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Predicting tropical insect herbivore abundance from host plant traits and phylogeny

TIMOTHY J. S. WHITFELD,[1,5] VOJTECH NOVOTNY,[2] SCOTT E. MILLER,[3] JAN HRCEK,[2] PETR KLIMES,[2]
AND GEORGE D. WEIBLEN[4]

[1]*University of Minnesota, Department of Forest Resources, 115 Green Hall, 1530 Cleveland Avenue North,*
St. Paul, Minnesota 55108-1095 USA
[2]*Czech Academy of Sciences, Biology Center and University of South Bohemia, Faculty of Science, Branisovska 31,*
37005 Ceske Budejovice, Czech Republic
[3]*National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 105, Washington, D.C. 20013-7012 USA*
[4]*University of Minnesota, Bell Museum and Department of Plant Biology, 250 Biological Sciences Center, 1445 Gortner Avenue,*
St. Paul, Minnesota 55108-1095 USA

Abstract. Phylogenetic ecology has identified patterns of diversity in communities that may find explanation in trophic interactions, and yet there have been few attempts to directly relate such patterns among trophic levels. Density-dependent processes involving pests and pathogens, for example, have been invoked to account for plant community phylogenetic patterns, but relatively little is known about how plant relatedness might affect community structure at other trophic levels. We examined the degree to which the abundance of herbivores in a rain forest community is explained by the phylogeny and functional traits of host plants. We destructively sampled all stems ≥ 5 cm diameter in two 1-ha plots of New Guinea primary and secondary lowland forest to test predicted relationships between herbivore abundance and plant resources. We analyzed per-tree caterpillar and leaf miner abundance, total leaf biomass (kg), percentage of immature foliage, specific leaf area (cm^2/g), leaf nitrogen content (percentage of dry mass), and presence of exudates in the context of a plant community phylogeny estimated from DNA barcodes.

Apart from nitrogen content and exudates, neither plant resources nor herbivore abundance showed evidence of phylogenetic signal in our community sample. The plant traits we measured could account for only 30% and 16% of variation in caterpillar and leaf miner abundance, respectively, among individual trees. Leaf biomass was a stronger predictor of herbivore abundance than either resource quality (leaf nitrogen content) or palatability (percentage of immature foliage, specific leaf area). The primary importance of resource quantity was also observed at the plant species level in analyses of species means and phylogenetic generalized least-squares regression. Plant relatedness did not account for much variation in herbivore abundance, but significant effects of exudates and leaf nitrogen content on caterpillar abundance illustrate how conserved traits at one trophic level may influence community-wide patterns at another.

Key words: comparative methods; food webs; herbivory; Lepidoptera; lowland rain forest; New Guinea; plant defense.

INTRODUCTION

A general aim of phylogenetic community ecology is to interpret patterns of species distribution and abundance in terms of evolutionary processes and ecological mechanisms (Kraft et al. 2007, Cavender-Bares et al. 2009). Diverse tropical forests have been particularly fertile ground for testing theories on mechanisms of species coexistence in communities (Wright 2002) where trophic interactions may affect patterns of plant community phylogenetic diversity (Lamarre et al. 2012). The idea that density-dependent processes involving specialized pests and pathogens could limit the recruitment of related plants in close proximity is not new (Janzen 1970, Connell 1971). Recent evidence suggests that trophic interactions indeed play a role in structuring the distribution of tropical tree community phylogenetic diversity (Wills et al. 2006, Comita et al. 2010, Metz et al. 2010), but it is less clear how the abundance of natural enemies is distributed with respect to the vegetation.

Insect herbivores feeding on tropical foliage are an obvious target for investigating this problem because tropical vegetation is extraordinarily diverse (Leigh 1999) and foliage can be particularly vulnerable to herbivory (Coley and Barone 1996). A broad array of plant morphological, physiological, and chemical de-

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[5] E-mail: whitf015@umn.edu

fenses are present (Agrawal and Fishbein 2006). For example, rapid leaf expansion (Coley and Aide 1991) and delayed greening (Kursar and Coley 1992) have been regarded as plant adaptations that limit herbivory and nutrient loss. Evidence that evolved defenses play a role in mediating plant–herbivore interactions (Agrawal 2005) has supported the view that a phylogenetic context is needed to test predictions about trophic relationships (Lamarre et al. 2012). The distribution of herbivore dietary preferences with respect to plant community phylogeny has further suggested that many tropical insect species are clade specialists (Tavakilian et al. 1997, Berkov and Tavakilian 1999, Novotny et al. 2002, 2004, 2010, Novotny and Basset 2005, Odegaard et al. 2005, Weiblen et al. 2006, Dyer et al. 2007, Hulcr et al. 2007). However, it is unclear what effect the phylogenetic distribution of plant traits might have on overall patterns of herbivore abundance at the community level.

Whether host plant phylogeny can predict the abundance of herbivores depends on the conservatism or lability of traits associated with herbivory (Fine et al. 2006). Phylogenetic ecology has identified ample evidence of particular plant defensive adaptations or herbivore specialization according to this approach (Weiblen et al. 2006, Agrawal et al. 2009*a*), but whether phylogenetic considerations improve predictive models relating plant traits to overall herbivore abundance in communities is unknown. We examined this possibility through analyses of a unique plant–herbivore community data set from New Guinea.

Ecological theory predicts that the abundance of consumers such as insect herbivores should be related to plant resources in a predictable manner. However, the abundance of herbivorous insects in forest communities is challenging to measure due to the dynamics of species populations in space and time (Lawton and Gaston 1989). Factors including disease, predators (Mooney et al. 2010), parasitoids, and a dynamic abiotic environment (e.g., seasonality) pose further complications for such a simple theory. Nonetheless, a few general predictions can be stated. First, the plants having greater biomass are expected to host greater numbers of leaf herbivores (Basset 1996, Marques et al. 2000). Second, plants of higher nutritional quality are expected to support more herbivores than plants of lower quality (Basset 1991, Poorter et al. 2004, Cornelissen and Stiling 2006). Third, the theory of plant life history trade-offs (Wright et al. 2010) predicts that plants investing relatively more resources in defense than in rapid growth should harbor fewer herbivores than plants at the other end of the resource allocation spectrum (Herms and Mattson 1992). Fourth, statistical power to detect such relationships will be higher in a phylogenetic context for conserved traits, whereas no effect is expected for traits that lack community phylogenetic signal (Fine et al. 2006, Gilbert and Webb 2007).

Destructive sampling of vegetation offers a rare opportunity to simultaneously investigate predicted relationships between leaf traits and leaf-chewing insect abundance at the community level. We harvested each tree (>5 cm dbh) in two hectares of New Guinea lowland rain forest to measure leaf availability, nutrient quality, and palatability, while collecting all leaf-chewing caterpillars and leaf miners. Almost all caterpillars were Lepidoptera, as were most leaf miners (mostly Gracillariidae), although some Diptera and Coleoptera leaf miners were included (Novotny et al. 2010). For simplicity, all are assumed to be Lepidoptera in this discussion, and this group was the focus of analysis because its members were the least likely to be separated from their host plants during felling due to their apterous condition and intimate associations (i.e., feeding internally between the epidermal layers of leaves in the case of miners; Sinclair and Hughes 2010). Gradual felling of all trees in primary- and secondary-forest plots over a two-year period provided instantaneous measures of these variables on a per-tree basis. We compared the relative strength of correlations among resource availability (as measured by total leaf biomass per plant), resource quality (as measured by leaf nitrogen content on a mass basis), palatability (as measured by specific leaf area [SLA] and the presence or absence of exudates), and herbivore abundance at the community level. Fresh leaf area divided by dry leaf mass (SLA) is a measure of plant investment in photosynthetic capacity relative to structural elements (Cornelissen et al. 2003) and, following Poorter et al. (2004), we used SLA as a proxy for palatability given the tendency for leaves with low SLA to have higher lignin content and C:N ratios. Plant exudates are often a conveyance for mechanical and chemical plant defense, including toxic secondary metabolites reducing palatability (Farrell et al. 1991, Coley and Barone 1996, Agrawal 2004, Agrawal and Fishbein 2006).

