduous species, as we showed here. Because of their lower growth rate, evergreen species may adopt resistance strategies to herbivores (Herms and Mattson 1992), and enhance their investments in defense as their leaf lifespan increases (Coley et al. 1985, Coley 1987), which can account for the negative correlation between leaf lifespan and herbivory in evergreen species.

We suggest that some patterns of herbivory detected recently on a global scale can be explained by our findings. In general, woody species suffer a considerably higher level of herbivory than do non-woody species (Turcotte et al. 2014*a*, Zhang et al. 2016). We also confirmed that pattern in this study (Appendix S1: Fig. S2); however, when the role of leaf lifespan was taken into account, growth form showed a negligible effect on herbivory. Non-woody species have much shorter leaf life spans than do woody species (see Appendix S1: Fig. S2, non-woody species concentrated in the lower-left tail of the hump-shaped plot), which limits the accumulation of herbivory on their leaves. Therefore, we suggest that the

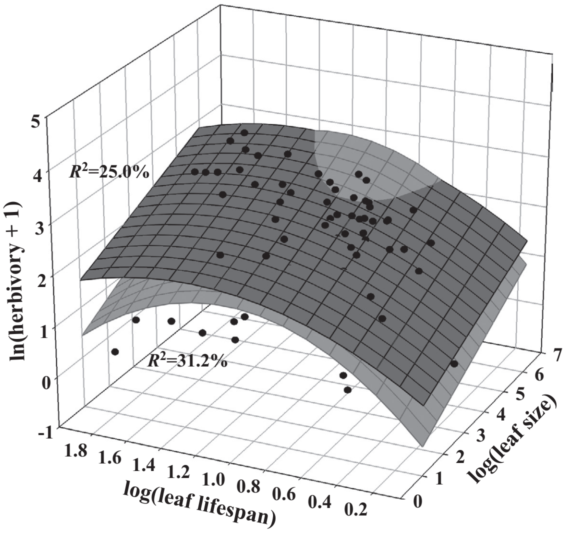

FIG. 3. The relationships of leaf lifespan and leaf size with herbivory in 126 plant species. Each dot represents a species. The gray mesh was fitted by ordinary least square regression and the black mesh was fitted by phylogenetic generalized least square regression.

lower temporal apparency of non-woody species for herbivores may be a key reason for their lower herbivory levels. Another pattern is the hemispheric asymmetry in herbivory: plants from the Southern Hemisphere had a 1.5 times higher level of herbivory than did plants from the Northern Hemisphere (Zhang et al. 2016). We also found that the leaf lifespan for species in the Southern Hemisphere was longer than that of species in the Northern Hemisphere (Appendix S1: Fig. S3). Species in the Southern Hemisphere were concentrated on the right near the center of the hump-shaped plot (Appendix S1: Fig. S3). Thus, a relatively longer leaf lifespan could lead to higher levels of herbivory in the Southern Hemisphere. In the resampling tests, we found little relationship between latitude and herbivory when the effects of leaf lifespan and MAT were taken into account. This result suggests that latitudinal variation in leaf lifespans also may be an important factor that shapes the latitudinal patterns of herbivory observed in recent studies (Kozlov et al. 2015*b*, Zhang et al. 2016).

Herbivory also showed a stable positive relationship with leaf size in our study. Within a species, a previous study also detected a similar pattern (Garibaldi et al. 2011). Species with large leaves often grow faster and are more tolerant of herbivores, which can result in higher levels of herbivory. Kozlov et al. (2015*a*) found a positive correlation between herbivory and SLA, but in our study, we detected no such relationship. The reason for this difference may lie in the variation in the data sets used. We collected data only from published studies; Kozlov et al. (2015*a*) also included a proportion of original data on

