

Herbivory, growth rates, and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity

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Abstract. Tropical plant diversity is extraordinarily high at both local and regional scales. Many studies have demonstrated that natural enemies maintain local diversity via negative density dependence, but we know little about how natural enemies influence beta-diversity across habitats and/or regions. One way herbivores could influence plant beta-diversity is by driving allocation trade-offs that promote habitat specialization across resource gradients. We therefore predicted that increasing resource availability should be accompanied by increasing herbivory rates and decreasing plant allocation to defense. Second, relative abundances within plant lineages are predicted to reflect patterns of habitat specialization and allocation trade-offs. A phylogenetic context is vital not only to compare homologous plant traits (including defense strategies) across habitat types, but also to connect evolutionary trade-offs to patterns of species diversification in each phylogenetic lineage.

We tested these predictions for trees in white-sand, clay terra firme, and seasonally flooded forests in Peru and French Guiana that represent the range of soil fertility, forest structure, and floristic compositions found throughout the Amazon region. We established 74 0.5-ha plots in these habitats and sampled all trees. Within 12 representative plots we marked newly expanding leaves of 394 saplings representing 68 species, including the most abundant species in each plot in addition to species from five focal lineages: *Swartzia* and *Inga* (Fabaceae), *Protieae* (Burseraceae), *Bombacoideae* (Malvaceae), and *Micropholis* (Sapotaceae). We measured total leaf production rates for each sapling and calculated relative herbivory impact as the ratio between herbivory rate and leaf production rate.

Herbivory rates averaged 2.1% per month, did not correlate with leaf production rate, and were similar across habitats. Relative herbivore impacts exceeded leaf production rates for most species. Leaf production rate averaged 2.8%, was significantly higher in seasonally flooded forests than the other two habitats, and exhibited significant correlations with specific leaf area. Species with high herbivory rates exhibited significantly lower relative abundances in terra firme forests. Overall, focal species within lineages present contrasting patterns regarding their herbivory rates and leaf production rate within habitats. These results highlight why a lineage-based approach is necessary when attempting to connect hypotheses regarding evolutionary trade-offs to community assembly patterns.

Key words: Amazon rainforest; beta-diversity; forest habitat; French Guiana; herbivory; natural enemies; Peru; plant defense traits; resource availability.

INTRODUCTION

Tropical plant diversity is extraordinarily high at both local and regional scales, including a significant component of beta-diversity, or the turnover in species composition across habitats and regions (Condit 2002,

Tuomisto et al. 2003, Fine et al. 2010, Swenson et al. 2012). Increasing evidence has demonstrated the critical role of natural enemies in maintaining local diversity via negative density dependence (Carson et al. 2008, Comita et al. 2010, Mangan et al. 2010, Metz et al. 2010), but we know very little about how natural enemies influence beta-diversity. Recently, Fine et al. (2004) proposed that herbivores contribute to plant beta-diversity by driving allocation trade-offs that promote habitat specialization across resource gradients.

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Plant defense theory predicts that, in low-resource environments, the impact of herbivory will be especially large because of the cost of replacing lost tissue, thereby driving natural selection for plant defenses (Janzen 1974, Coley et al. 1985). Investment in defenses, in turn, will cause even slower growth rates due to the impossibility of allocating energy simultaneously to both growth and defense (the growth–defense trade-off; Coley 1987). In high-resource environments, plants can invest more of their energy into growth rather than defense because resources are more available and thus tissue loss is less costly. Across habitats that differ in resource availability, herbivores are therefore predicted to reinforce convergence within habitats and divergence among habitats in allocation strategies of growth vs. defense investment and in the corresponding herbivory rates. In this way, herbivores can promote habitat specialization and beta-diversity in plants (Fine et al. 2004, 2006).

The Amazonian lowlands exhibit substantial habitat heterogeneity. Hoorn et al. (2010) present evidence that the complex geological history during the Miocene involving the Andean uplift, marine incursions, and major fluvial changes promoted environmental and topographic heterogeneity that has been a major driver of Amazonian diversification. In addition, there is a broad soil fertility gradient that corresponds with seasonality from the western Amazon (fertile clay soils, no annual dry season) to the Guianas (infertile eroded clays, well-established dry season). In the mega-diverse Amazonian lowlands there are three well-defined habitats: (1) white-sand forest habitat islands (WS) that are surrounded by (2) terra firme clay forests with higher nutrient availabilities (TF; see Plate 1); and, in low-lying areas near rivers and streams (3) seasonally flooded forests (SF) in which the water table never descends below 50 cm depth and where surface soils often remain submerged during periods of high precipitation. Each of these three habitat types harbors a unique floristic composition (Fine et al. 2010, Wittmann et al. 2010), and there is high beta-diversity among these three habitats due to the high propensity of habitat specialist species (Baraloto et al. 2007, Fine et al. 2010). Notably, many of the same lineages (i.e., genera) have representative habitat specialist species that occur in each of these habitats.

We focused on such lineages in addition to other species that are the most abundant in each habitat type, to investigate whether insect herbivores drive habitat specialization to white-sand, terra firme, and seasonally flooded forests. Here we expanded on the hypothesis that the growth–defense trade-off interacts with environmental gradients to promote habitat specialization in plants. We integrated multiple axes of divergent environmental gradients (soil fertility, drought, and flooding), and developed explicit predictions regarding how evolutionary trade-offs in plant allocation to growth, defense, and flood tolerance should influence

the evolution and maintenance of specialization to habitats, and hence, promote beta-diversity.

We posit that allocation to growth, anti-herbivore defense and flood tolerance is best conceptualized as a series of evolutionary trade-offs, because each costs energy and a plant cannot simultaneously invest in all three. Thus, we predict that in nutrient-poor WS soils, plants invest in defense at the expense of growth and flood tolerance. In SF forests, we predict that plants invest in flood tolerance, which reduces their investments to growth and/or defense. In nutrient-rich TF forests, we predict that plants should invest more in growth at the expense of defense and flood tolerance. We therefore predict, not only that species with higher investment in growth will incur lower defense investment, but also that the extent of this investment will depend on the resource availability of the habitat in which the species occurs (Fig. 1a). However, defense investment may not always correlate well with herbivore attack, especially with limited sampling effort (Fig. 1a, b). For example, plants with low defense investment and high growth rates can either experience high herbivory rates (e.g., pioneer species; Coley 1983, 1988) or low-to-high herbivory rates (Fig. 1b, diamond lineage) depending on whether some conspecific individuals are able to escape natural enemies via herbivore satiation or unpredictable phenology of leaf production (Aide 1988, 1993). Alternatively, species may be able to defend themselves at low cost or herbivores may not be important selective agents, in which case, we would predict no strong correlation between herbivory rates and growth rates.

Trade-offs in allocation between growth and defense may be mostly enforced by specialist herbivores that themselves are undergoing antagonistic coevolution with their host plants, which in turn, may have phylogenetically conserved defense strategies (Ehrlich and Raven 1964, Agrawal et al. 2009). As a result, phylogenetic relatedness of plants often mediates plant–insect interactions (Fine et al. 2006, Agrawal et al. 2009), and a phylogenetic context is necessary to make predictions about how the growth–defense trade-off may influence community composition and beta-diversity. Allocation strategies to growth, defense, and flood tolerance within and among plant lineages could be evolutionarily convergent (high variability within lineages) or conservative (low variability within lineages). If traits are convergent, then lineages may be comprised of multiple habitat specialists, and we would predict positive correlations between growth traits and herbivory rates within lineages, which in turn, may explain the relative abundance of species across habitats.