A community phylogeny estimate for tree species in the data set was obtained by Bayesian analysis of chloroplast DNA sequences in conjunction with minimum age estimates and well-supported relationships for major seed plant clades as described in Whitfeld et al. (*in press*). Trait relationships at the level of individual trees were examined using multiple and stepwise regression, whereas phylogenetic generalized least-squares regression examined these relationships among tree species means. Each trait was tested for evidence of phylogenetic signal in our community sample (Blomberg and Garland 2002, Losos 2008). This approach evaluated the conditions under which community phylogenetic information is expected to improve predictions of overall herbivore abundance from plant traits.

METHODS

Field plots

Two 100 × 100 m plots near Wanang (145°10′55″ E, 5°13′51″ S), Madang Province, Papua New Guinea were destructively sampled. The two plots were 800 m apart in a mosaic of primary and secondary rain forest vegetation at 100–200 m above sea level in an extensive mixed evergreen forest on latosols in the Ramu River basin (Paijmans 1976, Wood 1982). The climate is generally humid and relatively aseasonal. Historical readings from Madang (70 km east, 1956–1970; McAlpine et al. 1983) indicated mean annual rainfall of 3500 mm and mean monthly temperature between 26.2°C and 26.7°C. Mean monthly rainfall exceeded 100 mm throughout the year, except during August to September based on readings taken between January 1994 and December 1996 from a site 70 km east of the study area (Novotny and Basset 1998). A minimum age for the primary-forest plot was estimated from Royal Australian Survey Corps aerial photographs, where the presence of multi-layered canopy in 1973 suggests no anthropogenic disturbance since at least the late 1950s. Local landowners practice subsistence agriculture in 0.25–1.0 ha gardens planted after felling and burning of primary forest. Succession ensues when garden plots are abandoned after 2–3 years of low-intensity cultivation. The secondary-forest plot was located in a garden plot that had been abandoned a decade earlier according to interviews with landowners. All woody plants with diameter at breast height (dbh) $\geq$ 5cm were measured and identified to species prior to sampling.

Destructive sampling

We coordinated our sampling with local landowners who were planning to clear the sites for subsistence gardens. Each 100 × 100 m plot was subdivided into 20 × 20 m subplots. For each subplot, the understory (i.e., all vegetation $<$1.4 m in height) was cleared followed by removal of all trees $<$5 cm diameter with machetes while taking care to minimize disturbance to the remaining vegetation. Orderly felling of trees $\geq$5 cm in diameter with a chain saw proceeded one tree at a time from the midstory to the canopy by severing lianas and dropping trees into artificial gaps created during the course of subplot removal. This procedure minimized the disturbance of remaining vegetation as much as could be expected during logging. Immediately upon felling, trees were inspected for the presence of caterpillars and leaf miners by a team of eight field workers. Live caterpillars were hand-collected and placed in plastic vials for processing, whereas leaves containing miners were collected and stored in plastic bags. Caterpillar and leaf miner abundance per tree were obtained by summing total numbers of live insects. Following inspection of the foliage for herbivores, eight field workers manually stripped all leaves from each felled tree and weighed the total leaf biomass in kilograms.

Specific leaf area (SLA), defined as fresh leaf area divided by dry leaf mass, was estimated from leaf disks punched from multiple individuals for all species in the survey plots with the dual purpose of DNA collection. Disks were collected from fully expanded, mature leaves without obvious signs of pathogen or herbivore damage. The disks had a diameter of 2.3 cm and were punched from fresh leaves in the field, temporarily stored in paper envelopes over silica gel, and subsequently stored in a –80°C frozen tissue collection at the University of Minnesota (St. Paul, Minnesota, USA). Mean SLA per species was obtained by averaging multiple samples per species. The presence or absence of exudates including latex and resin was also noted.

Leaves were sampled from up to four individuals per tree species for the measurement of foliar nitrogen. Three randomly chosen leaf samples per tree were bulked and ground by hand in liquid nitrogen or in a Tissuelyzer (Qiagen, Valencia, California, USA). Analysis was carried out at the University of Nebraska (Lincoln, Nebraska, USA) using dry combustion gas chromatography on a Costech analytical elemental combustion system ESC 4010 (Costech, Valencia, California, USA). This method yields the mass of an element that is subsequently converted to a percentage of the total mass of the sample.

Community phylogeny

Estimation of community phylogeny followed the procedure outlined in Whitfeld et al. (*in press*) based on the gene for the large subunit of ribulose-1,5-bisphosphate carboxylase-oxygenase (*rbcL*), a conserved coding locus that is easily amplified and known to accurately place most land plant taxa in orders and families. We sequenced according to published protocols (Kress et al. 2005, 2009, Kress and Erickson 2007), and all sequences were deposited in GenBank (accession numbers JF738369–JF739166; *available online*).[6]

We estimated phylogenetic relationships among all species of woody plants including trees, shrubs, and vines $\geq$5 cm dbh that occurred in the two 100 × 100 m plots and a series of 0.25-ha satellite plots that were part of an effort to examine change in phylogenetic structure during succession (Whitfeld et al., *in press*). Sequences were analyzed using Bayesian methods under a general time-reversible model of molecular evolution with parameters for invariant sites and rate heterogeneity among sites (GTR+Γ+I) selected using the Akaike Information Criterion as implemented in ModelTest version 3.7 (Posada and Crandall 1998). Bayesian analysis was conducted using BEAST (Drummond and Rambaut 2007) under GTR+Γ+I so that phylogenetic relationships and divergence times could be estimated simultaneously. Topological constraints, based on major angiosperm clades (APG 2009) and assumptions of monophyly below the ordinal rank were enforced to incorporate prior knowledge of well-supported relationships (Beaulieu et al. 2012), while allowing unresolved relationships to be estimated from sequence variation in the community sample (Kress et al. 2010). Information

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[6] http://www.ncbi.nlm.nih.gov/genbank/

on the minimum ages of major angiosperm lineages was incorporated in the Bayesian analysis by setting node age priors in BEAST. Thirty-one nodes with ages based on Wikström et al. (2001) were identified using Phylomatic (*available online*).[7] We applied these as node age priors in Bayesian analysis along with *rbcL* sequences, model parameters, and topological constraints to estimate branch lengths. A Markov chain Monte Carlo simulation of 10 million generations was sampled every 1000 generations and the first 1000 trees were discarded as burn-in. Among the posterior distribution of 9000 trees, the topology with the highest likelihood was used to quantify community phylogenetic patterns. For the present study, the resulting estimate of community phylogeny was pruned to include only those species occurring in the two 100 × 100 m plots.

Phylogenetic trait conservatism

Phylogenetic signal was assessed using the K statistic (Blomberg et al. 2003) that compares the observed trait distribution in community samples to expectations under Brownian motion model of trait evolution. Calculations of K values for the traits included in this study were performed in Picante (Kembel et al. 2010) based on 2150 individuals representing 183 species for which comparable data were available. We also analyzed a subset of 84 species with ≥ 5 individuals out of concern that rarely sampled species yield inaccurate estimates of mean herbivore abundance and total leaf biomass given the extremes of intraspecific variability in these traits. Common species represented >90% of individuals in our plots.

