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LETTER

Plant traits affecting herbivory on tree recruits in highly diverse subtropical forests

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Abstract

Differences in herbivory among woody species can greatly affect the functioning of forest ecosystems, particularly in species-rich (sub)tropical regions. However, the relative importance of the different plant traits which determine herbivore damage remains unclear. Defence traits can have strong effects on herbivory, but rarely studied geographical range characteristics could complement these effects through evolutionary associations with herbivores. Herein, we use a large number of morphological, chemical, phylogenetic and biogeographical characteristics to analyse interspecific differences in herbivory on tree saplings in subtropical China. Unexpectedly, we found no significant effects of chemical defence traits. Rather, herbivory was related to the plants' leaf morphology, local abundance and climatic niche characteristics, which together explained 70% of the interspecific variation in herbivory in phylogenetic regression. Our study indicates that besides defence traits and apparency to herbivores, previously neglected measures of large-scale geographical host distribution are important factors influencing local herbivory patterns among plant species.

Keywords

BEF-China, ecosystem functioning, Gutianshan National Nature Reserve, latitudinal range, phenolics, phytochemical diversity, plant defence, plant–insect interaction, species richness, tannins.

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INTRODUCTION

Herbivory can strongly affect plant communities and might play an important structuring role in species-rich subtropical and tropical forests (Wright 2007; Viola *et al.* 2010). However, little is known about the main drivers causing interspecific differences in herbivore damage among tree species.

It is often assumed that the extent of herbivore damage is driven primarily by morphological or phytochemical plant traits (Coley & Barone 1996; Marquis *et al.* 2001; Poorter *et al.* 2004). Primary metabolites, such as nitrogen compounds, and morphological traits related to high growth rates, such as specific leaf area, increase nutritional quality and can make plants more susceptible to herbivory (Poorter *et al.* 2004). In contrast, the role of many secondary compounds not directly involved in primary metabolism, and the part played by many morphological characteristics, have often been attributed to chemical and physical defence against herbivores (Coley & Barone 1996). Tannins, total phenolics, or even overall phytochemical diversity, but also physical traits such as leaf toughness and dry matter content, are assumed to increase a plant's resistance to herbivory (Jones & Lawton 1991; Poorter *et al.* 2004). Yet, identifying general patterns across different species has proven difficult because the vast majority of studies incorporated only a limited number of traits and plant species; thus, results have often been ambiguous (see Carmona *et al.* 2011). Moreover, the potential effects of the phylogenetic interdependence of these relationships must be accounted for, as these can be influenced by a common evolutionary history which affects the degree of trait similarity between species (Freckleton *et al.* 2011).

In addition to palatability and defence traits, characteristics relating to the abundance and geographical distribution of plants might also strongly affect local herbivory levels. Abundant plant species can experience greater herbivore damage due to the effects of negative density dependence, a process which has frequently been studied for local distribution patterns (e.g. Terborgh 2012). However, a more evolutionary, but so far neglected, perspective might equally suggest that larger-scale geographical distribution of a host plant also affects local herbivory levels. Widespread plants provide increased opportunities for host-specialisation and should sustain more widely distributed populations of herbivores, thus reducing extinction probabilities and promoting the accumulation of herbivore species over time (Kennedy & Southwood 1984; Lewinsohn *et al.* 2005; Miller 2012). High herbivore diversity can intensify herbivore pressure not only via complementarity among herbivore species, but also by increasing the probability of important herbivores being present at local scales. Range characteristics probably also affect the long-term stability of these associations, as host range fragmentation and persistence in refugia during past glacial periods differed between plant species with different range sizes and geographical distributions (Qiu *et al.* 2011). Moreover,

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herbivores might cause greater damage at the hosts' geographical range margins. Plants often face stressful environmental conditions at the margins of their range (Brown 1984), which can affect their susceptibility to herbivory (Fine *et al.* 2004; Meyer *et al.* 2006). Range characteristics might thus mediate local herbivory patterns, but so far these aspects have not been incorporated into analyses of the drivers that determine herbivore damage levels.