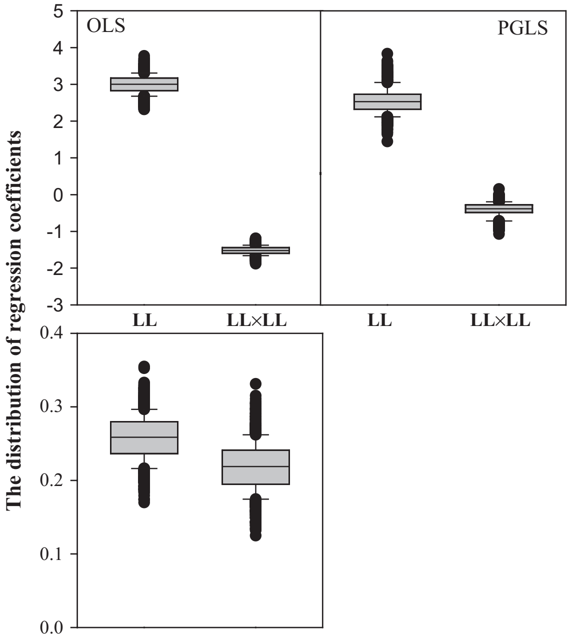

FIG. 4. The relationships of leaf lifespan (LL, upper panels) and leaf size (lower panel) with herbivory based on random resamplings tests (n = 1,000). Parameter estimation was conducted in each resampling by ordinary least square regression (OLS) and phylogenetic least square regression (PGLS).

TABLE 2. The effect of different factors on herbivory in 1,000 times resampling tests.

Variable	Proportion of $P < 0.05$ (%)
Full model	
OLS	
Latitude	0.3
Growth form	0.5
MAT	91.5
LL	99.9
LL × LL	100.0
PGLS	
Latitude	0.1
Growth form	0.1
MAT	61.7
LL	77.2
LL × LL	84.2
Simplified model	
OLS	
MAT	100.0
LL	100.0
LL × LL	100.0
PGLS	
MAT	92.7
LL	99.3
LL × LL	98.9

Notes: Ordinary least square regression (OLS) and phylogenetic generalized least square regression (PGLS) were conducted separately for each resampling. For abbreviations, LL, leaf lifespan; MAT, mean annual temperature.

herbivory, but herbivory in these two types of data differed significantly (Kozlov et al. 2015*b*). Nevertheless, SLA only explained 1% of the interspecific variation in herbivory in the previous study (Kozlov et al. 2015*a*), and thus its effect on herbivory should be much weaker compared to leaf lifespan and size. It is somewhat surprising that the nutritional quality of leaves showed little relationship with herbivory in our study. However, compared to previous studies (Loranger et al. 2012, Schuldt et al. 2012), our work included a much greater variety of species. At a broad phylogenetic scale, different nutritional traits have complex correlations with each other (Wright et al. 2004), and these traits act on herbivory in concert (Agrawal and Fishbein 2006, Carmona et al. 2011). For example, leaves with higher N content are predicted to be more attractive to herbivores, but N is also an important element in some defensive compounds (Bauerfeind and Fischer 2013), and this can make the relationship between a particular nutritional trait and herbivory undetectable. In addition to previous arguments (Agrawal and Weber 2015), we suggest that interspecific studies that include a wide variety of species also might be unsuitable for evaluating nutritional trait–herbivory relationships.

This study includes some limitations. First, we could not avoid completely the methodological weak points in interspecific studies raised by Agrawal and Weber (2015). Second, the nature of the data set prohibited us from evaluating the combined effects of different leaf traits on herbivory in a full model and taking into account the colinearity of different traits. Third, we did not consider the intraspecific variation in leaf traits in this study, which is a common weak point in global analyses of herbivory (Kozlov et al. 2015*a*). Further studies should address these issues whenever possible. More importantly, we suggest that a new framework to predict the intra- and interspecific variations in herbivory should be developed in the near future.