Values of the K statistic approaching zero approximate a random distribution of trait values with respect to the plant community phylogeny, whereas values approaching one imply trait values match expectations under a Brownian motion model of evolution (Ackerly 2009). P values were derived from the comparison of observed K to a null distribution obtained by 999 randomizations of trait values across the tips of the community phylogeny. We chose this approach over Mantel tests because the latter lacks power and is known to involve high Type I error with phylogenetic information, whereas Blomberg's K does not (Harmon and Glor 2010).

Regression analysis

Comparable functional trait and insect abundance data from the 2150 individual trees were analyzed under a general model incorporating resource quantity (leaf biomass, dbh), quality (foliar nitrogen), palatability (specific leaf area, percentage of immature foliage, and the presence of exudate), and the month in which trees were felled. The best-fit model was chosen based on the minimum AIC score. The sample size for regression analyses was not identical to the numbers of stems surveyed in the plots due to missing data for a small number of individual tree (i.e., leaf biomass was recorded but SLA was unavailable, and so on). Individual plants with zero values for leaf biomass (e.g., leafless trees at the time of felling) or zero herbivore abundance (e.g., foliage entirely lacking caterpillars or leaf miners) were included in the analysis. All analyses were performed using JMP version 8.0.1 (SAS Institute 2009). Individual-level and species-level regression analyses assumed the independence of trait values; however, phylogenetic trait conservatism violates this assumption. We used a phylogenetic generalized least-squares (PGLS) approach (Martins and Hansen 1997) to conduct regression incorporating phylogenetic relationships as the expected variance–covariance error matrix. The method incorporates tree topology and branch lengths to minimize variance of the regression slope and intercept using the generalized least-squares equation (a Gauss-Markov estimator; Grafen 1989, Martins and Hansen 1997, Garland and Ives 2000). Analysis of trait differences among sister groups was performed using COMPARE version 4.6b (available from E. P. Martins, Indiana University, Bloomington, Indiana, USA).

RESULTS

Stand characteristics of primary and secondary plots are provided in Table 1. The density of stems was comparable, whereas tree species richness, basal area, and leaf biomass per hectare was substantially higher in the primary forest. Overall caterpillar abundance in secondary forest was nearly twice that of primary forest, whereas leaf miner abundance was comparable. These trends at the stand level were consistent with significantly higher mean caterpillar abundance per tree and per kilogram of foliage in secondary vegetation than in primary forest, whereas miner abundance did not differ among plots. Specific leaf area and nitrogen content were also higher, on average, in secondary-forest trees. Evidence that total leaf biomass per tree was significantly lower in secondary forest, where trees were also smaller on average, is consistent with tree allometry relating leaf biomass as a log function of plant size ($r^2 = 0.56$, $P < 0.0001$; Fig. 1A). Herbivore abundance at the time of felling ranged from 475 caterpillars in one tree to no caterpillars in 29% of trees. Leaf miners were considerably less abundant, ranging from a maximum of 109 in one tree to none in 67% of trees at the time of felling. Herbivores per kilogram of foliage was not strongly related to plant size, although small trees hosted much higher densities on occasion than did large trees (Fig. 1B, C).

Results of multiple regression among plant traits and herbivore abundance on individual trees yielded highly similar results when primary and secondary-forest trees were treated separately or pooled, and here we report results based on the combined data set for the sake of

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[7] http://www.phylodiversity.net/phylomatic/phylomatic.html

TABLE 1. Plant traits and insect herbivore abundance in 1-ha plots of secondary and primary New Guinea lowland rain forest vegetation.

Trait	Rain forest vegetation type: Secondary	Rain forest vegetation type: Primary	P
A) Total per ha			
Stems $\geq$ 5 cm	1 206	1 336	NA
Basal area (m^2/ha)	13.6	29.9	NA
Species richness	90	213	NA
Leaf biomass (kg)	6 036	10 500	NA
Caterpillars	14 053	7 256	NA
Leaf miners	1 548	1 852	NA
B) Mean (SD)			
Leaf biomass per tree (kg)	5.72 (9.83)	9.60 (9.83)	<0.0001
Foliar nitrogen (%)	2.32 (0.48)	2.08 (0.52)	<0.0001
Specific leaf area (cm^2/g)	147.01 (35.23)	140.03 (39.95)	<0.0001
Caterpillars per tree	13.31 (36.60)	6.63 (16.19)	<0.0001
Caterpillars per kg foliage	3.03 (0.32)	1.82 (0.31)	<0.01
Leaf miners per tree	1.37 (5.69)	1.69 (5.37)	n.s.
Leaf miners per kg foliage	0.56 (2.53)	0.39 (2.04)	n.s.

Notes: Values in panel (A) are based on all woody stems with diameter at breast height (dbh) $\geq$5 cm in each 100 × 100 m plot, and values in panel (B) are based on per-plot means (with standard deviations in parentheses) for a subset of species with comparable data for all traits and insect abundances ($n = 1056$ and 1094 for secondary and primary forest, respectively). P values represent significance from ANOVA for traits, insect abundance per tree, and per-kilogram foliage.; n.s. indicates "not significant"; NA, "not applicable."

brevity. Plant traits including biomass (foliage and dbh), nutritional quality (foliar nitrogen), and palatability (specific leaf area, percentage of immature foliage, and exudate) were considered, along with the timing of sampling in the full regression model. The best-fit model, based on minimum AIC scores, explained 30% of variation in caterpillar abundance per tree and 13% for caterpillars per kilogram of foliage (Table 2A). Leaf miner abundance was explained to a lesser extent (Table 2B). Total leaf biomass, the percentage of immature foliage, and the month in which trees were sampled were consistently significant predictors of herbivore abundance, and leaf nitrogen was generally significant. The presence of exudate had a strong negative effect on per-tree caterpillar and leaf miner abundance (Fig. 2).

Species mean values for plant traits and herbivore abundance were more or less randomly distributed with respect to host plant community phylogeny according to generally low values of Blomberg's K (Table 3). Only leaf nitrogen content showed evidence of phylogenetic conservatism in the community sample. This was the case according to analyses of either the entire data set of 183 tree species or a subset of 84 common species represented by $\geq$5 individuals. In the case of exudate, we calculated the D statistic for phylogenetic signal as a binary trait (Fritz and Purvis 2010). The statistic is based on the sum of sister clade differences. Clustered traits have the same state in related species at the tips of the phylogeny such that the sum of sister clade differences is low compared to the case of over-dispersed traits where the sum of sister clade differences is high. Exudate D indicated a degree of phylogenetic clustering that is consistent with Brownian expectations (Fig. 3).

Regression analysis based on species trait means identified the strongest predictor of caterpillar abundance per tree to be total leaf biomass (Table 4A). This was true whether all species or only common species were considered and whether or not phylogenetic relationships between trees species were taken into account. Overall, the best-fitting model, explaining 34% of caterpillar abundance variation, included only common tree species and accounted for their phylogenetic relationships. Foliar nitrogen and SLA were also included in the best-fitting model, although the latter was not significant. Comparable results were obtained for caterpillars per kilogram of foliage, although less variation was explained (r^2 = 0.04–0.08; model not shown). Plant traits also explained more variation in leaf miner abundance per tree when only common species and their phylogenetic relationships were considered (Table 4B). No plant trait explained significant variation in leaf miners per kilogram of foliage (model not shown).

