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PHYLOGENETIC DISPERSION OF HOST USE IN A TROPICAL INSECT HERBIVORE COMMUNITY

GEORGE D. WEIBLEN,[1,6] CAMPBELL O. WEBB,[2,7] VOJTECH NOVOTNY,[3] YVES BASSET,[4] AND SCOTT E. MILLER[5]

[1]*Department of Plant Biology, University of Minnesota, Saint Paul, Minnesota 55108 USA*
[2]*Section of Evolution and Ecology, University of California, Davis, California 95616 USA*
[3]*Institute of Entomology, Czech Academy of Sciences and Biological Faculty, University of South Bohemia, 370 05 Ceske Budejovice, Czech Republic*
[4]*Smithsonian Tropical Research Institute, Balboa, Ancon, Panama*
[5]*National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012 USA*

Abstract. Theory has long predicted that insect community structure should be related to host plant phylogeny. We examined the distribution of insect herbivore associations with respect to host plant phylogeny for caterpillars (Lepidoptera), beetles (Coleoptera), and grasshoppers and relatives (orthopteroids) in a New Guinea rain forest. We collected herbivores from three lineages of closely related woody plants and from more distantly related plant lineages in the same locality to examine the phylogenetic scale at which host specificity can be detected in a community sample. By grafting molecular phylogenies inferred from three different genes into a supertree, we developed a phylogenetic hypothesis for the host community.

Feeding experiments were performed on more than 100 000 live insects collected from the 62 host species. We examined patterns of host use with respect to the host plant phylogeny. As predicted, we found a negative relationship between faunal similarity, defined as the proportion of all herbivores feeding on two hosts that are shared between the hosts, and the phylogenetic distance between hosts based on DNA sequence divergence. Host phylogenetic distance explained a significant fraction of the variance (25%) in herbivore community similarity, in spite of the many ecological factors that probably influence feeding patterns. Herbivore community similarity among congeneric hosts was high (50% on average) compared to overlap among host families (20–30% on average). We confirmed this pattern using the nearest taxon index (NTI) and net relatedness index (NRI) to quantify the extent of phylogenetic clustering in particular herbivore associations and to test whether patterns are significantly different from chance expectations. We found that 40% of caterpillar species showed significant phylogenetic clustering with respect to host plant associations, somewhat more so than for beetles or orthopteroids. We interpret this as evidence that a substantial fraction of tropical forest insect herbivores are clade specialists.

Key words: community ecology; community phylogenetics; herbivory; host specialization; host specificity; plant–insect interactions; phylogenetic dispersion; phylogeny; tropical rain forest.

INTRODUCTION

In the era before automated DNA sequencing and molecular phylogenetics, Daniel H. Janzen stated that "the systematics and taxonomy of interactions is hopeless" (Janzen 1977). As robust phylogeny estimates for plants and insects become available, investigating the evolutionary history of their interactions is no longer a fruitless endeavor. It is now possible to examine the historical associations of plants and insects by comparing molecular phylogenies for the interacting lineages (Becerra 1997, Weiblen and Bush 2002, Percy et al. 2004). Phylogenetic studies of host use by phytophagous insects have tended to focus on the reconstruction of ancestral associations for particular groups (Kelley and Farrell 1998) or whether particular insect groups and their host plants have diversified in parallel (Farrell and Mitter 1990, 1998). Other macroevolutionary studies have examined patterns of phylogenetic conservatism in the host plant associations of phytophagous insects (Farrell 1998, Janz and Nylin 1998, Ward et al. 2003).

Ecologists interested in patterns of herbivore community structure are faced with a different set of questions. For example, to what extent do insects feed on closely related host plants in a particular community? How likely are host shifts to occur between divergent host lineages? Few studies have attempted to integrate the knowledge of phylogeny in the study of community structure (Connor et al. 1980, Strong et al. 1984, Marquis 1991, Losos 1996, Ødegaard 2003, Ødegaard et al. 2005). Concern over the lack of statistical independence among species led Kelly and Southwood

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[6] E-mail: gweiblen@umn.edu
[7] Present affiliation: Arnold Arboretum of Harvard University.