An improved understanding of the relative contribution and interdependence of these different characteristics to herbivore damage levels requires a pluralistic approach which incorporates the whole suite of different traits and characteristics that potentially affect plant resistance (Agrawal 2007; Carmona *et al.* 2011; Moles *et al.* 2011). In intraspecific comparisons morphological and life-history traits have recently been found to have a greater effect on herbivory levels than secondary compounds, and this could also apply to interspecific patterns (Carmona *et al.* 2011). These traits might in turn be influenced by the distributional characteristics of the plants: apparency theory predicts that plant species which are obvious to herbivores (such as those plants with high local abundance) will evolve mechanisms to reduce their nutritional attractiveness (Feeny 1976; Agrawal 2007). This evolutionary response might also be encountered at larger scales for plant species with a high regional spread, i.e. a large-scale geographical availability (Bryant *et al.* 1989; Scriber 2010). Local abundance and geographical range characteristics might thus covary with, and to some extent influence, physical or chemical defence mechanisms (e.g. Moles *et al.* 2011). However, direct effects of range-size related aspects on the species richness and composition of herbivore assemblages (Lewinsohn *et al.* 2005; Lavandero *et al.* 2009) could also cause increased herbivore pressure independent of, and even outweighing, the effects of plant defences.

Herein, we analyse the combined effects of a large number of morphological, chemical and biogeographical characteristics, as well as the influence of phylogenetic relationships, on the herbivory levels of saplings of 21 dominant tree and shrub species (representing 16 genera of nine families) in an extraordinarily plant species-rich subtropical forest in southeast China. We focus on saplings (height range: 20–100 cm), as these recruits are particularly important for the long-term maintenance of tree and shrub diversity in these forests, forming future generations of the tree and shrub layers (Bruelheide *et al.* 2011). We test which plant characteristics primarily determine mean levels of herbivore damage on tree recruits, and to what extent the effects of the various characteristics are complementary. While we expect to find (1) negative effects of defence traits and (2) positive effects of traits that increase the plants' palatability to herbivores, we hypothesise that (3) local abundance, range size and the marginality of climatic conditions at the study site (relative to the host species' overall climatic niche) positively, and in part independent of the effects of chemical and morphological traits, affect local herbivory levels.

METHODS

Study plots

The study was conducted in the Gutianshan National Nature Reserve (29°14′ N, 118°07′ E), Zhejiang Province, in southeast China. The reserve covers about 8000 ha of semi-evergreen, broad-leaved subtropical forest. In 2008, 27 study plots (30 × 30 m) were established, distributed randomly across the whole reserve. Plot selection was based on stand age (ranging from < 20 to > 80 years) and woody plant species richness (25–69 species per plot), allowing quantification of herbivory as a mean value over a range of abiotic and biotic local conditions. For further details on plot selection and general plot characteristics see Bruelheide *et al.* (2011).

Herbivory assessment

We studied insect herbivory on leaves of saplings (height 20–100 cm) from 21 tree and shrub species (Fig. 1). The study species belonged to the dominant plants, accounting for 65% of the total biomass (as approximated by their local relative basal area) in the tree and shrub layers of the study plots. A maximum of ten saplings of each species were randomly sampled in each plot (see Appendix S1 in Supporting Information). Insect herbivory was measured as standing levels of leaf damage (Ness *et al.* 2011) at the end of the rainy season in June/July 2008, which also marks the end of a major activity period for arthropods in these forests (personal observations). To ensure that the analysis was consistent among species, we only used young leaves produced in the current growing season [time of leaf flush is very similar among the studied species (T. Fang, unpublished data) and did not affect herbivory levels: $R^2 = 0.05$, $P = 0.35$]. Leaf damage was assessed as the cumulative percentage of leaf area lost due to chewing, mining, galling and (if visible) sucking insects. Damage was estimated by visual inspection using a pre-defined percentage system of six classes of photosynthetic tissue removal for each leaf (Appendix S1). The validity of the estimates was checked using samples of randomly collected leaves; these were digitally scanned to determine the exact amount of leaf damage (expressed as the ratio of removed to estimated total leaf area). For the statistical analysis, we used the mean percentage