In this paper, we tested these predictions for trees in WS, TF, and SF forests in Peru and French Guiana. We integrate data on leaf production, herbivory rates, leaf traits, and species distribution across a network of 74 plots that represent the range of soil fertility, forest structure, and floristic compositions found throughout

the Amazon region. We used a comparative approach for both abundant species in each habitat type and for five focal lineages that comprise habitat specialists (*Swartzia* and *Inga* [Fabaceae], *Protieae* [Burseraceae], Bombacoideae [Malvaceae], and *Micropholis* [Sapotaceae]) to address three research questions: (1) How do allocation strategies related to growth and defense vary among species and lineages? (2) How does leaf production and herbivory vary among habitats and countries? (3) How do allocation trade-offs predict the relative abundance of a species across white-sand, clay terra firme, and seasonally flooded forests?

MATERIALS AND METHODS

Study sites and plot network

This study is based in a permanent vegetation plot network of 74 modified Gentry plots established during 2008–2010 to broadly sample geographic and environmental gradients in lowland tropical forests of South America (Baraloto et al. 2011). The plot network represents a factorial design, with multiple replicates in Loreto, Peru, and French Guiana, of the three broad habitat classes (SF, TF, and WS).

Focal species

We selected focal species to address our research questions using an expanded phylogenetic approach to ensure adequate representation of local floristic composition in each habitat and region. We focused our analyses on five lineages that are widespread in the Amazon Basin and Guiana Shield and contain multiple species associated with each of the three studied habitats: *Inga* and *Swartzia* (Fabaceae), *Protium* (Burseraceae), Bombacoideae (Malvaceae), and *Micropholis* (Sapotaceae) (Table 1). These lineages are phylogenetically dispersed within the eudicots, the dominant angiosperms in tropical rain forests, with representatives of asterids (Sapotaceae), fabids (Fabaceae), and malvids (Malvaceae and Burseraceae). Each of these lineages is known to employ diverse physical and chemical defense strategies (Table 1). We also studied at least three species in each plot that were among the species with the highest relative abundance in each habitat in each region. Overall, we focused on 68 species across the two regions (Fig. 2). Here we integrated three data sets collected for these species: censuses of sapling leaf production and leaf herbivory, measures of leaf functional traits related to plant growth and herbivore defense, and measures of habitat association from the floristics data of the 74 plots.

Leaf production and herbivory censuses

We marked newly expanding leaves of saplings of the focal taxa within 12 plots representing the three habitats in two locations of each geographic region (French Guiana and Peru). Overall, the 12 focal plots represent almost the entire range of variation in environmental

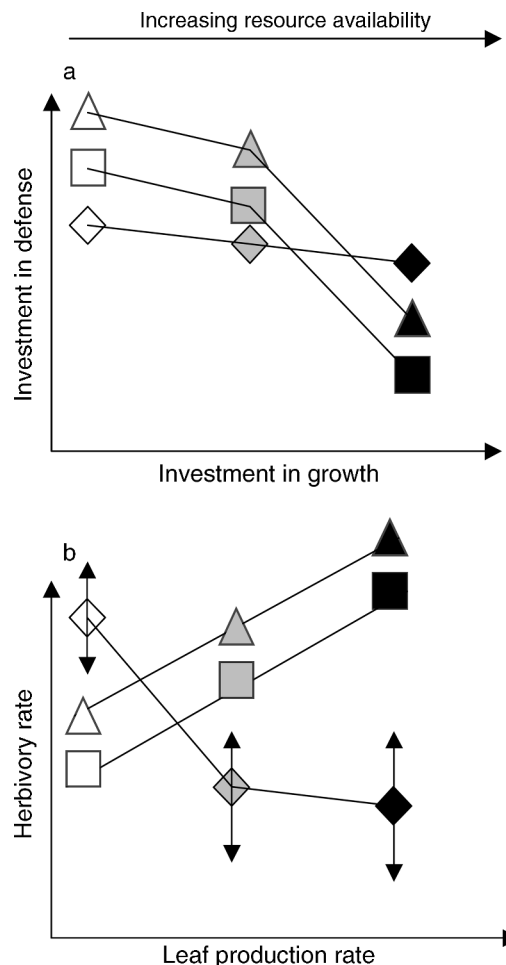


FIG. 1. A conceptual illustration of the predicted relationships among growth rates, defense investment, and herbivory rates and how they relate to habitat association. Three different lineages are shown by the three different shapes, and shading corresponds to habitat association arranged in a gradient of increasing resource availability from left to right (white is white-sand forest, gray is seasonally flooded forest, and black is terra firme forest). (a) Species from white-sand forests are predicted to have low growth and high investment in antiherbivore defenses, flooded forest species are predicted to have intermediate levels of growth and defense investment, and terra firme species are predicted to have high growth rates and low defense rates. (b) Predicted herbivory rates are plotted against leaf production rates for the same three lineages and across the same habitat gradient. Traits related to growth–defense trade-offs are shown to be phylogenetically convergent, allowing species from each lineage to adapt and specialize to habitats with divergent resource availabilities. Note that the diamond lineage employs an “escape” strategy by allocating leaf production unpredictably and synchronously to cause herbivore satiation in higher-resource habitats and can experience either high or low rates of herbivory, depending on which individuals are sampled.

factors observed in the plot network (Baraloto et al. 2011).

For each focal species present in each plot, we located 3–8 saplings from 1 to 5 m in height, to permit

TABLE 1. A summary of the focal lineages with preliminary results of distribution from plots in Peru and French Guiana (FG) including clay terra firme, seasonally flooded forest (SF), and white-sand (WS) habitats.

Lineage	No. spp. total	No. Amazonian spp.	No. spp. in Peru and FG	No. spp. shared between Peru and FG	No. spp. in two or more habitats	No. spp. in SF	No. spp. in WS	Existing DNA data, genes used (sources)	Chemical defense strategies (sources)
<i>Inga</i> (Fabaceae)	300	250	86	19	17	15	6	ITS, trnL-F (1)	phenolics, saponins, non-protein amino acids (6)
<i>Micropholis</i> (Sapotaceae)	40	35	16	5	5	2	4	ndhF, rbcL, trnL, rps16 (2)	latex (2, 7)
<i>Pachira</i> (<i>s.l.</i>) (Malvaceae)	48	45	9	2	3	3	2	trnL-F matK, ITS (3)	mucilaginous latex, fungicides (7)
Tribe Protieae (Burseraceae)	180	100	45	14	6	4	6	phyC, ETS, ITS, trnL-F, rps16 (4)	terpenes, lignans, coumarins, phenolics (8)
<i>Swartzia</i> (Fabaceae)	180	140	21	4	5	3	5	atpB-rbcL, trnL-F, Aat, ITS (5)	saponins, terpenes, isoflavones, pterocarpans (9)

Sources: (1) Richardson et al. 2001, Lavin 2006; (2) Anderberg and Swenson 2003, Swenson and Anderberg 2005; (3) Duarte et al. 2011; (4) Fine et al. 2005, Weeks et al. 2005, A. Weeks (*unpublished data*); (5) Lavin et al. 2005, Torke and Schaal 2008; (6) Coley et al. 2006, Lokvam and Kursar 2005, Lokvam et al. 2006; (7) Schultes and Raffauf 1990; (8) Fine et al. 2006, Zoghbi et al. 1994, Ramos et al. 2000, Siani et al. 1999, Almeida et al. 2002; (9) DuBois and Sneden 1996, Orphelin et al. 1996.

comparisons with other studies investigating herbivory rates in tropical forests (e.g., Coley 1983). Saplings were chosen to represent understory light conditions in each habitat, with crown exposure indices (Poorter et al. 2006) between 1 and 2.5. The crown exposure index of each sapling was noted as a covariate in all analyses. We followed all individuals once every two weeks to monitor leaf production and herbivory. As buds burst, we marked a cohort of 5–8 leaves for each individual and tracked their fates once every two weeks until leaves were fully expanded. In French Guiana, surveys began in March 2010 with the final census in December 2010; this period corresponds to the end of the rainy season and most of the dry season (Bonal et al. 2008). In Peru, there is generally no marked dry season, and monitoring was initiated in July 2010 with the final census in June 2011.