(1999) to control for phylogenetic effects in demonstrating that host plant abundance can predict herbivore species richness in the temperate forest of Britain. But still more can be learned from phylogeny. The members of any biotic community are related in some fashion, and insights can be gained by examining ecological patterns with respect to patterns of descent from common ancestors.

The incorporation of phylogenetic knowledge in ecological studies can inform our understanding of community structure (Webb et al. 2002) and of evolutionary constraints on the distribution of traits in ecological communities (Chazdon et al. 2003). A useful approach is to apply clustering indices to the phylogenetic distribution of species that belong to a particular community sample drawn from a larger species pool (Futuyma and Gould 1979, Webb 2000). Such indices were first applied to the distribution of phytophagous insects across a host plant phylogeny in order to quantify diet breadth (Symons and Beccaloni 1999, Beccaloni and Symons 2000). Early studies of diet breadth failed to consider the phylogenetic nonequivalence of taxonomic ranks (e.g. families and orders), and the phylogenetic diversity index and the clade dispersion index, in particular, were proposed to address this problem (Symons and Beccaloni 1999). However, these indices measured relatedness in terms of the branching order, not branch lengths, of phylogenies. Branch lengths are especially critical for studies of phylogenetic dispersion in ecological communities with an uneven distribution of closely related and distantly related species (Cavender-Bares et al. 2004). Consider lowland tropical rain forest tree communities, for example, which are often dominated by a relatively small number of highly species-rich genera and families (Novotny et al. 2002). In such cases, narrow host specificity of herbivores has been invoked to explain the maintenance of high insect species richness, but this conclusion was reached with little regard for host plant relatedness (Basset 1992).

The analysis presented here builds on an earlier study (Novotny et al. 2002), expanding a New Guinea host plant assemblage from 51 to 62 species and applying new indices of phylogenetic dispersion to herbivore associations. The island of New Guinea is the third largest remaining area of tropical forest wilderness in the world and includes ~5% of global plant and insect diversity while occupying only 0.5% of the land area (Miller 1993). Our study site near Madang, on the north coast of Papua New Guinea, includes ~150 tree species/ha that measure >5 cm dbh, and species richness is dominated by approximately a dozen genera.

We quantified the relationship between the herbivore community similarity of host trees and the phylogenetic distance between hosts. We defined similarity as the ratio of the number of herbivore species sharing two hosts to the total number of herbivore species feeding on the pair of hosts. Phylogenetic distance between host species was based on DNA sequence divergence integrated across three genes and rate-smoothed across the community phylogeny using penalized likelihood. If herbivores tend to feed on closely related plants more than on distantly related plants, as we expect, then faunal similarity should decline with increasing phylogenetic distance between host species.

Indices of phylogenetic dispersion that incorporate null models can be especially useful as quantitative tests of host specificity in community samples. We used the nearest taxon index (NTI) and net relatedness index (NRI) to quantify the extent of phylogenetic clustering in particular herbivore associations and to test whether patterns are significantly different from chance expectations (Webb 2000, Webb et al. 2002). These indices measure the mean phylogenetic distance between plants that share a particular herbivore, relative to the mean and standard deviation of herbivore associations randomly distributed on the phylogeny, as obtained by multiple iteration. The NRI measures the average distance between all plants that share an herbivore species (i.e., the extent of overall clustering), while the NTI measures the average minimal distance between plants that share an herbivore species (i.e., the extent of terminal clustering).