DISCUSSION

Recent ecological studies of plant–herbivore interactions have argued for the importance of phylogenetic context to identify the mechanisms responsible for patterns in trophic relationships (Lamarre et al. 2012). Although this may be the case for particular plant defenses (Fine et al. 2006, Agrawal et al. 2009*a*) and the dietary specialization of particular herbivore species (Weiblen et al. 2006), the overall abundance of leaf-chewing herbivores and most of the leaf traits we examined showed little evidence of phylogenetic signal (Table 3). Whether phylogenetic considerations improved the fit of trait-based models predicting herbivore

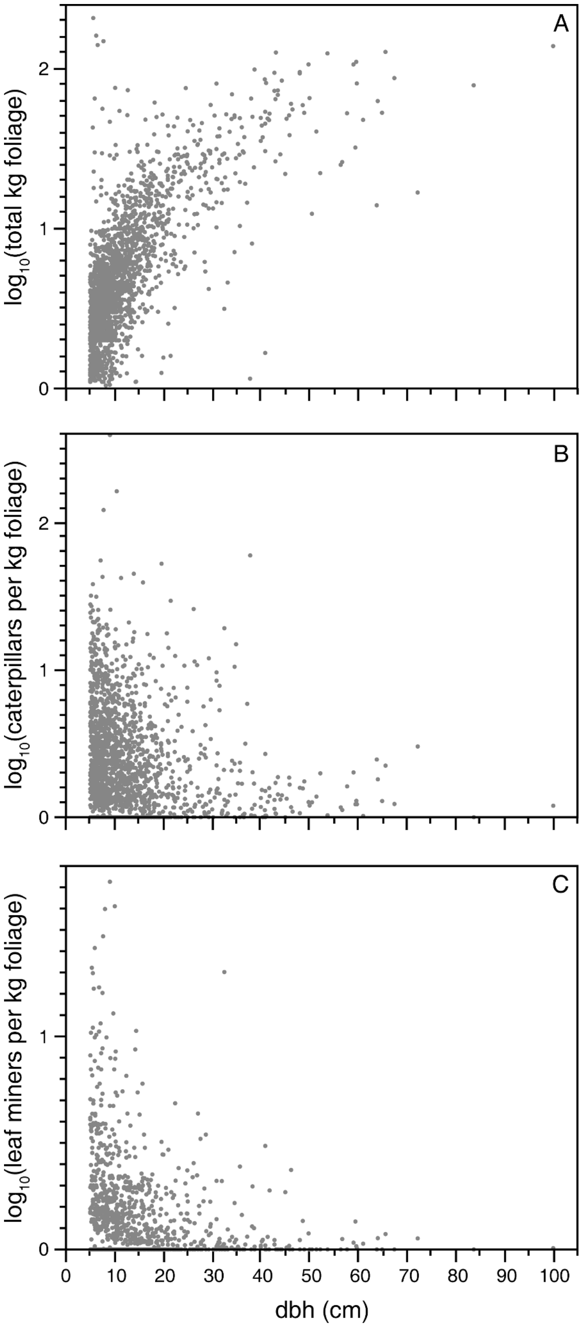

FIG. 1. Total leaf biomass and herbivore abundance per tree as functions of diameter at breast height (dbh) based on 2150 stems in two hectares of New Guinea lowland rain forest for (A) leaf biomass, (B) caterpillar density per kilogram foliage, and (C) leaf miner density per kilogram foliage.

abundance depended on the size of the plant species pool (Table 4). Models incorporating phylogeny were less predictive when all plant species were analyzed, but proved more predictive when only common species were analyzed.

We would expect the power to detect phylogenetic effects to decline with the size of the species pool but, to the contrary, we found stronger effects with the subset of common species that we attribute to improved accuracy in estimating species means. Leaf biomass and herbivore abundance per plant were extremely variable among individuals in species populations such that sampling only a few individuals could introduce considerable error to comparisons at the species level.

The dynamism of populations in space and time that results from seasonal variation in the abiotic environment (Lawton and Gaston 1989) or trophic cascades involving natural enemies of herbivores (Mooney et al. 2010) could also weaken relationships between plant traits and instantaneous measures of herbivore abundance. Although the study site is relatively aseasonal, with mean monthly rainfall exceeding 100 mm in all months of the year but two (Novotny and Basset 1998), the month in which a tree was sampled explained a major component of variation in folivore abundance (Table 2). Seasonal patterns of insect abundance are best examined in particular tree species that were felled throughout the year rather than in the entire sample because our design did not control for monthly variability in the size or species composition of felled trees. Significant monthly variation in herbivore density per kilogram of foliage was detected in half of the 12 tree

TABLE 2. Results of best-fit multiple regression for (A) caterpillar abundance and (B) leaf miner abundance per tree and per kilogram of foliage.

Parameter	SS	*F*	*P*
A) Caterpillars			
Per tree ($r^2 = 0.30$)			
Total leaf biomass	138.97	648.502	<0.0001
Foliar nitrogen	22.66	105.73	<0.0001
Month sampled	31.20	13.24	<0.0001
Immature foliage (%)	10.72	50.02	<0.0001
Exudate	1.63	7.61	0.006
Per kg foliage ($r^2 = 0.13$)			
Month sampled	13.72	11.81	<0.0001
Immature foliage (%)	8.04	76.17	<0.0001
Foliar nitrogen	7.60	72.00	<0.0001
Total leaf biomass	2.16	20.43	<0.0001
Exudate	0.83	7.89	0.005
B) Leaf miners			
Per tree ($r^2 = 0.16$)			
Month sampled	11.86	11.34	<0.0001
Total leaf biomass	3.98	41.89	<0.0001
dbh	2.86	30.06	<0.0001
Foliar nitrogen	1.28	13.41	0.0002
Immature foliage (%)	0.58	6.07	0.01
Per kg foliage ($r^2 = 0.06$)			
Month sampled	2.59	6.78	<0.0001
Total leaf biomass	1.38	39.80	<0.0001
dbh	0.42	12.30	0.00035
Immature foliage (%)	0.26	7.41	0.007
Specific leaf area	0.23	6.63	0.01

Notes: Data drawn from 2150 individual trees on two hectares of New Guinea lowland rain forest. The full model combined traits reflecting resource quantity (leaf biomass, dbh), quality (leaf nitrogen), and palatability (specific leaf area, percentage of immature foliage, exudate) with seasonality. The best-fitting model was chosen based on minimum AIC score.

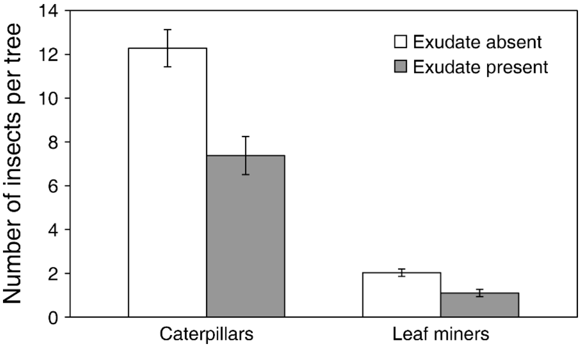

FIG. 2. Mean (±SE) abundance of caterpillars and leaf miners per tree in the presence or absence of exudates including latex and resin. Samples included 1040 exudate-bearing trees and 1110 non-exudate-bearing trees in two hectares of New Guinea lowland rain forest. Both guilds were significantly less abundant in the presence of exudate (ANOVA; $F_{2,2148} = 16.19$, $P < 0.0001$ for caterpillars; $F_{2,2148} = 15.28$, $P < 0.0001$ for leaf miners).

species that were sampled during at least 10 months of the year. For example, herbivores per kilogram of foliage in *Trichospermum pleiostigma* (Malvaceae) exhibited relatively strong seasonal variation (Fig. 4) such that abundance peaked following the wettest months and declined with the onset of the driest months.