In general, we found that leaf lifespan and size, rather than nutritional traits, correlated with herbivory across a wide variety of plant species. This finding can explain certain general patterns of herbivory demonstrated in recent studies. Because many key functional traits that could affect herbivory (photosynthetic assimilation rates, toughness, secondary metabolites, and leaves' palatability to herbivores) are related closely to leaf lifespan (Wright et al. 2004, Kitajima and Poorter 2010, Ripple et al. 2016), we suggest that leaf lifespan could be used as a "common currency" to explain the high variability of herbivory in natural communities.

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LITERATURE CITED

Agrawal, A. A. 2007. Macroevolution of plant defense strategies. Trends in Ecology & Evolution 22:103–109.

Agrawal, A. A. 2011. Current trends in the evolutionary ecology of plant defence. Functional Ecology 25:420–432.

Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. Ecology 87:S132–S149.

Agrawal, A. A., and M. G. Weber. 2015. On the study of plant defence and herbivory using comparative approaches: How important are secondary plant compounds. Ecology Letters 18:985–991.

Andrew, N. R., I. R. Roberts, and S. J. Hill. 2012. Insect herbivory along environmental gradients. Open Journal of Ecology 2:202–213.

Anstett, D. N., K. A. Nunes, C. Baskett, and P. M. Kotanen. 2016. Sources of controversy surrounding latitudinal patterns in herbivory and defense. Trends in Ecology & Evolution 31:789–802.

Auger, S., and B. Shipley. 2013. Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. Journal of Vegetation Science 24:419–428.

Bauerfeind, S. S., and K. Fischer. 2013. Increased temperature reduces herbivore host-plant quality. Global Change Biology 19:3272–3282.

Becerra, J. X. 2015. On the factors that promote the diversity of herbivorous insects and plants in tropical forests. Proceedings of the National Academy of Sciences USA 112:6098–6103.

Carmona, D., M. J. Lajeunesse, and M. T. J. Johnson. 2011. Plant traits that predict resistance to herbivores. Functional Ecology 25:358–367.

Chen, F. S., K. J. Niklas, G. S. Chen, and D. Guo. 2012. Leaf traits and relationships differ with season as well as among species groupings in a managed Southeastern China forest landscape. Plant Ecology 213:1489–1502.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs 53:209–233.

Coley, P. D. 1987. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74:531–536.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305–335.

Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science 230:895–899.

Díaz, S., et al. 2016. The global spectrum of plant form and function. Nature 529:167–171.

Escudero, A., J. M. D. Arco, I. C. Sanz, and J. Ayala. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. Oecologia 90:80–87.

Garibaldi, L. A., T. Kitzberger, and A. Ruggiero. 2011. Latitudinal decrease in folivory within *Nothofagus pumilio* forests: Dual effect of climate on insect density and leaf traits? Global Ecology and Biogeography 20:609–619.

Hahn, P. G., and J. L. Maron. 2016. A framework for predicting intraspecific variation in plant defense. Trends in Ecology & Evolution 31:646–656.

Heard, M. J., and D. F. Sax. 2013. Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. Ecology Letters 16:206–213.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology 67:283–335.

Ho, L. S. T., and C. Ané. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63:397–408.

Hulshof, C. M., C. Violle, M. J. Spasojevic, B. McGill, E. Damschen, S. Harrison, and B. J. Enquist. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. Journal of Vegetation Science 24:921–931.

Joern, A., T. Provin, and S. T. Behmer. 2012. Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. Ecology 93:1002–1015.

Karban, R. 2007. Deciduous leaf drop reduces insect herbivory. Oecologia 153:81–88.

Karban, R. 2008. Leaf drop in evergreen *Ceanothus velutinus* as a means of reducing herbivory. Ecology 89:2446–2452.

Kattge, J., et al. 2011. TRY—a global database of plant traits. Global Change Biology 17:2905–2935.

Kitajima, K., and L. Poorter. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. New Phytologist 186: 708–721.