Methods

Community ecology

Leaf-chewing insects were collected from 62 plant species representing 41 genera and 18 families (Table 1). Sampling effort was equalized across all host plants to provide quantitative estimates of herbivore relative abundance. Parataxonomists and village collectors surveyed 1500 m^2 of foliage over nearly 1600 field-days and $>6 \times 10^4$ tree inspections. Live insects were subjected to feeding trials with fresh foliage of the plant species from which they were collected in the field. These procedures are detailed in Novotny et al. (2002). We recorded 961 species and 62 193 individuals feeding on the 62 host plant species. Additionally, 40 000 insects that failed to feed on the plant from which they were collected were discarded. Local parataxonomists assigned feeding specimens to morphospecies (Basset et al. 2000), and taxonomic specialists later identified known taxa. Details on plant and insect identification are reported in Miller et al. (2003). One-quarter of all species were identified to named species, and 44% were identified to genus, but taxonomic knowledge varied from group to group. For example, 90% of the Lepidoptera species were assigned to a genus, and 72% were associated with a known species, while only 39% of beetles were assigned to genus and 19% to species. The locality, collection date, and host plant species for 37 972 mounted specimens are also available in our database. Digital photographs of many species are archived and *available online*.[8] Sampling included 388 species and

[8] ⟨http://www.entu.cas.cz/png/index.html⟩

TABLE 1. Plant species and gene sequences included in a phylogenetic study of host use in a tropical insect herbivore community.