In spite of seasonality, a significant component of variation among individual trees in leaf-chewing insect abundance could be explained by the leaf traits we measured, and more so for caterpillars than for leaf miners (Table 2). Among the relationships between leaf traits and herbivore abundance, we predicted that resource availability would have the greatest influence. As expected, total leaf biomass in terms of kilogram foliage per tree was generally more important than either resource quality (approximated by N content) or palatability (percentage of immature foliage and SLA). Leaf biomass as a major determinant of leaf-chewing insect abundance is consistent with the prediction of the resource availability hypothesis (Herms and Mattson 1992) and evidence from other systems (Basset 1996, Marques et al. 2000). Our finding that overall insect abundance was related more strongly to resource availability than to other plant traits has been observed in other systems (Crist et al. 2006, Pringle et al. 2010).

Even though foliage availability appears to be a first-order predictor of folivore abundance variation among individual trees and tree species, we expected plants with higher nutritional quality to support more herbivores. Foliar nitrogen did show evidence for resource quality affecting community structure at the next trophic level. Nitrogen is known to influence the growth and abundance of insect populations (Basset 1991, Cornelissen and Stiling 2006), and a small but significant component of abundance variation among trees in our community sample can be attributed to this factor. Further investigation is needed to determine whether the observation that nitrogen content is generally more important for caterpillars than leaf miners (Tables 2 and 4) results from life history differences among these guilds (Novotny et al. 2010) or is due to a lack of statistical power arising from the relative rarity of leaf miners in our data set (Table 1).

The prediction that trees with low SLA, and therefore relatively greater investment in leaf structural components, would host fewer numbers of herbivores (Poorter et al. 2004) did not draw support from comparisons among individual trees except in the case of leaf miners per kilogram of foliage (Table 2). It was also only rather weakly supported at the tree species level (Table 4). Although SLA is thought to be correlated with a general life history trade-off between rapid plant growth and avoidance of mortality by investment in anti-herbivore defense (Fine et al. 2006, Wright et al. 2010), it is far from a direct measure of palatability, and it clearly did not account for the overall abundance of leaf-chewing insect communities or for leaf biomass, which is a function of plant size (Fig. 1). These findings would seem to favor the importance of resource availability over plant defense for community-wide patterns of herbivory, but direct investigation of palatability by way of plant secondary chemistry (Agrawal et al. 2009*b*, Kursar et al. 2009) at the community level is needed.

Exudates, including the latex and resins that convey the defensive plant secondary metabolites of foliage to herbivores, provide a somewhat more direct measure of palatability than SLA. The presence of exudate is often implicated in plant defense (Farrell et al. 1991, Coley

TABLE 3. Tests for plant trait phylogenetic conservatism based on Blomberg's K statistic (D statistic for exudate presence) for a community sample of all 183 woody plant species with dbh ≥ 5 cm (K_{all}) and 84 species with ≥ 5 stems (K_{common}) in two hectares of New Guinea lowland rain forest.

Trait	K_{all}	K_{common}	P
Stem density per hectare	0.06	0.06	n.s.
Diameter at breast height (cm)	0.09	0.19	n.s.
Leaf biomass per tree (kg)	0.06	0.17	n.s.
Leaf nitrogen content (% dry mass)	0.16	0.24	<0.005
Specific leaf area (cm^2/g)	0.10	0.18	n.s.
Caterpillar abundance per tree	0.12	0.16	n.s.
Caterpillar abundance per kg foliage	0.18	0.13	n.s.
Leaf miner abundance per tree	0.06	0.15	n.s.
Leaf miner abundance per kg foliage	0.09	0.11	n.s.
Presence of exudate†	0.19	0.11	NA

Notes: In the case of K, values approaching 0 approximate a random distribution of trait values with respect to the plant community phylogeny whereas values approaching 1 imply trait values matching expectations under the Brownian motion model of evolution. P values are derived from the comparison of observed K to a null distribution obtained by 999 randomizations of trait values across the tips of the community phylogeny; n.s. stands for not significant. Significance was comparable for the full data set and the reduced data set.

† The D statistic (D_{all}, D_{common}) is shown for the presence of exudate. In the case of D, values near 0 approximate Brownian expectations, whereas values approaching 1 suggest a phylogenetically random trait distribution (Fritz and Purvis 2010); NA stands for not applicable.

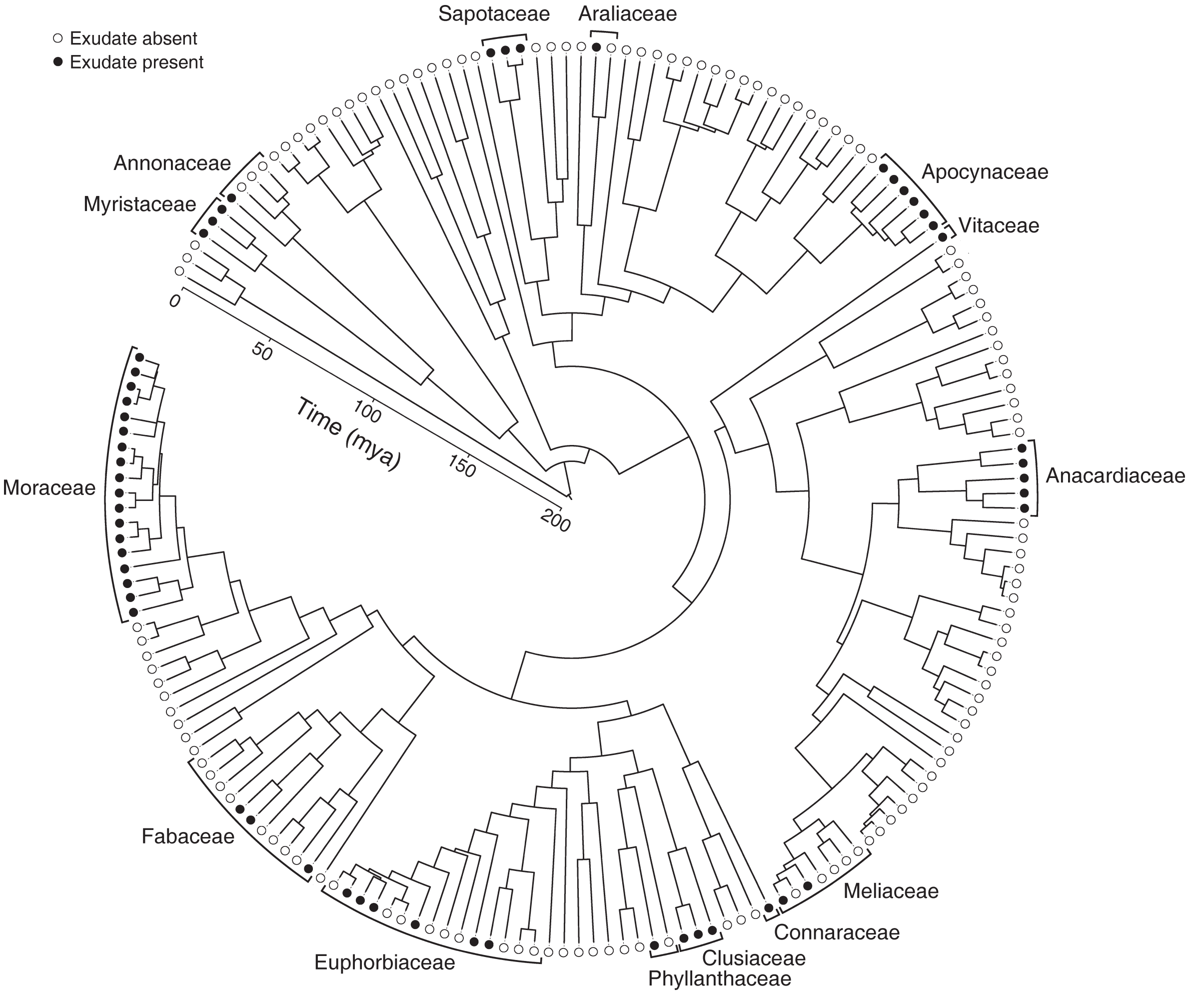

FIG. 3. A community phylogeny of 183 woody plant species with ≥5 cm diameter at breast height (dbh) encountered in 2 ha of New Guinea lowland rain forest. The maximum-likelihood tree among a Bayesian posterior distribution of 9000 phylogenetic trees is displayed with branch lengths proportional to time in millions of years (mya). The presence or absence of exudate (including latex and resins) is indicated by open and solid circles at the tips of the trees, respectively. Only families with at least one species containing exudate are named to illustrate the convergence in this trait.