At each census, we estimated the proportion of full expansion surface area of the leaf developmental stage, and we evaluated surface area removed by herbivores using a plastic grid (0.25-cm² squares). All removed parts caused by herbivorous insects, as a loss of photosynthetic surface, necrosis, leaf mines, and galls, were considered to be likely natural enemy attacks. Other types of physical damage were not considered to be herbivore damage. The proportion of area damaged at each census was estimated visually and confirmed in the laboratory by analyzing in situ pictures using WinFolia software (Regent Instruments, Toronto, Canada).

From the field measurements, we calculated three indices describing leaf production (a proxy for growth allocation) and herbivory (a proxy of defense allocation). First, we defined leaf production rate (LPR;

leaf·leaf⁻¹·month⁻¹) for time t (initial and final) for each individual based on measures of net assimilation rate (Hunt 1978) to standardize the amount of biomass allocated into leaf tissue production per unit time by initial plant size as follows:

$$\text{LPR} = [\log(\text{leaf blade count at } t_{\text{fin}}) - \log(\text{leaf blade count at } t_{\text{init}})] / (t_{\text{fin}} - t_{\text{init}}).$$

We then estimated herbivory rate (HR; leaf·leaf⁻¹·month⁻¹) for each individual using a linear approximation of surface area removed during leaf expansion, averaged for all observed leaves to a composite measure for each individual as

$$\text{HR} = \sum_{i=1}^L \left(\frac{\text{Area removed}}{\text{Total area}} \right) / \text{Expansion time}$$

where L is the total number of leaves per individual and leaf expansion time was estimated, to the nearest week, as the time from bud opening to attain maximum leaf size. This measure standardizes leaf surface removed by herbivores among plants with different leaf expansion rates. Nevertheless, it may overestimate total herbivory because it assumes a linear extrapolation across leaf lifetime, even though most herbivory is expected to occur during leaf expansion (Coley and Barone 1996).

The consequence of herbivory on the opportunity cost for the plant will depend not only on the amount of biomass removed by herbivores, but also on the rate at which this biomass can be replaced (Coley 1987, Cyr and Pace 1993, Cebrian and Duarte 1994). We therefore estimated an index of herbivore impact (HI) as the ratio

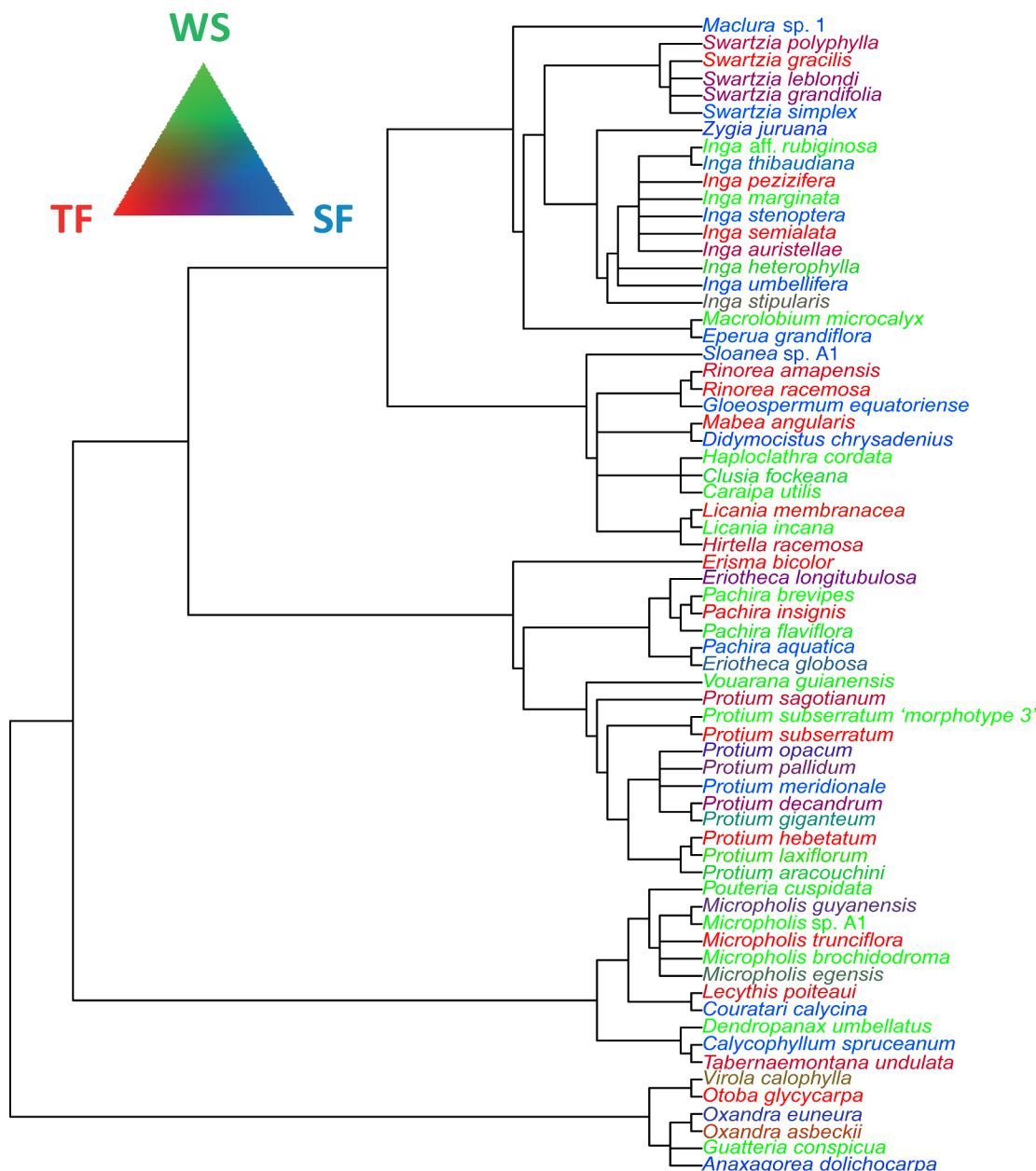


FIG. 2. Evolutionary relationships and habitat associations for the focal taxa in Peru and French Guiana. The cladogram is based on the Angiosperm Phylogeny Group (APG) III classification and nomenclature (APG 2009). Colors of species epithets are scaled to the proportion of stems of each species found across 74 0.5-ha plots in each of clay terra firme (red, TF), white-sand (green, WS), and seasonally flooded (blue, SF) forests.

of herbivory rates and leaf production rates:

$$HI = \frac{HR}{LPR}$$

This index is unit-less because it represents the ratio of two parameters with the same units. An HI of 1 indicates that leaf biomass is transferred to the herbivore trophic level at a rate equivalent to its production. An HI >1 indicates that herbivore consumption outpaces

foliar production, whereas if the index is <1, then tissue loss from herbivory is less than that produced.