Species	Code	Family	Order	Clade	GenBank
Amaracarpus nymanii Valeton	AMA	Rubiaceae	Gentianales	euasterids 1	AJ002176†
Artocarpus camansi Blanco	ART	Moraceae	Rosales	eurosids 1	AY289288
Breynia cernua (Poir.) Muell. Arg	BRE	Phyllanthaceae	Malphigiales	eurosids 1	AY374311
Casearia erythrocarpa Sleum.	CAS	Flacourtiaceae	Malphigiales	eurosids 1	AF206746†
Celtis philippensis Blanco	CEL	Ulmaceae	Rosales	eurosids 1	D86309†
Codiaeum ludovicianum Airy Shaw	COD	Euphorbiaceae	Malphigiales	eurosids 1	AY374312
Dolicholobium oxylobum K. Schum.	DOL	Rubiaceae	Gentianales	euasterids 1	AJ318445
Dracaena angustifolia Roxb.	DRA	Agavaceae	Asparagales	monocots	AF206729†
Endospermum labios Schodde	END	Euphorbiaceae	Malphigiales	eurosids 1	AY374313
Eupomatia laurina R. Br.	EUP	Eupomatiaceae	Magnoliales	basals	L12644†
Excoecaria agallocha L.	EXC	Euphorbiaceae	Malphigiales	eurosids 1	AY374314
Ficus bernaysii King	BER	Moraceae	Rosales	eurosids 1	AF165378
Ficus botryocarpa Miq.	BOT	Moraceae	Rosales	eurosids 1	AF165379
Ficus conocephalifolia Ridley	CON	Moraceae	Rosales	eurosids 1	AF165381
Ficus copiosa Steud.	COP	Moraceae	Rosales	eurosids 1	AF165382
Ficus dammaropsis Diels	DAM	Moraceae	Rosales	eurosids 1	AF165383
Ficus hispidioides S. Moore	HIS	Moraceae	Rosales	eurosids 1	AF165388
Ficus microcarpa L.	MIC	Moraceae	Rosales	eurosids 1	AF165393
Ficus nodosa Teysm. & Binn.	NOD	Moraceae	Rosales	eurosids 1	AF165395
*Ficus phaeosyc*e Laut. & K. Schum.	PHA	Moraceae	Rosales	eurosids 1	AF165401
Ficus pungens Reinw. ex Bl.	PUN	Moraceae	Rosales	eurosids 1	AF165404
Ficus septica Burm. f.	SEP	Moraceae	Rosales	eurosids 1	AF165409
Ficus tinctoria Forst.	TIN	Moraceae	Rosales	eurosids 1	AF165413
Ficus trachypison K. Schum.	TRA	Moraceae	Rosales	eurosids 1	AF165414
Ficus variegata Bl.	VAR	Moraceae	Rosales	eurosids 1	AF165415
Ficus wassa Roxb.	WAS	Moraceae	Rosales	eurosids 1	AF165418
Gardenia hansemannii K. Schum.	GAR	Rubiaceae	Gentianales	euasterids 1	AJ318446
Gnetum gnemon L.	GNE	Gnetaceae	Gnetales	outgroup	AY056577
Homalanthus novoguineensis (Warb.) K. Schum.	HON	Euphorbiaceae	Malphigiales	eurosids 1	AY374315†
Hydriastele microspadix (Becc.) Burret.	ARE	Arecaceae	Arecales	monocots	AY012504†
Kibara cf. *coriacea* (Bl.) Tul.	STG	Monimiaceae	Laurales	basals	AF050221†
Leucosyke capitellata (Poir.) Wedd.	LEU	Urticaceae	Rosales	eurosids 1	AY208707†
Macaranga aleuritoides F. Muell.	MAA	Euphorbiaceae	Malphigiales	eurosids 1	AY374319
Macaranga bifoveata J. J. Smith	MAP	Euphorbiaceae	Malphigiales	eurosids 1	AY374321
Macaranga brachytricha A. Shaw	MAF	Euphorbiaceae	Malphigiales	eurosids 1	AY374316
Macaranga densiflora Warb.	MAD	Euphorbiaceae	Malphigiales	eurosids 1	AY374317
Macaranga novoguineensis J. J. Smith	MAU	Euphorbiaceae	Malphigiales	eurosids 1	AY374320
Macaranga quadriglandulosa Warb.	MAQ	Euphorbiaceae	Malphigiales	eurosids 1	AY374318
Mallotus mollissimus (Geisel.) Airy Shaw	MAL	Euphorbiaceae	Malphigiales	eurosids 1	AY374322
Melanolepis multiglandulosa (Reinw. ex Bl.) Reichb. f.	MEL	Euphorbiaceae	Malphigiales	eurosids 1	AY374323
Morinda bracteata Roxb.	MOR	Rubiaceae	Gentianales	euasterids 1	AJ318448
Mussaenda scratchleyi Wernh.	MUS	Rubiaceae	Gentianales	euasterids 1	AJ318447
Nauclea orientalis (L.) L.	SAR	Rubiaceae	Gentianales	euasterids 1	AJ318449
Neonauclea clemensii Merr. & Perry	NEO	Rubiaceae	Gentianales	euasterids 1	AJ318450
Neuburgia corynocarpa (A.Gray) Leenh.	NEU	Loganiaceae	Gentianales	euasterids 1	AJ001755
Osmoxylon sessiliflorum (Lauterb.) W.R.Philipson	OSM	Araliaceae	Apiales	euasterids 2	U50257†
Pavetta platyclada Lauterb. & K. Schum.	PAV	Rubiaceae	Gentianales	euasterids 1	AJ318451
Phyllanthus lamprophyllus Muell. Arg.	PHY	Phyllanthaceae	Malphigiales	eurosids 1	AY374325
Pimelodendron amboinicum Hassk.	PIM	Euphorbiaceae	Malphigiales	eurosids 1	AY374324
Pometia pinnata Forster	POM	Sapindaceae	Sapindales	eurosids 2	AJ403008†
Premna obtusifolia R.Br.	PRE	Verbenaceae	Lamiales	euasterids 1	U28883†
Psychotria leptothyrsa Miquel	PSF	Rubiaceae	Gentianales	euasterids 1	AJ318452
Psychotria micralabastra (Laut. & Schum.) Val.	PSM	Rubiaceae	Gentianales	euasterids 1	AJ318453
Psychotria micrococca (Laut. & Schum.) Val.	PSS	Rubiaceae	Gentianales	euasterids 1	AJ318454
Psychotria ramuensis Sohmer	PSL	Rubiaceae	Gentianales	euasterids 1	AJ318455
Pterocarpus indicus Willd.	PTE	Fabaceae	Fabales	eurosids 1	AF308721†
Randia schumanniana Merrill & Perry	MEN	Rubiaceae	Gentianales	euasterids 1	AJ318456
Sterculia schumanniana (Lauterb.) Mildbr.	STR	Malvaceae	Malvales	eurosids 2	AJ233140†
Tabernaemontana aurantica Gaud.	TAB	Apocynaceae	Gentianales	euasterids 1	X91772†
*Tarenna buruens*is (Miq.) Val.	TAR	Rubiaceae	Gentianales	euasterids 1	AJ318457
Timonius timon (Spreng.) Merr.	TIT	Rubiaceae	Gentianales	euasterids 1	AJ318458
Versteegia cauliflora (K. Schum. & Laut.)	VER	Rubiaceae	Gentianales	euasterids 1	AJ318459

