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 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, plant defence, plant–insect interaction, species richness, and geographical distributions (Qiu et al. 2010) may play a role in herbivore damage. 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 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, 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,
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.](Image 324x113 to 554x337)
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 (Díaz 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 (cm² 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 × 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 florras (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 × 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 co-inertia 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 congeneric species 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 limited 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 $\lambda$ with a maximum likelihood approach. The value of $\lambda$ 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 ($\text{AIC}_c$, 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 $\text{AIC}_c$ was obtained. Model residuals were checked for assumptions of normality and homoscedasticity. Variance partitioning (Legendre & Legendre 2004) was used to determine the independent and shared effects of the explanatory variables on mean levels of herbivore damage (Fig. 1). The explanatory variables on mean levels of herbivore damage (Fig. 1) 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>
<thead>
<tr>
<th>Variable</th>
<th>Estimate (standardised)</th>
<th>SE</th>
<th>$t$</th>
<th>$P$</th>
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<tbody>
<tr>
<td>(Intercept)</td>
<td>1.499</td>
<td>0.071</td>
<td>21.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Leaf dry matter content</td>
<td>0.335</td>
<td>0.076</td>
<td>4.4</td>
<td>0.0004</td>
</tr>
<tr>
<td>Mean local abundance (log-transf.)</td>
<td>0.282</td>
<td>0.074</td>
<td>3.8</td>
<td>0.0016</td>
</tr>
<tr>
<td>Climatic niche breadth</td>
<td>0.303</td>
<td>0.093</td>
<td>3.3</td>
<td>0.0049</td>
</tr>
<tr>
<td>Niche marginality</td>
<td>0.234</td>
<td>0.093</td>
<td>2.5</td>
<td>0.0233</td>
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Adjusted $R^2 = 0.703$; $F_{5,16} = 12.84$; $P < 0.001$. ML estimation of $\lambda = 0$. © 2012 Blackwell Publishing Ltd/CNRS
display 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.

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.
Wood 1984; Ness populations of herbivores across their ranges (Kennedy & South-encounter rates and the support of larger, less extinction-prone Bra¨ ndle & Brandl 2001; Lavandero matic conditions face a larger and more diverse set of herbivore plants' climatic niches. Plants covering a broader range of cli-
not only the area of distribution but also the breadth of the
Terborgh 2012). Our measures of niche breadth and niche
biogeographical characteristics can thus improve our understand-
ing of differences in the levels of herbivore damage among plant
Our findings also provide little evidence for the assump-
tion 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; Térborgh 2012). Our measures of niche breadth and niche

Most importantly, however, our findings (2) and (3) confirm

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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 her-

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ACKNOWLEDGEMENTS

We thank the administration of the Gutianshan National Nature Reserve and members of the BEF China consortium for support. We are particularly grateful to Teng Fang (Gutianshan NNR) for help with plot establishment, species identification and data on leaf flush phenology. Data on basal area of trees were provided by Martin Baruffol and Martin Böhne. Alrun Siebenkäs and Gunnar Seidler contributed to the compilation of range characteristics. Christian Ristok carried out part of the phenolic and tan-nin analysis. We gratefully acknowledge funding by the German

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Research Fund (DFG FOR 891/1 and 891/2) and the National Science Foundation of China (NSFC 30710103907 and 30930005), as well as various travel grants for project preparation financed by the DFG, NSFC and the Sino-German Centre for Research Promotion in Beijing (GZ 524, 592, 698 and 699). We thank C. E. Timothy Paine and two anonymous reviewers for helpful comments that improved the manuscript.

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.

REFERENCES


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Editor, Vojtech Novotny
Manuscript received 11 January 2012
First decision made 13 February 2012
Second decision made 27 March 2012
Manuscript accepted 4 April 2012

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