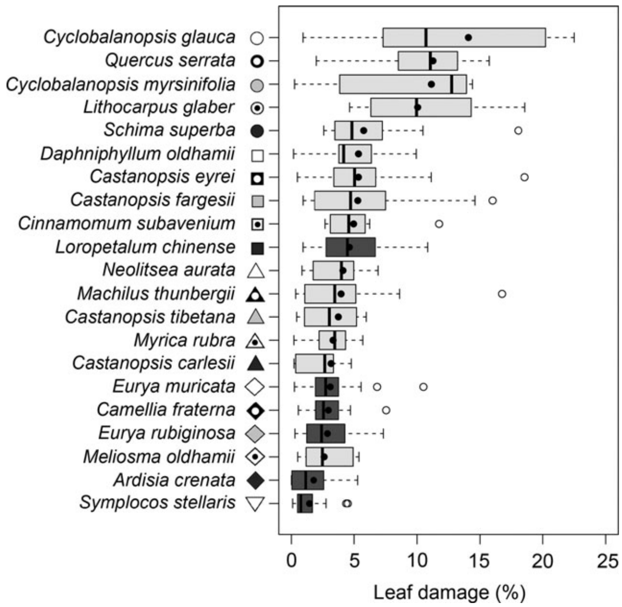

Figure 1 Leaf damage (%) on young, fully expanded leaves of 21 tree (light grey) and shrub (dark grey) species in subtropical forests of southeast China. Species are ordered by mean leaf damage levels. Filled circles indicate mean values, black lines show medians across the 27 study plots. Each species is assigned a unique symbol (next to species name) for identification in Fig. 2.

of herbivory determined from the sampled and scanned leaves for each percentage class (see Appendix S1 and Schuldt *et al.* 2010 for details).

Plant characteristics

We used a comprehensive set of morphological, chemical, biogeographical and phylogenetic characteristics of the plant species as predictors of species-specific levels of herbivory. Details of measurements and calculations of these variables are provided in Appendix S1.

The morphological leaf traits included in our analyses were leaf area, specific leaf area (SLA), leaf dry-matter content (LDMC) and leaf toughness. Larger leaves might attract more herbivores and thus show greater damage (Garibaldi *et al.* 2011). The SLA, which is often positively related to plant growth rate and leaf quality, can have similar effects (Diaz *et al.* 2004). The LDMC, on the other hand, is often considered to be related to leaf robustness and toughness (Poorter *et al.* 2009; Kitajima & Poorter 2010).

A wealth of phytochemical compounds and compound classes has been identified as potential defence against herbivores (Coley & Barone 1996). We tested for total phenolics and tannins as 'classical' chemical defences (Coley & Barone 1996). However, a variety of compounds are effective against different herbivores and might also act together to affect herbivores (Rasmann & Agrawal 2011). Thus, we also used chemical diversity and chemical uniqueness (expressed as the Shannon Index and the proportion of unique retention time peaks, respectively, of leaf extracts in HPLC analysis) as measures of the general phytochemical diversity (Lavandero *et al.* 2009). The method records UV spectra of a multitude of both non-polar and weakly polar compounds, among them a large number of compounds with UV spectra that point to flavonoids such as kaempferol and quercetin derivatives. Herbivores might have difficulties dealing with chemical mixtures, and high phytochemical diversity or unique phytochemical features not shared by many other plants might thus reduce a plant species' overall susceptibility to herbivory (Jones & Lawton 1991; Lavandero *et al.* 2009; Rasmann & Agrawal 2011). As chemical traits that determine the nutritional quality of the plants, we included leaf C and N content (%) and the C/N ratio, which have often been used as measures of palatability to herbivores (Poorter *et al.* 2004).

As a measure of mean local abundance, we used the total basal area (cm^2 per plot) of each species averaged across study plots (see Appendix S1 and Bruelheide *et al.* 2011).