and Barone 1996, Agrawal 2004, Agrawal and Fishbein 2006), and herbivory is known to increase when exudate production is disrupted experimentally (Dussourd and Eisner 1987). This trait appears to have a substantial impact on herbivore community abundance (Fig. 2) that is consistent with predictions from plant defense theory (Herms and Mattson 1992, Agrawal and Fishbein 2006). It is striking that exudates were recorded in more than half of all trees measured in our New Guinea forest plots, and it is arguable that the ecological importance of such evolved defenses could influence the community distribution of plant–herbivore interactions (Agrawal 2005). Although exudates are conserved in several lineages, they also appear to have evolved repeatedly and independently (Fig. 3). Trophic interactions could facilitate the co-occurrence of diverse lineages with similar defenses (Farrell et al. 1991) if exudate-bearing trees shared a competitive advantage relative to non-exudate bearing trees in the presence of abundant herbivores. When functional trait parallelism and convergence are widespread, ecologists should take care not to use phylogeny as a proxy for ecological similarity in explaining community-wide patterns. We also argue that phylogeny need not contribute to the solution of every problem in ecology. In the case of trophic interactions at the community level, we think it is important for ecologists to recognize the limitations of a phylogenetic approach, especially as it has gained popularity in recent literature on plant–insect interactions.

Nitrogen content illustrates how a conserved plant trait might influence herbivore community abundance patterns. Phylogenetic signal in nutrient availability has been observed in another tropical forest (Kraft and Ackerly 2010, Kraft et al. 2010), and in our study, PGLS demonstrated that consideration of host plant related-

TABLE 4. Results of best-fit multiple regression for (A) caterpillar abundance per tree and (B) leaf miner abundance against plant traits drawn from two hectares of New Guinea lowland rain forest.

Parameter	SS	*F*	*P*
A) Caterpillars per tree			
All species			
AH ($r^2 = 0.25$)			
Total leaf biomass	7.04	53.05	<0.0001
Specific leaf area	2.12	15.98	<0.0001
PGLS ($r^2 = 0.20$)			
Total leaf biomass	146.32	37.61	<0.0001
Specific leaf area	11.05	2.84	0.09
Foliar nitrogen	9.11	2.34	0.13
Common species			
AH ($r^2 = 0.28$)			
Total leaf biomass	2.18	26.96	<0.0001
Foliar nitrogen	0.28	3.51	0.06
PGLS ($r^2 = 0.34$)			
Total leaf biomass	0.07	25.59	<0.0001
Foliar nitrogen	0.03	11.84	0.0009
Specific leaf area	0.01	2.65	0.11
B) Leaf miners per tree			
All species			
AH ($r^2 = 0.09$)			
Total leaf biomass	0.94	19.19	<0.0001
Specific leaf area	0.11	2.29	0.13
PGLS ($r^2 = 0.06$)			
Total leaf biomass	16.13	10.82	0.001
Specific leaf area	4.26	2.86	0.09
Common species			
AH ($r^2 = 0.21$)			
dbh	0.42	21.49	<0.0001
PGLS ($r^2 = 0.35$)			
Exudate	0.01	13.18	0.0005
dbh	0.01	9.66	0.003
Total leaf biomass	0.001	1.72	0.19

Notes: Species means were analyzed for all 183 woody plant species with dbh ≥5 cm (all species) and a community sample of 84 species with ≥5 stems (common species) and based on ahistorical correlations (AH) and phylogenetic generalized least-squares regression (PGLS). The full model combined traits reflecting resource quantity (leaf biomass, dbh), quality (leaf nitrogen), and palatability (specific leaf area, exudate). The best-fitting model was chosen based on minimum AIC score.

ness did increase the power of leaf nitrogen to predict caterpillar abundance on a per-tree and per-unit of foliage basis. This provides evidence that the community phylogenetic distribution of a trait at one trophic level can to some extent affect overall community structure at another trophic level.

A logical next step in these investigations is to assess herbivore species distributions with respect to plant phylogeny and traits where we expect the strength of relationship between the community distribution of plant defensive traits and specialized herbivores to be stronger (Weiblen et al. 2006). DNA barcoding of herbivores may aid in identifying not only species but also patterns of dietary specialization (Craft et al. 2010) in relation to the phylogenetic distribution of particular plant defenses (Agrawal et al. 2009*b*).

Although our un-replicated plot design weakens the comparison of secondary and primary-forest attributes, differences in plant functional traits observed in our New Guinea plots are consistent with other tropical forests (Popma et al. 1992, Poorter et al. 2004) and predictions from resource allocation theory. That the trees of secondary forest had higher SLA and foliar nitrogen than primary-forest trees is typical for this high-light environment where low investment in structural defense, high growth rates, and relatively high rates of photosynthesis per unit of mass are commonly observed (Schadler et al. 2003, Poorter et al. 2004, Agrawal and Fishbein 2006).

Observed patterns of SLA and foliar nitrogen associated with secondary and primary forests may reflect a trade-off between plant growth syndromes associated with survival in two rather different environments. Trees of high-resource secondary forests maximize photosynthesis and growth (high SLA and foliar nitrogen), while investing less in structural defenses and

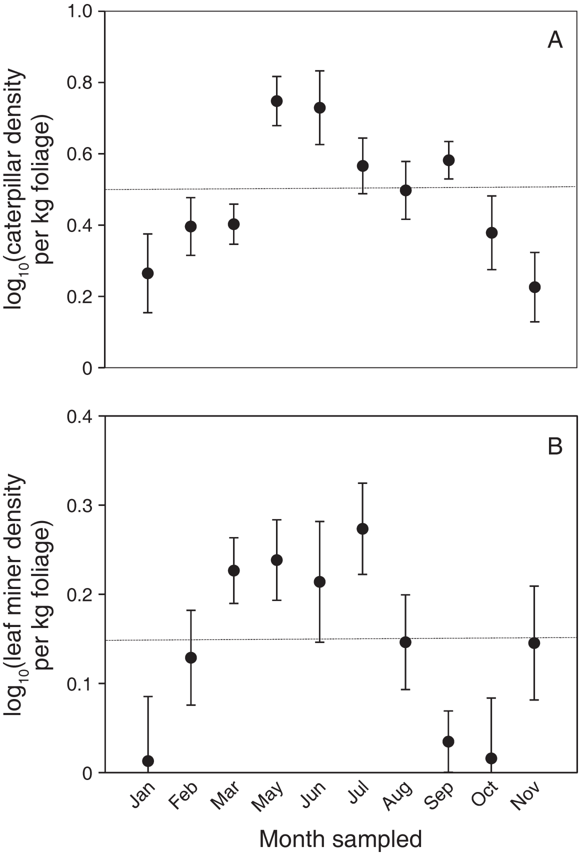

FIG. 4. Seasonality of (A) caterpillar and (B) leaf miner abundance on *Trichospermum pleiostigma* (Malvaceae) based on insects per kilogram of foliage (mean ± SE) on 151 individual trees in two hectares of New Guinea lowland rain forest. The horizontal lines show the overall mean number of insects per kilogram of foliage.

relying on abundant exudate to deter herbivores. This puts secondary forests at one end of a spectrum that is interpreted as trade-off between the rate of investment in biomass and the speed of return on that investment (Reich et al. 2003, Wright et al. 2004). The greater leaf biomass of older forests (Guariguata et al. 1997, Chazdon 2003) is consistent with this view.