Leaf functional traits

We measured six leaf functional traits related to growth and herbivory on at least one individual of each species in each of the 12 plots. We sampled individuals other than those censused for herbivory and leaf production because our methods included destructive

sampling. On three leaves per individual, leaf chlorophyll content was estimated using three values from a Minolta SPAD 502DL meter (Spectrum Technologies, Plainfield, Illinois, USA) with calibrations after Coste et al. (2010); leaf thickness was measured as the mean of three measurements with a digital micrometer (Mitutoyo Instruments, Singapore), and leaf toughness was measured as the average of three punch tests with a Chatillon penetrometer (Ametek, Largo, Florida, USA). The leaves were scanned using a portable scanner (LiDE 60; Canon, Lake Success, New York, USA), and their area was determined by image analyses with Winfolia software (Regent Instruments, Toronto, Canada). The leaves were dried at 60°C for 72 h, and their dry mass was weighed to determine specific leaf area (SLA; leaf area divided by its dry mass). All leaves were then pooled together and ground to fine powder using a ball mill (Retsch MM200, Retsch, Haan, Germany). Their C and N contents (%) were determined by mass spectrometry at the Mass Spectrometry Facility of the University of Florida, Gainesville, Florida.

Habitat association

For each focal species, we compiled data from all 74 plots to determine its relative abundance in each habitat (e.g., Baraloto et al. 2007). We then used the indicator species value following the method of Dufrene and Legendre (1997) as a measure of habitat association for each species in each habitat. This measure scales from 0 to 1 and integrates both the relative frequency of each species across plots in a given habitat, with its relative abundance in each habitat.

Data analyses

We tested relationships between LPR and HR (Question 1) using standardized major axis regression (SMA) to account for variance in both variables (Warton 2007). We performed SMA analyses on the entire dataset and within each lineage.

To examine phylogenetic signal in LPR, HR, and HI (Question 1), we constructed a phylogenetic topology for the focal species using the backbone of the APG3 megatree (R20091110) provided by the Phylomatic utility (Webb and Donoghue 2005), in addition to existing published and unpublished work from each lineage's molecular phylogenetic analyses (Fine et al. 2005, Torke and Schaal 2008, Dexter et al. 2009, Duarte et al. 2011; P. Fine, *unpublished data*; C. Baraloto, J. Vieu, and J. Chave, *unpublished data*). We updated polytomies below the family level using Mesquite (Maddison and Maddison 2010) when further resolution from more than one gene indicated higher than 90 posterior probability or bootstrap support. We then calculated Blomberg's *K* (2003) for all 68 focal taxa, and examined differences among the five focal lineages conducting an analysis of variance (ANOVA). To examine relationships between leaf functional traits

and LPR, HR, and HI (Question 1), we performed correlation analyses with and without phylogenetically independent contrasts based on the topology of our phylogenetic tree.

We then conducted an ANOVA to test for differences in LPR, HR, and HI among habitats and countries (Question 2).

We tested for relationships between LPR and HR and habitat associations within each habitat (Question 3) using 95% quantile regressions to determine if LPR and HR constrained the extent to which species had high indicator values in a particular habitat (Koenker 2005).

All analyses were conducted in the R statistical platform, version 2.11 (R Core Development Team 2010), using the packages smatr (Warton 2007), picante (Kembel et al. 2010), APE (Paradis et al. 2004), vegan (Oksanen et al. 2010), labdsv (Roberts 2010), and quantreg (Koenker 2011).

RESULTS

Leaf production and herbivory rates in species and lineages

Leaf production rates varied almost 50-fold among the studied species, from 0.002 leaves·leaf⁻¹·month⁻¹ in *Oxandra euneura* (Annonaceae, Peru SF) to 0.12 leaves·leaf⁻¹·month⁻¹ in *Didymocistus chrysadenius* (Euphorbiaceae, Peru SF; Fig. 3). Herbivory rates were also highly variable, ranging from 0.1% per month in *Lecythis poiteaui* (Lecythidaceae, French Guiana TF) to 7.8% per month in *Pachira aquatica* (Malvaceae, Peru SF). We found no relationship between LPR and HR using major axis regressions among all species or within each of the five focal lineages. Indeed, the ratio of HR to LPR, as measured by HI, was also highly variable. *Oxandra euneura* was estimated to have lost leaf tissue 14 times faster than it replaced it over the study period, whereas *Protium subserratum* 'morphotype 3' (see Daly and Fine 2011; Burseraceae, Peru WS) replaced tissue nearly 20 times faster than it was lost. Overall, about half of the studied taxa lost tissue faster than it was replaced (i.e., HI > 1) during the study period (above the 1:1 line in Fig. 3).

Phylogenetic signal in leaf production and herbivory rates

None of the three indices describing growth–defense trade-offs showed significant phylogenetic correlations across the 68 studied taxa; all three indices had very low Blomberg's *K* indices < 0.066 (see the Appendix), within the range of confidence intervals under the null hypothesis of no phylogenetic correlation. Indeed, we observed as much variation among species within *Protium*, *Inga*, and Bombacoideae as among most genera (see Fig. 3). Nevertheless, we did find overall differences in leaf production and herbivory rates among the five focal genera (Fig. 4), with *Micropholis* exhibiting significantly lower LPR than *Pachira* and lower HR and HI than *Inga*.

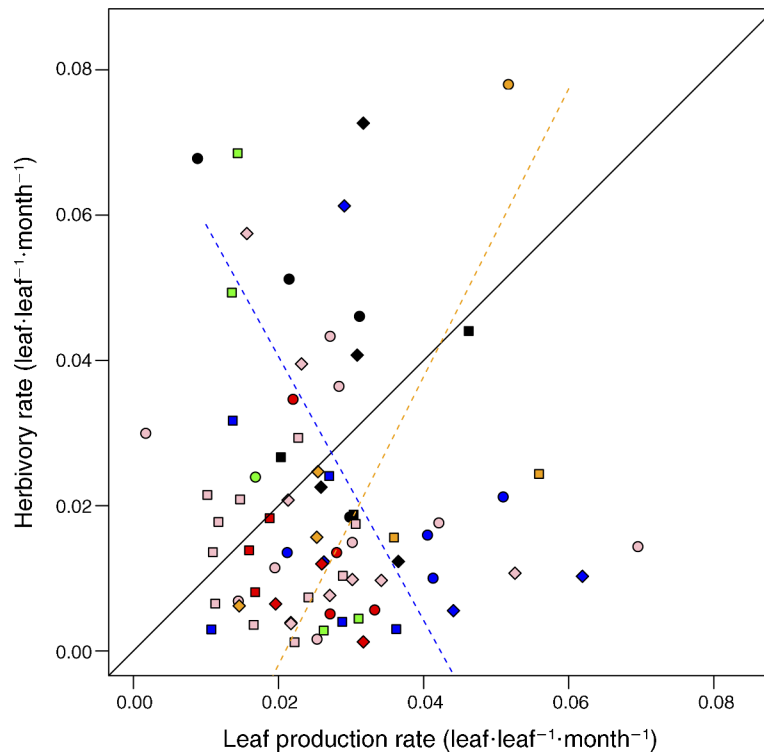


FIG. 3. Relationships between herbivory rates and leaf production rates for abundant species (pink symbols) in each habitat (circles, seasonally flooded forest; squares, terra firme clay; and diamonds, white-sand forest) and the five focal lineages: *Swartzia* (green), *Inga* (black), Protieae (blue), Bombacoideae (orange), and *Micropholis* (red). The black diagonal line indicates a rate of herbivory equivalent to a rate of leaf production (herbivore impact [HI] index = 1). Trend lines for *Protium* and Bombacoideae are shown to illustrate contrasting patterns, even though no relationship within genus or overall was significant for major axis regression ($P > 0.05$).