Notes: When sequences were not available for particular species, substitutions of near relatives from GenBank were made (⟨http://www.ncbi.nlm.nih.gov⟩). For example, *rbc*L sequences from *Artocarpus altilis* (AF500345) and *Ficus heterophylla* (AF500351) were substituted for ART and VAR, respectively. Additional substitutions are footnoted.

† Substituted *rbc*L sequences *Amaracarpus* sp. (AMA), *Casearia sylvestris* (CAS), *Celtis sinensis* (CEL), *Agave ghiesbreghtii* (DRA), *Eupomatia bennetti* (EUP), *Gnetum parvifolium* (GNE), *Kibara rigidifolia* (STG), *Hydriastele wendlandiana* (ARE), *Urtica dioica* (LEU), *Teraplasandra hawaiensis* (OSM), *Talisia nervosa* (POM), *Premna microphylla* (PRE), *Willardia mexicana* (PTE), *Sterculia apetala* (STR), and *Tabernaemontana divaricata* (TAB).

24 481 individuals for beetles (Coleoptera), 464 species and 31 108 individuals for moths and butterflies (Lepidoptera; see Plate 1), and 109 species and 6605 individuals of orthopteroids (Orthoptera and Phasmatodea). Among the caterpillars, ~14 000 were matched with adults, amounting to 298 species of Lepidoptera with known larval and adult stages.

Molecular phylogenetics

Phylogenetic relationships for the 62 host plant species were drawn from multiple molecular data sets including a three-gene phylogeny for all angiosperms (Soltis et al. 1998). We used additional molecular markers for species of Moraceae, Rubiaceae, and Euphorbiaceae, including the internal transcribed spacer (ITS) region of nuclear ribosomal DNA for *Ficus* (Weiblen 2000), *rbc*L, encoding the large subunit of ribulose-1,5-bisphosphate carboxylase, and the 30S ribosomal protein S16 gene (*rps*16) for Rubiaceae (Novotny et al. 2002), and *ndh*F, encoding a subunit of NADH-plastoquinone oxidoreductase, for the Euphorbiaceae. Phylogenetic analyses of Euphorbiaceae based on *ndh*F are presented in the Appendix.

Community phylogenetics

A phylogeny estimate for the community sample was obtained by grafting less inclusive single-gene phylogenies for *Ficus*, Euphorbiaceae, and Rubiaceae into a more inclusive phylogeny of angiosperms based on three genes (Soltis et al. 1998). The assembly of a community phylogeny can follow supertree methods (Sanderson et al. 1998) or other approaches (Lapointe and Cucumel 1997), but one crucial difference is that only members of the community are retained in the supertree, while all other lineages are pruned away.