Variables related to the plant species' geographical range were latitudinal range, minimum latitude of the species' range, geographical range size (approximated as the number of occupied $0.25 \times 0.25'$ grid cells), climatic niche breadth (calculated from temperature and precipitation ranges of the occurrence data points) and marginality of climatic conditions at the study site, i.e. the minimum distance in PCA space to the margin of the species' niche (see below). Larger range size, latitudinal range and niche breadth might promote the accumulation of herbivore species adapted to a plant species over time (Lewinsohn *et al.* 2005). A lower minimum latitude of the plant species' range might have a similar effect, as it can indicate a higher long-term stability of plant-herbivore associations in historical time (see Discussion). Finally, deviations from the mean climatic niche conditions of the plant species (high niche marginality) at the study site might increase environmental stress and affect the plants' susceptibility to herbivory. Distribution data were derived from data bases, published range maps and regional floras (see Appendix S1 for a complete list of data sources). Species occurrence data were geo-referenced and digitised to calculate species ranges. Corresponding climate data ($0.25 \times 0.25'$ resolution) were extracted from the Worldclim database (http://www.worldclim.org). The niche position and niche breadth along climatic axes were quantified using a multivariate coinertia analysis computing an Outlying Mean Index (Dolédec *et al.* 2000). The analysis results in species-specific descriptions of the niche ranges along the main principal components of the environmental data space of all considered species. In this context, the species-specific niche position is a measure of the deviations of the mean climatic conditions of the study location from the range-wide habitat conditions of each species, calculated as the mean of marginality distances on each principal components axis (see Appendix S1 for details).

Phylogenetic relationships between species were constructed from rbcL and matK sequences, downloaded from NCBI Genbank (http://www.ncbi.nlm.nih.gov; Table S2 in Appendix S1). Sequences were aligned in Bioedit, and a first phylogenetic hypothesis was generated using maximum likelihood (ML) in MEGA5 (Tamura *et al.* 2011). A second ultrametric tree was computed based on the ML tree (Figure S1 in Appendix S1) using penalised likelihood. The branch lengths in this tree are a measure of divergence time. For each of our study species we also included the number of congenerics growing in the 27 study plots as a measure of taxonomic isolation. This can provide additional insight into plant community effects on interspecific patterns of herbivore damage (Ness *et al.* 2011).

Data analysis

We used phylogenetic general least squares (PGLS) regression, based on the ultrametric phylogenetic tree, to test for the effects of biogeographical, morphological and chemical plant traits on insect herbivory levels. Damage was expressed as the mean leaf damage per species averaged across plots to match it with the explanatory variables, which were available in most cases only as species-level data (due to the nature of the data or because traits were measured from pooled samples). This also hinders the integration of potential effects of intraspecific trait variation on herbivory and phylogenetic relationships in our models (cf. Ives *et al.* 2007). This would have required trait measurements at the plot or individual level, and limits our analyses to an interspecific perspective based on mean trait values. However, variance components analysis of the herbivory data on the individual plant level (regressing herbivory on species and plots as random effects) revealed that 29.2% of the variation was explained by species, 5.5% by plots (pooled over species) and 65.3% was residual variation, indicating that intraspecific variation in herbivory due to changes in environmental conditions among the 27 study plots was low compared with interspecific variation in herbivory levels across species.

Phylogenetic analysis assumes that the residual error of the regression (and not necessarily the independent and dependent variables) is affected by phylogenetic relationships among the species studied (Revell 2010). In many cases, the strength of this phylogenetic signal is not known *a priori* and thus it is not possible to determine in advance whether phylogenetically explicit modelling should be used (Freckleton 2009). We thus followed the approach suggested by Revell (2010) and simultaneously estimated the phylogenetic signal in the regression residuals with the regression parameters, quantifying Pagel's λ with a maximum likelihood approach. The value of λ is adjusted to, and optimised for, the strength of the phylogenetic signal in the error structure (where $\lambda = 0$ indicates no phylogenetic signal and $\lambda = 1$ a strong phylogenetic signal according to a Brownian motion model of trait evolution; Freckleton *et al.* 2011). This ensures that potential phylogenetic effects are adequately considered and reduces the risk of over or underestimating this effect (Revell 2010; Freckleton *et al.* 2011). As the presence or absence of phylogenetic effects is already automatically accounted for in this regression, the approach is statistically more straightforward than a comparison between phylogenetically corrected and uncorrected models (cf. Freckleton 2009). We also checked for the strength and significance of the phylogenetic signal in the regression residuals by calculating K statistics (Blomberg *et al.* 2003). For additional information on the individual variables see Table S1 in Appendix S1.