Leaf production, herbivory rates, and leaf functional traits

Leaf production rates were correlated with some leaf functional traits describing the leaf economics spectrum (Fig. 5). Leaf production was faster in species with higher SLA and lower leaf toughness, especially when phylogenetically independent contrasts were employed (Table 2). However, neither HR nor HI was significantly correlated with any leaf traits for the studied taxa (Fig. 5).

Leaf production and herbivory rates in contrasting habitats

Leaf production rates differed among both habitats and countries (Fig. 6), with consistently higher rates in SF forests in both countries ($F_{2,349} = 8.4$, $P < 0.001$) and Peruvian forests in general ($F_{1,349} = 3.6$, $P = 0.06$). Herbivory rates were also nearly twice as high in Peru as in French Guiana ($F_{1,349} = 8.4$, $P < 0.001$), but there was no significant difference in herbivory rates among habitats ($F_{2,349} = 0.6$, $P = 0.54$). The relative impact of herbivory reflects the balance between leaf biomass produced and eaten by herbivores. Overall, this index did not differ significantly among habitats, but saplings in Peru had nearly twice the relative herbivory impact as

did those studied in French Guiana ($F_{1,349} = 7.0$, $P = 0.008$; Fig. 6).

Growth–defense trade-offs and habitat specialization

The focal taxa exhibited striking contrasts in habitat association across the 74 plots, with more than two-thirds of the focal species showing clear preference for a single habitat. This can be visualized by the range of colors represented by species names in Fig. 2. We found strong support for divergent patterns of habitat associations within each of the five focal lineages, and we were able to study specialists to each of the three habitats in each of the five lineages. Species that were strongly associated with TF forests exhibited significantly lower rates of leaf production and lower herbivory (Fig. 7), such that no species with high LPR or high HR was dominant in that habitat. Species strongly associated with the other habitats also tended to have lower LPR and HR, but the triangular trend was not as strong (Fig. 7).

The five lineages we studied in detail showed contrasting patterns with respect to their herbivory and leaf production rates and habitat association. In *Protium* and *Swartzia*, relative abundances in TF forests

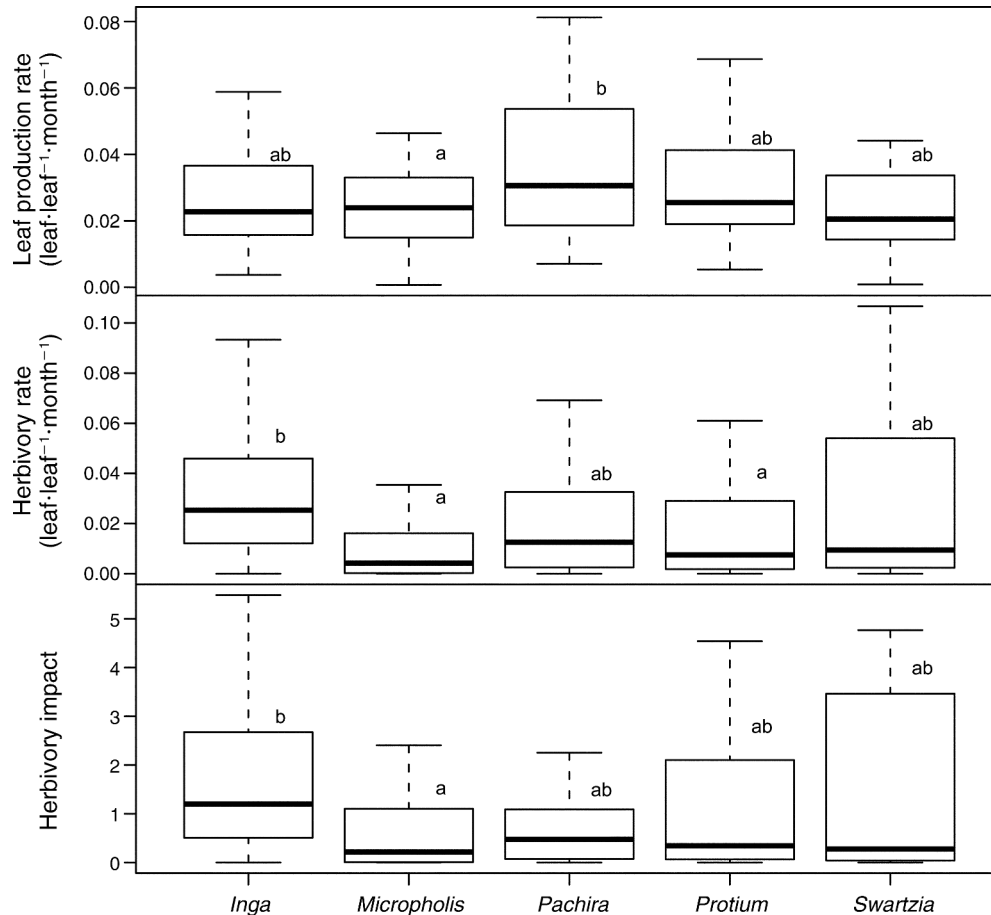


FIG. 4. Boxplots illustrating differences among the five focal genera for (a) herbivory rates, (b) leaf production rates, and (c) the relative impact of herbivory. The bottom and top of the box represent the 25th and 75th percentile, and the band near the middle of the box shows the median. The ends of the whiskers represent the minimum and maximum ranges of the data. Lowercase letters denote groups with significantly different means calculated with Tukey HSD post hoc tests following one-way ANOVA on log-transformed variables.

are well explained by the herbivory rates of saplings (Fig. 7), and to a lesser extent by their leaf production rates.

DISCUSSION

Variation in growth and defense strategies

Our study represents the most comprehensive examination of leaf production and herbivory rates in tropical trees, including both a phylogenetic approach to species selection and a broad gradient of environmental conditions. We predicted that we would find a general positive relationship between LPR and HR (or HI) and that differences in HR and HI would be found among habitats, consistent with the hypothesis that the growth–defense trade-off contributes to observed patterns of habitat specialization in trees (Fig. 1a, b). Instead, we found no general positive relationship between HR and LPR (Fig. 3), although we did find some significant differences among habitats (Fig. 6).

Potential explanations for the lack of correlation between HR and LPR include (1) herbivores may not be important selective agents for these trees, and/or not at this particular life stage; (2) our sample included only shade-tolerant species; (3) fast-growing species in our sample may be flushing their leaves synchronously and satiating their specialist enemies and/or flushing their leaves at unpredictable times, and thereby escaping their enemies; or (4) fast-growing species may have some novel defense that is effective, but does not entail a large allocation cost and thus does not trade-off with LPR. We treat each of these explanations in turn.