It is important to consider the impact of branch length considerations on indices of phylogenetic clustering drawn from community samples. When branch lengths are assumed equal, using the number of intervening nodes as a proxy for phylogenetic distance (Novotny et al. 2002), relationships between intensively sampled congeneric species are given the same weight as relationships among representatives of major clades. Branch length information can distinguish between these two very different cases, short distances between congenerics and long distances between members of major lineages. Therefore, to incorporate information from all three molecular data sets, we scaled branch lengths in the supertree to the relative rate of change in two genes compared between pairs of taxa. For example, the relative rate of ITS to *ndh*F was calculated by counting the absolute number of character differences in each gene between *Ficus microcarpa* and *F. variegata*. Including all characters, there were 15 *ndh*F differences between these species and 58 ITS differences, yielding a relative rate of 0.259 for *ndh*F to ITS (Weiblen 2000, Datwyler and Weiblen 2004). Fifty-eight pairwise differences between *Artocarpus camansi* and *Ficus variegata* for *rbc*L and 111 for *ndh*F yielded a rate of 1.914 for *ndh*F relative to *rbc*L. We rescaled the branch lengths by these rates to approximate the phylogenetic distance between taxa sampled for genes showing radically different rates of molecular divergence. The assumption of this method is that rates of divergence for each gene are homogeneous among the lineages comprising the community sample. In the case of plant families other than Moraceae, Rubiaceae, and Euphorbiaceae, *rbc*L sequences were not necessarily available from the particular species, and in these instances sequences from related species or genera were obtained from GenBank as indicated in Table 1.

The next challenge is to obtain a phylogeny for which all distances from the root of the tree to the tips are equal, also known as an ultrametric tree. Ultrametricity is necessary to make direct comparisons of phylogenetic distance (as measured by rescaled molecular branch lengths) among pairs of host species distributed across the phylogeny. Each individual data set rejected a molecular clock assumption, so we applied nonparametric rate smoothing and penalized likelihood as implemented in the program r8s (Sanderson 2002) to the rescaled branch lengths of the supertree to obtain an ultrametric tree accommodating rate heterogeneity across lineages. Penalized likelihood is a semiparametric method that allows substitution rates to vary among lineages according to a smoothing parameter (Sanderson 2002). The optimal smoothing parameter was chosen on the basis of the data by cross-validation involving the sequential pruning of taxa from the tree and parameter estimation to best predict the branch length of the pruned taxon (Sanderson 2003). We compared 20 cross-validation parameters beginning with zero and increasing by increments of $\log_{10}(0.05)$ and chose the optimal smoothing parameter to minimize χ^2 error. Cross-validation was performed with the age of the root node fixed at one. Penalized-likelihood search parameters included 2000 maximum iterations, 10 multiple starts, and 30 optimization runs.

Phylogenetic dispersion of herbivore associations

Herbivore associations with each of the 62 host species were coded as either present or absent under two different assumptions, including or excluding solitary observations. Where r denotes the number of feeding records for a particular herbivore species on a particular host species, associations were coded as present when $r > 1$ or when $r > 0$ to exclude or include singletons, respectively. Varying this threshold allowed us to examine the sensitivity of findings based on presence/absence to extreme variation in herbivore abundance. We examined the distribution of herbivore associations across the host phylogeny, with indices of phylogenetic clustering as implemented in the program Phylocom (Webb et al. 2004).