Prior to analysis, we checked for collinearity among explanatory variables. Minimum latitude, latitudinal range and distribution area were strongly correlated with the climatic niche breadth (Pearson's $r = 0.75$, $P < 0.001$; $r = -0.68$, $P < 0.001$; and $r = 0.70$, $P < 0.001$ respectively), C/N ratio with N content ($r = -0.93$, $P < 0.001$) and phenolic content with tannins ($r = 0.80$, $P < 0.001$). To avoid problems of multicollinearity, we only retained those variables most strongly related to herbivory in each of the above-mentioned sets. Differences in the number of plant individuals sampled for herbivory (the 27 plots did not necessarily have 10 saplings from each of the 21 species) had no effect on mean leaf damage ($r = -0.19$, $P = 0.935$) and we did not include this variable in the regression analyses. The full model thus included leaf area, SLA, LDMC, leaf toughness, chemical diversity, chemical uniqueness, C content, N content, tannin content, mean local abundance, climatic niche breadth, niche marginality, congeneric isolation and growth form (tree or shrub) as predictors of the differences in herbivory levels between species (Table S1 in Appendix S1). Mean leaf damage, mean local abundance, leaf area and tannin content were log-transformed to increase normality of the data.

We used model simplification based on the Akaike Information Criterion (AIC_c, corrected for small sample sizes; Burnham & Anderson 2004). Variables were eliminated from the full model until a minimal, best-fit model with the lowest global AIC_c was obtained. Model residuals were checked for assumptions of normality and homoscedasticity. Variance partitioning (Legendre & Legendre 1998) was used to determine the independent and shared effects of the explanatory variables on mean levels of herbivore damage between the 21 tree and shrub species. Statistical analyses were performed with R 2.12.0 (http://www.R-project.org).

RESULTS

Overall, we assessed herbivory on 1602 individuals (on a total of 36 752 leaves) of the 21 tree and shrub species. Mean leaf damage by insect herbivores ranged from 1.4 to 14.1% per plant species (Fig. 1), with an overall mean of 5.3%.

The best PGLS-model ($\text{AIC}_c = 24.9$, compared to $\text{AIC}_c = 159.6$ for the full model) accounted for 70.3% of the among-species variation in herbivory ($F_{5,16} = 12.84$; $P < 0.001$) and included LDMC ($t = 4.4$; $P < 0.001$), mean local abundance ($t = 3.8$; $P = 0.0016$), climatic niche breadth ($t = 3.3$; $P = 0.0049$) and niche marginality ($t = 2.5$; $P = 0.0233$) as predictors (Table 1). Simultaneous consideration of phylogeny with the regression parameters showed that there was no phylogenetic signal in the residual error of the regression model (Pagel's $\lambda = 0$). This was also confirmed by an additional analysis of the residuals using K statistics as an alternative measure ($K = 0.17$; $P = 0.11$). Yet, results were essentially the same even when (incorrectly, see Revell 2010) assuming phylogenetic effects (with $\lambda = 1$) due to signals in individual variables, thus underlining the robustness of our results (Table S3 in Appendix S2).

All four explanatory variables were significantly positively related to leaf damage by insects, i.e. mean herbivory levels increased with LDMC, local abundance, the breadth of the climatic niche and niche marginality (Table 1; Fig. 2). Leaf chemical traits were not included in the minimal model and did not show significant correlations with leaf damage in single regressions (not shown). The only exception was C content, which was also not included in the minimal model, but showed a significant positive relationship with herbivory in single regression ($R^2 = 0.17$; $P = 0.039$) and was correlated with LDMC (Pearson's $r = 0.61$; $P = 0.003$). In contrast, leaf toughness was not significantly related to herbivory ($R^2 = 0.09$; $P = 0.193$), nor was it correlated with LDMC ($r = 0.09$; $P = 0.674$).

Partitioning the total explained variance among the four predictors showed that LDMC, mean local abundance and climatic niche breadth and niche marginality accounted for largely independent fractions of explained variance (Fig. 3). The LDMC (32.3%) had the strongest independent effect on leaf damage levels, followed by mean local abundance (23.5%). The independent effects of the range size variables, climatic niche breadth and niche marginality accounted for 15% of the variance in the herbivory data (Fig. 3).