Our results may reflect the fact that herbivores are not important selective agents in these forests; more specifically, the sapling stage may not be the most appropriate stage at which to evaluate the impact of herbivory. Saplings are commonly the focus of woody-plant herbivory studies (Coley 1983, Endara and Coley 2011, Moles et al. 2011), perhaps in large part because

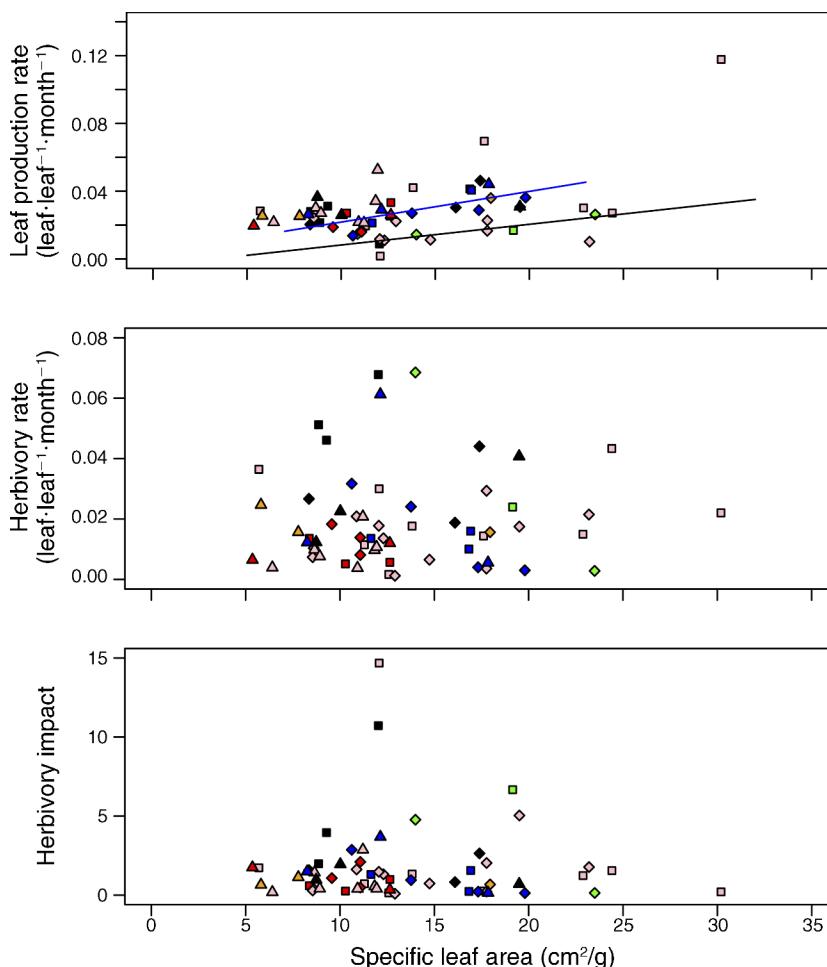


FIG. 5. Relationships between a leaf functional trait related to plant growth strategy, specific leaf area (SLA), and (a) leaf production rates, (b) herbivory rates, and (c) the relative impact of herbivory. Symbols are coded as in Fig. 3, with abundant species in each habitat (pink symbols) and the five focal lineages: *Swartzia* (green), *Inga* (black), Protieae (blue), Bombacoideae (orange), and *Micropholis* (red). Trend lines are shown for significant major axis regression coefficients overall (black) or within lineages (by color).

they are easy to survey. However, saplings are known to have lower levels of defense than seedlings (Boege and Marquis 2005), and in general, tropical tree seedlings experience less herbivory-related mortality as they age

(Baraloto et al. 2005, Fine and Mesones 2011). Previous work on WS and TF plants that reported significant differences in growth rates, defense allocation, and herbivory-related mortality between habitats for multi-

TABLE 2. Pairwise correlations between leaf production rate (LPR), herbivory rate (HR), herbivory impact (HI), and leaf traits.

Trait	LPR	HR	HI	SLA	LA	Thick	Tough	LN	LC:N
LPR	1	-0.113	-0.355	0.427	0.021	-0.036	-0.270	-0.009	-0.024
HR	-0.014	1	0.571	0.026	-0.171	-0.175	0.071	0.083	-0.050
HI	-0.222	0.658	1	-0.036	-0.086	-0.175	0.183	0.143	-0.088
SLA	0.473	-0.038	-0.021	1	-0.282	-0.555	-0.705	0.515	-0.544
LA	-0.174	0.086	0.044	-0.392	1	0.206	0.421	-0.143	0.151
Thick	0.327	-0.112	-0.148	-0.533	0.199	1	0.699	-0.480	0.566
Tough	-0.495	0.267	0.327	-0.697	0.412	0.628	1	-0.529	0.620
LN	0.379	-0.081	-0.083	0.524	-0.115	-0.398	-0.561	1	-0.914
LC:N	-0.421	0.053	0.103	-0.544	0.092	0.588	0.647	-0.907	1

Notes: Pearson correlation coefficients for species means (above diagonal) and phylogenetically independent contrasts (below diagonal) are shown in boldface type when significant, following Bonferroni-corrected alpha values ($P < 0.0014$). Leaf functional traits include: specific leaf area (SLA), total leaf area (LA), leaf thickness (Thick), leaf toughness (Tough), leaf nitrogen content (mass based; LN), and leaf carbon–nitrogen content ratios (LC:N).

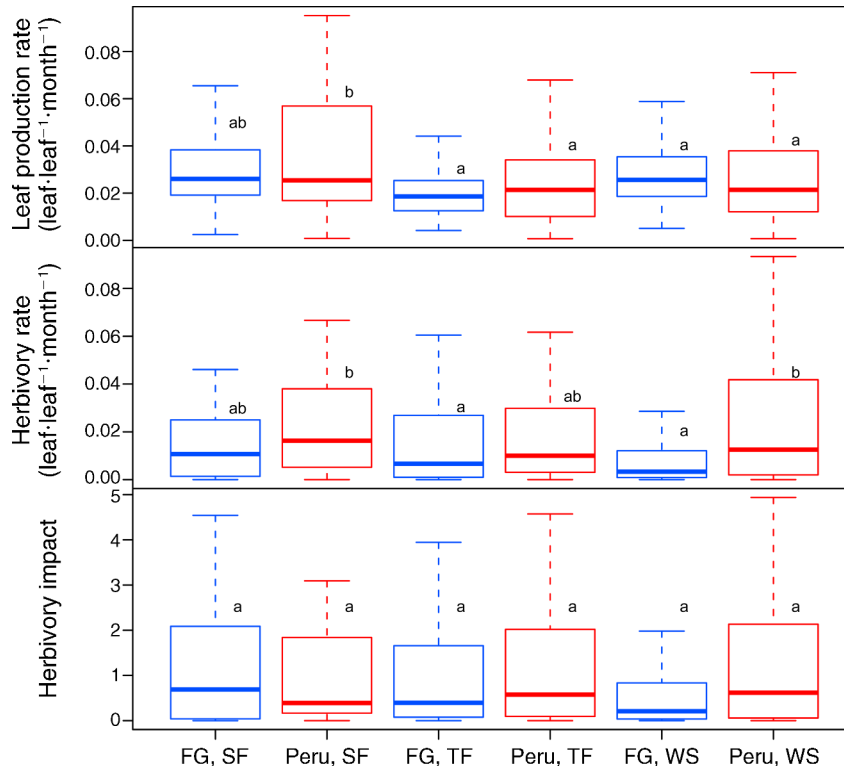


FIG. 6. Boxplots illustrating differences among countries (Peru and French Guiana [FG]) and habitats (seasonally flooded [SF], clay terra firme [TF], and white-sand [WS] forests) for (a) herbivory rates, (b) leaf production rates, and (c) the relative impact of herbivory. The bottom and top of each box represent the 25th and 75th percentile, and the band near the middle of the box shows the median. The ends of the whiskers represent the minimum and maximum ranges of the data. Lowercase letters denote groups with significantly different means calculated with Tukey HSD post hoc tests following two-way ANOVA on log-transformed variables.

ple lineages was based on seedlings, not saplings (Fine et al. 2004, 2006).