While previous studies have demonstrated the potential importance of herbivorous insects on habitat specialization of plants (Fine et al. 2004, 2006), few other studies have attempted to compare the abundance of insect herbivores between different successional stages. Higher rates of herbivory in early succession (Herms and Mattson 1992, Poorter et al. 2004) and in communities dominated by shade-intolerant trees (Basset 1996) have been reported in some previous studies, whereas others (Leps et al. 2001) found little evidence of differences in herbivore species abundance among successional stages. The higher overall total abundance of caterpillars per hectare, per tree, and per kilogram of foliage in younger secondary forest is consistent with expectations based on foliage quality and palatability. However, we found the strongest predictor of insect abundance was leaf biomass, making the higher abundance of insects in secondary forest seem paradoxical in light of the larger trees and greater biomass of primary forests. Nevertheless, Fig. 1B and C indicate that the density of herbivores per unit foliage declines with tree size. That smaller trees appear to be disproportionately attacked by herbivores appears to explain the lesser overall abundance of caterpillars in primary forest. Whether the apparent lower density of herbivores on larger trees has a biological explanation or is an artifact of our destructive sampling will require further investigation. Although we focused on non-volant herbivores (i.e., leaf miners, leaf-tying and leaf-rolling caterpillars), we would expect caterpillars as well as leaves containing miners to more likely become detached from large trees than small trees during felling. Whether this is true of our method could be determined in future by analysis of herbivory rates based on an extensive archive of digitally photographed leaves from each tree in our data set. If this pattern proves not to be an artifact, it potentially provides a mechanism for density-dependent mortality (Wills et al. 2006, Comita et al. 2010, Metz et al. 2010).

We conclude with a discussion of the implications of these findings for tropical-forest management in light of the current overall trend toward conversion of primary forest to secondary forest. Disturbance leads to well-documented changes in the structural and functional diversity of plant communities (Guariguata et al. 1997, Chazdon 2003, Poorter et al. 2004, Santos et al. 2010), and we observed generally similar trends in New Guinea. The impacts of forest conversion on herbivorous insects are less well understood. Based on our comparison of secondary and primary forests, younger vegetation appears to support greater numbers of insect herbivores per hectare, per tree, and per kilogram of biomass. Given the unprecedented rate and extent of tropical-forest conversion worldwide, the predicted increase in abundance of leaf-chewing caterpillars poses a challenge for forest management, especially where outbreaks may threaten forest regeneration after logging and small areas of remaining intact forests.

In light of observed decreases in host plant phylogenetic diversity in secondary vs. primary forest in New Guinea (Whitfeld et al., *in press*) and Costa Rica (Letcher 2010), an assessment of insect herbivore richness in early and late succession is needed to understand the full impact of forest conversion on overall biodiversity. Also, investigation of plant secondary chemistry could examine the extent to which chemical defenses are deployed and their cost relative to structural defenses in protecting host plants from insect herbivores. Analysis of the degree to which these chemicals are phylogenetically conserved or convergent in host plants would enable further predictions to be made about the degree to which host plants have adapted to their herbivore enemies. A better understanding of diversity in secondary forests is particularly important as these communities become a dominant feature of tropical landscapes and their role in species conservation (Chazdon et al. 2009) becomes more important.

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LITERATURE CITED

Ackerly, D. 2009. Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. Proceedings of the National Academy of Sciences USA 106:19699–19706.

Agrawal, A. A. 2004. Resistance and susceptibility of milkweed: competition, root herbivory, and plant genetic variation. Ecology 85:2118–2133.

Agrawal, A. A. 2005. Natural selection on common milkweed (*Asclepias syriaca*) by a community of specialized insect herbivores. Evolutionary Ecology Research 7:651–667.

Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. Ecology 87:132–149.

Agrawal, A. A., M. Fishbein, R. Halitschke, A. P. Hastings, D. L. Rabosky, and S. Rasmann. 2009*a*. Evidence for adaptive radiation from a phylogenetic study of plant defenses. Proceedings of the National Academy of Sciences USA 106:18067–18072.

Agrawal, A. A., J. P. Salminen, and M. Fishbein. 2009*b*. Phylogenetic trends in phenolic metabolism of milkweeds (*Asclepias*): evidence for escalation. Evolution 63:663–673.

APG [Angiosperm Phylogeny Group]. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161:105–121.

Basset, Y. 1991. Influence of leaf traits on the spatial-distribution of insect herbivores associated with an overstory rain-forest tree. Oecologia 87:388–393.

Basset, Y. 1996. Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. Ecology 77:1906–1919.

Beaulieu, J. M., R. H. Ree, J. Cavender-Bares, G. D. Weiblen, and M. J. Donoghue. 2012. Synthesizing phylogenetic knowledge for ecological research. Ecology 93(Supplement):S4–S13.

Berkov, A., and G. Tavakilian. 1999. Host utilization of the Brazil nut family (Lecythidaceae) by sympatric wood-boring species of Palame (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini). Biological Journal of the Linnean Society 67:181–198.

Blomberg, S. P., and T. Garland. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15:899–910.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57:717–745.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51–71.

Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork, and S. E. Miller. 2009. The potential for species conservation in tropical secondary forests. Conservation Biology 23:1406–1417.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant diseases in temperate and tropical broadleaf forests. Pages 25–49 *in* P. W. Price, T. M. Lewisohn, G. W. Fernamdes, and W. W. Benson, editors. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York, New York, USA.

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

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. Science 329:330–332.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 *in* P. J. D. Boer and G. Gradwell, editors. Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

Cornelissen, T., and P. Stiling. 2006. Responses of different herbivore guilds to nutrient addition and natural enemy exclusion. Ecoscience 13:66–74.

Craft, K. J., S. U. Pauls, K. Darrow, S. E. Miller, P. D. N. Hebert, L. E. Helgen, V. Novotny, and G. D. Weiblen. 2010. Population genetics of ecological communities with DNA barcodes: An example from New Guinea Lepidoptera. Proceedings of the National Academy of Sciences USA 107:5041–5046.

Crist, T. O., S. V. Pradhan-Devare, and K. S. Summerville. 2006. Spatial variation in insect community and species responses to habitat loss and plant community composition. Oecologia 147:510–521.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214–218.

Dussourd, D. E., and T. Eisner. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. Science 237:898–901.

Dyer, L. A., et al. 2007. Host specificity of Lepidoptera in tropical and temperate forests. Nature 448:696–699.

Farrell, B. D., D. E. Dussourd, and C. Mitter. 1991. Escalation of plant defense: do latex and resin canals spur plant diversification? American Naturalist 138:881–900.

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science 305:663–665.

Fine, P. V. A., Z. J. Miller, I. Mesones, S. Irazuzta, H. M. Appel, M. H. H. Stevens, I. Saaksjarvi, L. C. Schultz, and P. D. Coley. 2006. The growth–defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87(Supplement):S150–S162.

Fritz, S. A., and A. Purvis. 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conservation Biology 24:1042–1051.