DISCUSSION

By incorporating rarely tested biogeographical characteristics and the large number of morphological and chemical traits of a large proportion of the dominant plant species, our study provides a more comprehensive analysis of interspecific herbivory patterns than previous studies. It thus yields new insights into the relative importance and interdependence of drivers that might cause differences in mean levels of herbivory and promote the maintenance of woody plant diversity in plant species-rich forests. Three major conclusions arise from our study: whereas (1) our herbivory data do not reveal an effect of chemical compounds generally assumed to

Table 1 Regression results for the minimal-adequate phylogenetic general least squares model for mean herbivore damage levels (log-transformed) of 21 tree and shrub species in subtropical China

Variable	Estimate (standardised)	SE	t	P
(Intercept)	1.499	0.071	21.1	< 0.001
Leaf dry matter content	0.335	0.076	4.4	0.0004
Mean local abundance (log-transf.)	0.282	0.074	3.8	0.0016
Climatic niche breadth	0.303	0.093	3.3	0.0049
Niche marginality	0.234	0.093	2.5	0.0233

Adjusted $R^2 = 0.703$; $F_{5,16} = 12.84$; $P < 0.001$.
ML estimation of $\lambda = 0$.

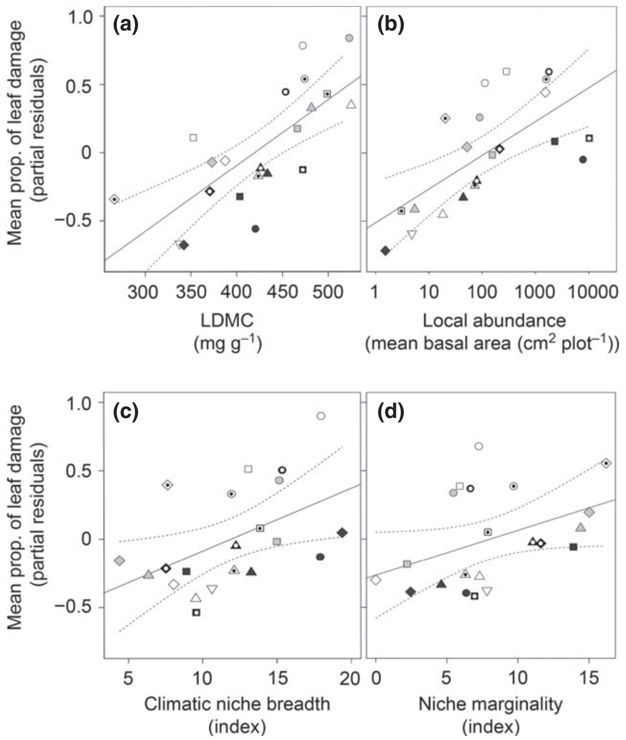

Figure 2 Independent effects of (a) leaf dry matter content, (b) mean basal area as a measure of local abundance, (c) climatic niche breadth and d) niche marginality on the mean proportion of leaf damage (partial residuals and 95% confidence bands with the effects of all other variables partialled out) by insect herbivores across 21 tree and shrub species in subtropical China. Niche breadth and marginality are dimensionless index values calculated from coinertia analyses (see Methods). All relationships are significant at $P < 0.05$ (see Table 1). Each species is assigned a unique symbol (see Fig. 1).

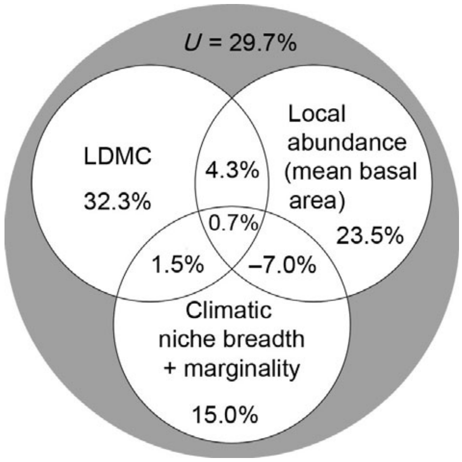

Figure 3 Partitioning of between-species variance in herbivory of young, fully expanded leaves of the 21 study species into independent and shared effects (percent explained variance) of morphological (leaf dry matter content), local (mean basal area as a measure of local abundance), and biogeographical (climatic niche breadth and niche marginality) variables. Shared effects are shown in the intersecting parts of the circles. *U* is the unexplained variation.

play an important role in plant defence, (2) distributional characteristics have strong effects on local herbivory patterns and (3) these distributional characteristics are largely independent of palatability and defence traits.