Second, whereas previous studies that have found a positive relationship between growth and herbivory across resource gradients have also studied saplings, they have included both pioneers and shade-tolerant species in high-light environments (Coley 1988, Endara and Coley 2011). In our study, by not including true pioneer species or light gaps, we have excluded those trees (both within and among species) that are likely to have the highest relative growth rates (see the top right quadrant in Fig. 1). This fact is especially important when considering that the seasonally flooded and Peruvian terra firme habitats generally have large light gaps with abundant pioneer species (e.g., *Cecropia*, *Trema*, and so on) that were not included in our sample (and that never occur in white-sand forests; Fine et al. 2010). Saplings in the understory are thought to be mostly light limited, waiting for a gap to allow them the chance to grow to the canopy and become a reproductive adult (Wright 2002). Insect herbivores are also less likely to be attracted to shady environments (Richards and Windsor 2007), and in general, lower overall leaf biomass and insect herbivore abundances are found in the understory of undisturbed forests compared to edges

of light gaps (Whitfield et al. 2012). Further research integrating herbivory rates for the same species across different life history stages, and across light environments, will be critical to fully evaluate the true relationship between growth and herbivory rates.

A third explanation for the lack of a general relationship between LPR and HR is that some species may be experiencing low herbivory rates without investing in defenses, by escaping through time and/or space. *Protium* species (Fig. 3) that have high LPR appear to be escaping their herbivores, perhaps via synchronous leaf flushing and herbivore satiation (Aide 1988, 1993). However, herbivory rates in such “escape” species are thought to be extremely variable, because some individuals in a population will be heavily defoliated while others will be left untouched, perhaps due to herbivore satiation (Coley and Kursar 1996). Alternatively, plants may be escaping their enemies through space, perhaps with unpredictable leaf flushing. This explanation is very similar to apparency theory (Feeny 1976). Endara and Coley (2011) argue strongly that apparency theory does not explain plant defense strategies, as there is no evidence that “unapparent” plant species suffer more damage from specialist herbivores than from generalist herbivores, nor is there

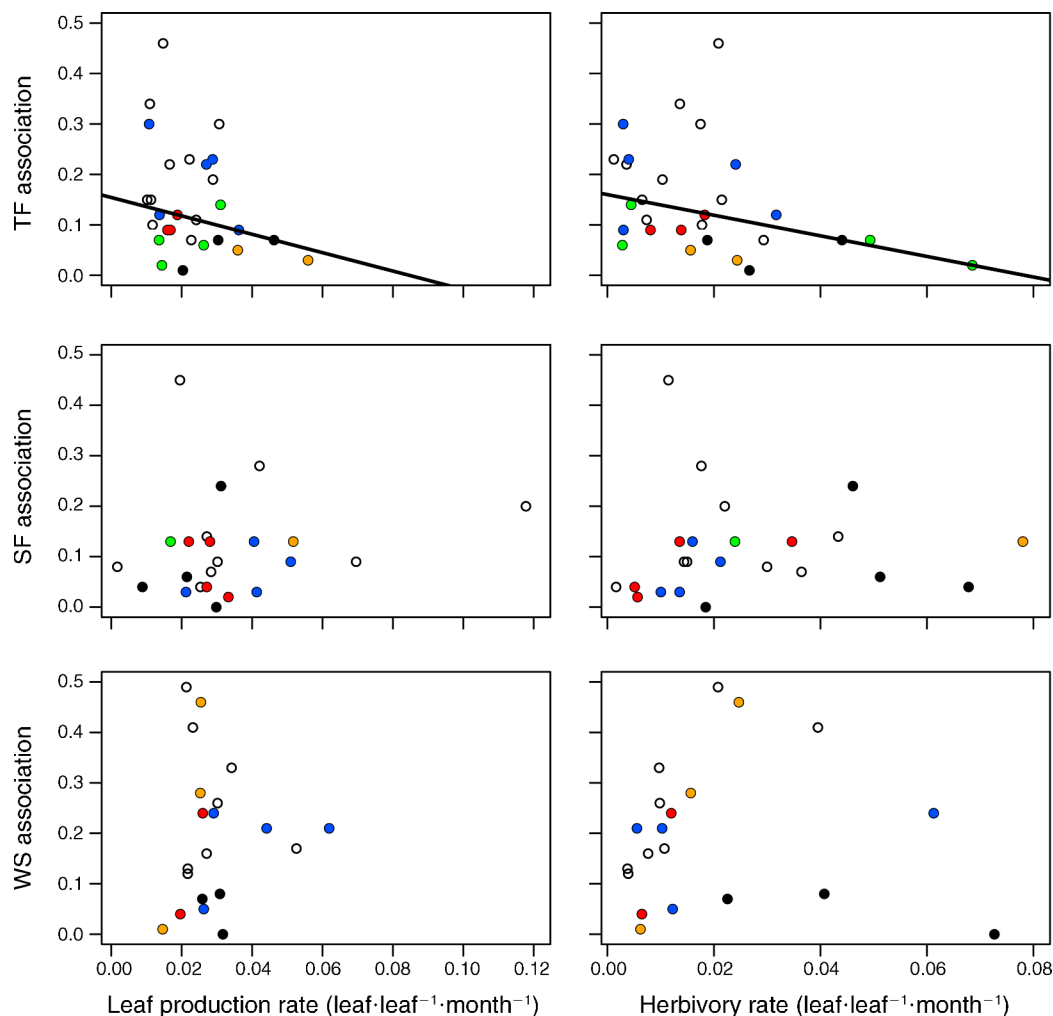


FIG. 7. Relationships between leaf production and herbivory rates and habitat association indices (indicator values of Dufrene and Legendre [1997]). Symbol colors are coded as in Fig. 3 for abundant species from each habitat (open symbols) and the five focal lineages. Trend lines are shown for lineages for which 95% quantile regression coefficients were significant at $P < 0.05$.

any evidence that herbivores have any difficulty in locating their host plants. Our comparative analysis focused on a large number of species, with the compromise of relatively low sample sizes (between three and eight individuals per species per plot). We posit that with such small sample sizes it is likely that we failed to observe the full breadth of variation in herbivore attack. As a result, the fast-growing species that appear to be escaping their herbivores in Fig. 3 are unlikely to do so over larger spatial and temporal scales. Larger sample sizes will allow better characterization of the relative importance of stochastic processes in herbivory rates within communities (Barber and Marquis 2011).

Finally, it is possible that the growth–defense trade-off is not universal, and that some species are able to defend themselves adequately at little cost, allowing them to produce high LPR and escape herbivory.

Although this possibility is important to consider, a recent meta-analysis of 50 studies evaluating the growth–defense trade-off found strong general support for the trade-off, suggesting that plant defenses are indeed costly and come at the expense of growth rates (Endara and Coley 2011). In agreement with our results, this meta-analysis found no significant differences in defenses or herbivory rates among habitats differing in resource availabilities, a pattern the authors attributed to the difficulty in sampling herbivory appropriately through time and space (Endara and Coley 2011).

Phylogenetic signal and correlations of growth and defense strategies

We found strong patterns of convergence in herbivory rates, leaf production, and our index of relative impact of herbivory throughout the 68 species, with species within our five focal lineages exhibiting high variation in

the rates of both leaf production and herbivore attack (Figs. 3 and 4). These results are consistent with the idea that there are plant defense syndromes that are evolutionarily convergent within and among lineages (Agrawal and Fishbein 2006). Fine et al. (2006) found a similar pattern studying a much smaller subset of species from three of these same focal lineages in Peru; and here we confirm this pattern across broader phylogenetic, spatial, and environmental scales, including 68 species from 17 plant families in WS forests, SF forest, and TF forests in two different regions on opposite sides of the Amazon Basin. Similarly, Whitfield et al. (2012) found high phylogenetic lability in latex production within their sample of trees, which was an important predictor of herbivory levels in their study. Furthermore, they found that neither insect abundance nor diversity in a New Guinean forest was predicted by plant phylogenetic information.