Kozlov, M. V., V. Lanta, V. Zverev, and E. L. Zvereva. 2015*a*. Background losses of woody plant foliage to insects show variable relationships with plant functional traits across the globe. Journal of Ecology 103:1519–1528.

Kozlov, M. V., V. Lanta, V. Zverev, and E. L. Zvereva. 2015*b*. Global patterns in background losses of woody plant foliage to insects. Global Ecology and Biogeography 24:1126–1135.

Kozlov, M. V., V. Zverev, and E. L. Zvereva. 2014. Confirmation bias leads to overestimation of losses of woody plant foliage to insect herbivores in tropical regions. PeerJ 2:e709.

Krober, W., H. Heklau, and H. Bruelheide. 2015. Leaf morphology of 40 evergreen and deciduous broadleaved subtropical tree species and relationships to functional ecophysiological traits. Plant Biology 17:373–383.

Kurokawa, H., D. A. Peltzer, and D. A. Wardle. 2010. Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. Functional Ecology 24:513–523.

Li, X. C. 2014. Leaf fall phenology and patterns of 22 evergreen woody species in subtropical evergreen forest in Tiantong Zhejiang, China. Dissertation. Zhejiang Normal University, Jinhua, China.

Li, F. L., X. Liu, and W. K. Bao. 2016. Leaf lifespan is positively correlated with periods of leaf production and reproduction in 49 herb and shrub species. Ecology & Evolution 6:3822–3831.

Lim, J. Y., P. V. A. Fine, and G. G. Mittelbach. 2015. Assessing the latitudinal gradient in herbivory. Global Ecology and Biogeography 24:1106–1112.

Loranger, J., S. T. Meyer, B. Shipley, J. Kattge, H. Loranger, C. Roscher, and W. W. Weisser. 2012. Predicting invertebrate herbivory from plant traits: evidence from 51 grassland species in experimental monocultures. Ecology 93:2674–2682.

Metcalfe, D. B., et al. 2014. Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecology Letters 17:324–332.

Pearse, I. S. 2011. The role of leaf defensive traits in oaks on the preference and performance of a polyphagous herbivore, *Orgyia vetusta*. Ecological Entomology 36:635–642.

Pearse, I., and R. Karban. 2013. Leaf drop affects herbivory in oaks. Oecologia 173:925–932.

Poorter, L., and F. Bongers. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. Ecology 87:1733–1743.

Reich, P. B., M. B. Walters, D. S. Ellsworth, J. M. Vose, J. C. Volin, C. Gresham, and W. D. Bowman. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia 114:471–482.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a trophic cascade? Trends in Ecology & Evolution 31:842–849.

Schuldt, A., et al. 2012. Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests. Ecology Letters 15:732–739.

Siefert, A., et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Silva, J. O., M. M. Espírito-Santo, and H. C. Morais. 2015. Leaf traits and herbivory on deciduous and evergreen trees in a tropical dry forest. Basic and Applied Ecology 16: 210–219.

Tian, Y. P. 2007. Study on growth and development of plant in subtropical evergreen broad-leaved forest. Dissertation. East China Normal University, Shanghai, China.

Turcotte, M. M., T. J. Davies, C. J. M. Thomsen, and M. T. J. Johnson. 2014*a*. Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. Proceedings of the Royal Society B 281:20140555.

Turcotte, M. M., C. J. M. Thomsen, G. T. Broadhead, P. V. A. Fine, R. M. Godfrey, G. P. A. Lamarre, S. T. Meyer, L. A. Richards, and M. T. J. Johnson. 2014*b*. Percentage leaf herbivory across vascular plant species. Ecology 95:788–788.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics 24:2098–2100.

Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. Molecular Ecology Notes 5:181–183.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Zhang, S., Y. Zhang, and K. Ma. 2016. Latitudinal variation in herbivory: hemispheric asymmetries and the role of climatic drivers. Journal of Ecology 104:1089–1095.

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