Our finding (1) is in contrast to the results of many previous studies, which, however, often focused on either a single or on a few, and similar, plant species (e.g. Eichhorn *et al.* 2007; Lavandero *et al.* 2009; Muola *et al.* 2010). However, it corroborates recent results of a more global analysis which indicates that secondary metabolites are of less importance as a defence against herbivory than morphological and life-history traits (Carmona *et al.* 2011). Unfortunately, we were not able to consider potential effects of intraspecific variation in defence traits in our results (cf. Ives *et al.* 2007). Yet, intraspecific variation among study plots was low compared with variation in herbivory among species (see Methods). Moreover, Carmona *et al.* (2011) showed that general support for an impact of secondary metabolites is also weak for intraspecific patterns. We did not consider the full range of potential chemical defence compounds, but the compounds we measured are frequently considered to have a particularly strong effect on herbivory (Coley & Barone 1996; Moles *et al.* 2011). Many specific chemical defence mechanisms might be overcome by the multitude of herbivore species adapted to, and able to deal with, phytochemical compounds of their hosts (see also Kurokawa & Nakashizuka 2008) to such an extent that in an interspecific context, other plant characteristics may have a stronger bearing on mean herbivore damage levels. Our study shows that even without finding a strong signal of chemical defence traits, a large proportion (70%) of the interspecific variation in herbivory can be explained by such alternative characteristics.

The strongest predictor in our analysis was LDMC. However, although high values of LDMC and analogous measures are often related to traits that convey physical resistance to herbivores (i.e. leaf toughness: Coley & Barone 1996; Perez-Harguindeguy *et al.* 2003; Poorter *et al.* 2009), we found an increase in herbivory with LDMC. Our results indicate that effects other than physical toughness are responsible in our case: LDMC was not related to leaf toughness in our study, and our direct measure of leaf toughness had no effect on herbivory. Leaf toughness does not necessarily pose an obstacle to herbivores adapted to tough leaves. Herbivores with strong mouthparts, particularly external leaf chewers, such as many beetles (which also caused a large proportion of the overall damage in our system; Schuldt *et al.* 2010), are not constrained in their feeding by physical leaf structure and can thus select leaves on the basis of other criteria (see also Marquis *et al.* 2001; Perez-Harguindeguy *et al.* 2003). This may apply in particular to regions such as our subtropical forests, where the leaves of most plant species are generally relatively tough, and may explain the deviating results of other studies from, for instance, temperate regions (see also Marquis *et al.* 2001; Perez-Harguindeguy *et al.* 2003). In view of the lack of support for physical defence effects, the positive relationship of both LDMC and C content (which did not, however, enter the final regression model) to herbivory might point to a different underlying mechanism: higher C content, and concomitantly higher LDMC, can represent a higher amount of structural components (Poorter *et al.* 2009). This, in turn, can cause herbivores to increase leaf consumption to compensate for lower nutrient content relative to structural compounds (Berner *et al.* 2005; Stiling & Cornelissen 2007). This may be particularly important as higher LDMC also means reduced leaf water content, which, in turn, can decrease nitrogen accumulation rates of herbivores

(Scriber & Slansky 1981). We did not find a direct relationship between herbivory and traits such as leaf N content and C/N-ratio. Although N content is often related to leaf palatability (Coley & Barone 1996; Poorter *et al.* 2004), it can also include N-based compounds which are used as a defence against herbivores (Baraza *et al.* 2007). A lack of effects of N content on herbivory at an interspecific level has also been reported by several other studies (e.g. Berner *et al.* 2005; Eichhorn *et al.* 2007).