The strong correlations between LPR and leaf functional traits (Fig. 5, Table 2) suggest that our measure of leaf production rates was consistent with a general pattern of growth strategy among these species (Baraloto et al. 2010). Indeed, we expect species with thinner, cheaper leaves to exhibit higher growth rates (Poorter et al. 2006) and more rapid leaf turnover (Coley 1983). However, leaf traits associated with the leaf economics spectrum (Wright et al. 2004) were not correlated with herbivory rates across species (Table 2). We suggest this may be due to variable investment in chemical defenses that may not correlate with other leaf morphological and physiological characteristics.

It is important to note that the predictions in Fig. 1 regarding the growth–defense trade-off and its role in beta-diversity refer to defense investment (i.e., energy allocated to defense), rather than to defense type (terpenes vs. alkaloids, for example). Indeed, even though we found convergence in herbivore rates (our proxy for defense), defense type could still be phylogenetically conserved (e.g., all *Bursera* species produce monoterpenes; Becerra 1997). Defense type is thought to influence the degree of specialization by herbivores (Ehrlich and Raven 1964). Although general predictions regarding plant investment in growth vs. defense focus on the amount of defense, the type of defense and its influence on host plant specialists may impact both measurement of the growth–defense trade-off, as well as patterns of community assembly within and across habitats (Cavender-Bares et al. 2009).

Measuring herbivory in tropical forests

To what extent do our measures of leaf production and herbivory represent appropriate proxies of allocation strategies of growth and defense? Our method of scaling HR with LPR represents a synthesis of plant defense theory with community-level trophic analyses (Coley 1987, Cyr and Pace 1993, Cebrian and Duarte 1994). This approach allows for comparisons of the relative impact of herbivory across plants of different

sizes and across habitats with different resource availabilities, and gives an estimate of the relative amount of plant biomass that is transferred to higher trophic levels.

Previous studies have generally sampled herbivory using much less labor-intensive methods, sampling percentage of leaf area eaten sometimes only once or twice, but rarely repeatedly over several months (reviewed in Coley and Barone 1996, Moles et al. 2011). When one samples herbivory rates without also calculating LPR, it is difficult to interpret what “percentage of leaf area eaten” means to the plant and to the community of herbivores. In our opinion, including both of these measures is critical. Global comparisons of herbivory rates (Moles et al. 2011) should consider herbivory rate in the context of LPR and leaf lifetime before drawing conclusions about whether or not tropical forests have higher herbivory rates than temperate forests, because it is necessary to standardize herbivory rate and impact across resource gradients and growth forms (see also Johnson and Rassman 2011). Our measure of herbivory impact as the ratio of herbivory to leaf production reveals that most plants in these tropical forests are experiencing high rates of herbivory scaled to the amount of biomass produced, suggesting that herbivory represents a significant cost to plants.

Variation in the growth–defense trade-off across habitats and countries

The contrasts in herbivore impacts between TF and WS forests have been well studied in Peru (Fine et al. 2004, 2006). From this work, we predicted that plants in nutrient-poor white-sand soils will invest in defense at the expense of growth, leading to slow turnover of leaf tissues (low LPR) that are well defended (low HR; e.g., Fig. 1a). In this study, we found some evidence for lower rates of leaf production and lower herbivory in WS forests of French Guiana (Fig. 6), as found in previous studies (Coomes and Grubb 1998, Fine et al. 2004, 2006). In nutrient-rich TF forests, we predicted the opposite trend, with plants investing more in growth at the expense of defense, leading to high LPR and high HR, a pattern for which we did not find support (Fig. 6).

We found significantly higher LPR in SF forests. This result correlates with the higher soil resources found in these habitats and rapid rates of turnover of stems in these forests due to seasonal flooding (Ferry et al. 2010, Baraloto et al. 2011). However, higher LPR was not accompanied by higher HR. We posit that this may be explained in part by predators and parasitoids of herbivores, which play a crucial role in tropical forests by regulating herbivore populations (Raw 1998, Dyer and Letourneau 2003, Van Bael et al. 2003). Both plant defense theory and trophic cascade theory predict that plant defenses should be lower in high-resource plant communities and higher in low-resource plant communities. Differences in herbivory rates across habitats may



PLATE 1. Five *Heliconius* caterpillars (Nymphalidae: Heliconiinae) feeding in a terra firme forest plot near the Nanay River, Loreto, Peru. Photo credit: G. P. A. Lamarre.

therefore be dependent on the strength of a trophic cascade. Indeed, pressure on herbivores from a third trophic level can allow plants in high-resource environments to persist with a lower defense investment (Van Bael et al. 2003, Richards and Coley 2007, Mooney et al. 2010).

Because of the higher variability of soil fertility among habitats in Peru (Baraloto et al. 2011), we expected the differences in LPR and HR among habitats to be much more marked in Peru than in French Guiana, which was not the case. Still, these results must be interpreted in their temporal context given an extreme drought event that occurred in the western Amazon during the study period, reducing precipitation by more than two-thirds in some of our Peruvian study sites (Lewis et al. 2011). We suggest that the 2010 drought may have induced substantial drought stress in our study sites in Peru, resulting in lower leaf production than typical years, and perhaps, driving down herbivory rates in SF and TF. Moreover, drought may have provoked cascading interactions at higher trophic levels. Indeed, previous research at Barro Colorado Island in Panama has documented that in years of extreme drought, herbivore

abundances greatly decreased and caused major die-offs in the third trophic level (Wright et al. 1999).

Finally, we found significantly higher HR in Peru than in French Guiana. Seasonality differs between the eastern and western Amazon, with aseasonal ever-wet rain forests common near the equator in the west, and strong two-to-three-month dry seasons in the east (Baraloto et al. 2011). Insect abundance is predicted to be higher in aseasonal regions (Basset et al. 2003). In addition, the western Amazon contains edaphic habitats that range from fertile to extremely infertile while the rest of the basin has much lower variance in soil fertility, being composed of brown sand, eroded ancient clays and similar white-sand quartzite edaphic habitats (Hoorn et al. 2010). Plant productivity tracks soil fertility and also correlates with insect abundance (Kaspari et al. 2000). Thus, we expect that the higher rates of herbivory found in Peru were due to both the higher soil fertility overall and aseasonal climates.

Growth-defense strategies and habitat specialization

Herbivory rates influence the relative abundance of plant species across contrasting habitat types, as we found that species suffering high herbivory rates do not

become dominant in any of the three habitats we studied (Fig. 7). For TF forests, there was a significant and negative correlation between both LPR and HR with relative abundance. Thus, herbivory rates do affect beta-diversity in these forests, but not directly as we predicted, with different species experiencing divergent impacts of herbivory in different habitats. Instead, we observed that no species was common within any habitat if it suffered high herbivory rates (Fig. 7). We envision a hierarchical model by which species are filtered among habitat types based on environmental filtering across abiotic gradients (Kraft et al. 2008), with local abundances determined by herbivore assemblages. We also expect herbivores to influence the evolution of functional traits that are linked to habitat association, although we acknowledge that these interactions do not appear to be very important at the sapling life stage.

Our approach represents several advances, with a strong integration of novel indices relating herbivory and species traits to species distributions across contrasting habitats in two biogeographic regions, and with contrasts among multiple monophyletic lineages. However, the strength of the relationships we observed was relatively weak. Our results underline the need for long-term studies integrating a phylogenetic context with field observations to better understand the role of species interactions in shaping regional patterns of biodiversity.

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SUPPLEMENTAL MATERIAL

Appendix

A summary of phylogenetic signal tests (*Ecological Archives* E093-186-A1).