Garland, T., and A. R. Ives. 2000. Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. American Naturalist 155:346–364.

Gilbert, G. S., and C. O. Webb. 2007. Phylogenetic signal in plant pathogen-host range. Proceedings of the National Academy of Sciences USA 104:4979–4983.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London B 326:119–157.

Guariguata, M. R., R. L. Chazdon, J. S. Denslow, J. M. Dupuy, and L. Anderson. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology 132:107–120.

Harmon, L. J., and R. E. Glor. 2010. Poor statistical performance of the Mantel test in phylogenetic comparative analyses. Evolution 64:2173–2178.

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

Hulcr, J., M. Mogia, B. Isua, and V. Novotny. 2007. Host specificity of ambrosia and bark beetles (Col., Curculionidae: Scolytinae and Platypodinae) in a New Guinea rainforest. Ecological Entomology 32:762–772.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463–1464.

Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs 80:401–422.

Kraft, N. J. B., W. K. Cornwell, C. O. Webb, and D. D. Ackerly. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. American Naturalist 170:271–283.

Kraft, N. J. B., M. R. Metz, R. S. Condit, and J. Chave. 2010. The relationship between wood density and mortality in a global tropical forest data set. New Phytologist 188:1124–1136.

Kress, W. J., and D. L. Erickson. 2007. A two-locus global DNA barcode for land plants: the coding *rbcL* gene complements the non-coding *trnH-psbA* spacer region. PLoS ONE 2:e508.

Kress, W. J., D. L. Erickson, F. A. Jones, N. G. Swenson, R. Perez, O. Sanjur, and E. Bermingham. 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. Proceedings of the National Academy of Sciences USA 106:18621–18626.

Kress, W. J., D. L. Erickson, N. G. Swenson, J. Thompson, M. Uriarte, and J. K. Zimmerman. 2010. Advances in the use of DNA barcodes to build a community phylogeny for tropical trees in a Puerto Rican forest dynamics plot. PLoS ONE 5:e15409.

Kress, W. J., K. J. Wurdack, E. A. Zimmer, L. A. Weigt, and D. H. Janzen. 2005. Use of DNA barcodes to identify flowering plants. Proceedings of the National Academy of Sciences USA 102:8369–8374.

Kursar, T. A., and P. D. Coley. 1992. Delayed greening in tropical leaves: an antiherbivore defense. Biotropica 24:256–262.

Kursar, T. A., K. G. Dexter, J. Lokvam, R. T. Pennington, J. E. Richardson, M. G. Weber, E. T. Murakami, C. Drake, R. McGregor, and P. D. Coley. 2009. The evolution of antiherbivore defenses and their contribution to species coexistence in the tropical tree genus Inga. Proceedings of the National Academy of Sciences USA 106:18073–18078.

Lamarre, G. P. A., C. Baraloto, C. Fortunel, N. Dávila, I. Mesones, J. G. Ríos, M. Ríos, E. Valderrama, M. V. Pilco, and P. V. A. Fine. 2012. Herbivory, growth rates, and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity. Ecology 93(Supplement):S195–S210.

Lawton, J. H., and K. J. Gaston. 1989. Temporal patterns in the herbivorous insects of bracken: a test of community predictability. Journal of Animal Ecology 58:1021–1034.

Leigh, E. G. 1999. Tropical forest ecology: A view from Barro Colorado Island. Oxford University Press, New York, New York, USA.

Leps, J., V. Novotny, and Y. Basset. 2001. Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. Journal of Ecology 89:186–199.

Letcher, S. G. 2010. Phylogenetic structure of angiosperm communities during tropical forest succession. Proceedings of the Royal Society B 277:97–104.

Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1003.

Marques, E. S. D., P. W. Price, and N. S. Cobb. 2000. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. Environmental Entomology 29:696–703.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. American Naturalist 149:646–667.

McAlpine, J. R., G. Keig, and R. Falls. 1983. Climate of Papua New Guinea. SCIRO and Australian National University Press, Canberra, Australia.

Metz, M. R., W. P. Sousa, and R. Valencia. 2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. Ecology 91:3675–3685.

Mooney, K. A., R. Halitschke, A. Kessler, and A. A. Agrawal. 2010. Evolutionary trade-offs in plants mediate the strength of trophic cascades. Science 327:1642–1644.

Novotny, V., and Y. Basset. 1998. Seasonality of sap sucking insects (Auchenorrhyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea. Oecologia 115:514–522.

Novotny, V., and Y. Basset. 2005. Review. Host specificity of insect herbivores in tropical forests. Proceedings of the Royal Society B 272:1083–1090.

Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. Nature 416:841–844.

Novotny, V., et al. 2010. Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. Journal of Animal Ecology 79:1193–1203.

Novotny, V., S. E. Miller, J. Leps, Y. Basset, D. Bito, M. Janda, J. Hulcr, K. Damas, and G. D. Weiblen. 2004. No tree an island: the plant-caterpillar food web of a secondary rain forest in New Guinea. Ecology Letters 7:1090–1100.

Odegaard, F., O. H. Diserud, and K. Ostbye. 2005. The importance of plant relatedness for host utilization among phytophagous insects. Ecology Letters 8:612–617.

Paijmans, K., editor. 1976. New Guinea vegetation. Elsevier Scientific, Amsterdam, The Netherlands.

Poorter, L., M. V. de Plassche, S. Willems, and R. G. A. Boot. 2004. Leaf traits and herbivory rates of tropical tree species differing in successional status. Plant Biology 6:746–754.

Popma, J., F. Bongers, and M. J. A. Werger. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain-forest in Mexico. Oikos 63:207–214.

Posada, D., and K. Crandall. 1998. Model test: testing the model of DNA substitution. Bioinformatics 14:817–818.

Pringle, R. M., D. F. Doak, A. K. Brody, R. Jocqué, and T. M. Palmer. 2010. Spatial pattern enhances ecosystem functioning in an African savanna. PLoS Biology 8:e1000377.

Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: Traits, spectra, and strategies. International Journal of Plant Sciences 164:S143–S164.

Santos, B. A., V. Arroyo-Rodriguez, C. E. Moreno, and M. Tabarelli. 2010. Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. PLoS ONE 5:e12625.

SAS Institute. 2009. JMP. Version 8.0.1. SAS Institute, Cary, North Carolina, USA.

Schadler, M., G. Jung, H. Auge, and R. Brandl. 2003. Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. Oikos 103:121–132.

Sinclair, R. J., and L. Hughes. 2010. Leaf miners: The hidden herbivores. Austral Ecology 35:300–313.

Tavakilian, G., A. Berkov, B. Meurer-Grimes, and S. Mori. 1997. Neotropical tree species and their faunas of *Xylophagous longicorns* (Coleoptera: Cerambycidae) in French Guiana. Botanical Review 63:303–355.

Weiblen, G. D., C. O. Webb, V. Novotny, Y. Basset, and S. E. Miller. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. Ecology 87(Supplement):S62–S75.

Whitfeld, T. J. S., W. J. Kress, D. L. Erickson, and G. D. Weiblen. *In press*. Changes in community phylogenetic structure during tropical forest succession: evidence from New Guinea. Ecography. http://dx.doi.org/10.1111/j.1600-0587.2011.07181.x

Wikström, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. Proceedings of the Royal Society B 268:2211–2220.

Wills, C., et al. 2006. Nonrandom processes maintain diversity in tropical forests. Science 311:527–531.

Wood, A. W. 1982. The soils of New Guinea. Pages 73–86 *in* J. Gressitt, editor. Biogeography and ecology of New Guinea. W. Junk, The Hague, The Netherlands.

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

Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14.

Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664–3674.