Most importantly, however, our findings (2) and (3) confirm our initial hypothesis that distribution characteristics also play a role in influencing local patterns of herbivory, independent of local abundance and other plant characteristics. Incorporation of biogeographical characteristics can thus improve our understanding of differences in the levels of herbivore damage among plant species. Our findings also provide little evidence for the assumption of the apparency theory that more apparent plants exhibit a higher degree of defensive traits or reduced palatability (see also Agrawal 2007). Leaf traits important for herbivory, such as LDMC, were little affected by local abundance in our study. They were also not influenced by biogeographical characteristics. However, this also means that the local-abundance and biogeographical effects we found were not caused by covarying effects of morphological or chemical plant traits. Rather, they might be related to the direct effects of herbivores. Locally more apparent, or more widespread, plants should be more visible, or regionally more widely available, to herbivores and thus face higher herbivore pressure (Chew & Courtney 1991; Brändle & Brandl 2001; Terborgh 2012). Our measures of niche breadth and niche marginality highlight the factors potentially underlying biogeographical effects that have also become evident in studies of latitudinal range effects on herbivore diversity and spatial patterns in herbivory (Jones & Lawton 1991; Brändle & Brandl 2001; Lavandero *et al.* 2009; Moles *et al.* 2011). Both of our measures incorporate temperature and precipitation and thus characterise not only the area of distribution but also the breadth of the plants' climatic niches. Plants covering a broader range of climatic conditions face a larger and more diverse set of herbivore species in their distribution ranges (Chew & Courtney 1991; Brändle & Brandl 2001; Lavandero *et al.* 2009). Besides higher encounter rates and the support of larger, less extinction-prone populations of herbivores across their ranges (Kennedy & Southwood 1984; Ness *et al.* 2011), widespread plant species might have had a higher probability of persisting (together with a larger proportion of their herbivores) in climatically suitable areas during past climatic changes. Niche breadth was strongly positively related to minimum latitude of the distribution range in our study (Pearson's $r = 0.75$, $P < 0.001$). This could indicate a higher long-term stability of plant–herbivore associations for these species, as glacial refuges for subtropical species were primarily located in southern China (Qiu *et al.* 2011). These large-scale geographical effects of host availability can influence local-scale patterns. Interrelations between regional and local species pools (Lewinsohn *et al.* 2005; Harrison & Cornell 2008) increase the probability of a locally more diverse set of herbivores adapted to these plants and concomitantly the likelihood that important herbivore species which increase herbivore pressure are present. Moreover, the observed positive relationship between herbivory and niche marginality indicates that plants are more susceptible to herbivory at their environmental range margins. One explanation would be that herbivory directly contributes to limiting the host species ranges. However, it is also conceivable that climatically marginal conditions at the study site affect plant physiology and morphology and make them more susceptible to herbivory (Fine *et al.* 2004; Meyer *et al.* 2006).

Although our study excludes very rare species and their contribution to interspecific trait variability, mean local abundance of the studied species varied by several orders of magnitude. Likewise, the species showed high interspecific variation in their morphological, chemical and biogeographical characteristics (Table S1), such that our set of species is representative of a large part, but obviously not all tree and shrub species occurring in the study region.

Our results were not affected by phylogenetic relationships among the studied species, which is in line with the results of related studies (cf. Brändle & Brandl 2001). Range size-related characteristics and abundances can be evolutionary labile and can differ strongly between closely related species (Losos 2011). On the other hand, convergent selection may have contributed to similar leaf morphology among species, with the majority of species in our forest ecosystem, for instance, having relatively tough leaves compared with species from more temperate regions.

CONCLUSIONS

Variance partitioning showed that morphological traits, local abundance and biogeographical characteristics had largely independent effects on mean herbivory levels, but together explained a large proportion (70%) of the overall herbivory found among the 21 tree and shrub species. Effects on mean herbivory levels were thus complementary, with morphological traits and local abundance, for instance, being largely unaffected by the biogeographical characteristics of the plants (cf. Garibaldi *et al.* 2011). The latter also applied to chemical plant traits, which were of less importance in our study, but were in some cases correlated with morphological traits. A clear message from our findings is that distributional, morphological and chemical characteristics need to be considered simultaneously if we are to improve our understanding of interspecific patterns of herbivory. This approach has rarely been applied in previous studies, but can provide a better knowledge of the main drivers influencing herbivore damage levels. In addition to leaf traits that reflect palatability or defence, the apparency of plant species on a local scale, and the availability to herbivores on a larger geographical scale emerge as important, but – in the case of geographical distribution measures – previously neglected, factors that influence mean herbivory levels. Apparency and range characteristics might thus potentially contribute to maintaining patterns of coexistence between plant species in ecosystems with high plant diversity.

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AUTHORSHIP

AS, HB, MF, WH, KM, BS, TA designed the study. AS, WD, DE, WK, SM, WUP, EW, HZ collected and prepared the data. AS carried out statistical analyses and wrote the manuscript, with input from all coauthors.

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