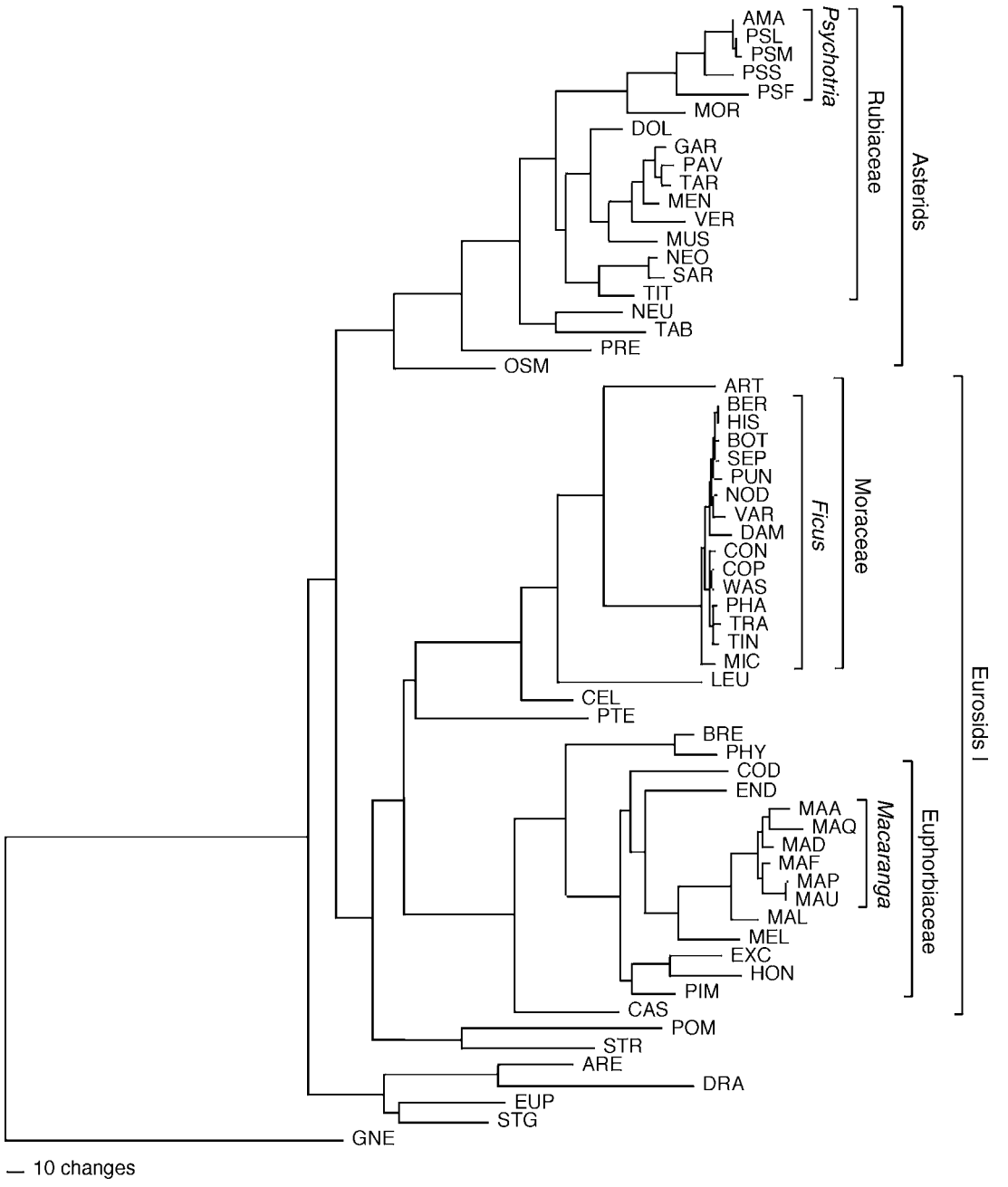

FIG. 1. Phylogenetic relationships of host plant species included in the study (see Table 1 for abbreviations). Brackets indicate the three major angiosperm clades that were sampled intensively. A supertree was assembled from separate analyses of DNA sequences for Rubiaceae (Novotny et al. 2002), *Ficus* (Weiblen 2000), Euphorbiaceae (see the Appendix), and angiosperms as a whole (Soltis et al. 1998, Angiosperm Phylogeny Group 2003). Branch lengths based on ITS, *rbc*L, and *ndh*F sequences for partially overlapping sets of taxa were rescaled in proportion to pairwise differences between selected species with published ITS and *ndh*F, or *ndh*F and *rbc*L, sequences (see *Methods*). Branch lengths as shown are proportional to absolute numbers of nucleotide changes under parsimony. The scale bar indicates 10 changes.

The net relatedness index measured the mean phylogenetic distance between all plants sharing a particular herbivore: $\text{NRI} = -(X_{\text{net}} - X(n))/\text{SD}(n)$ where X_{net} is the mean phylogenetic distance between all pairs of n host plants sharing an herbivore, and $X(n)$ and $\text{SD}(n)$ are the mean and standard deviation of phylogenetic distance for n host plants randomly distributed on the phylogeny, obtained by multiple iteration. The nearest taxon index measured the distance between the two nearest hosts sharing a particular herbivore. This index is calculated in the same manner as NRI, except that X_{near} is substituted for X_{net}, where X_{near} is the shortest

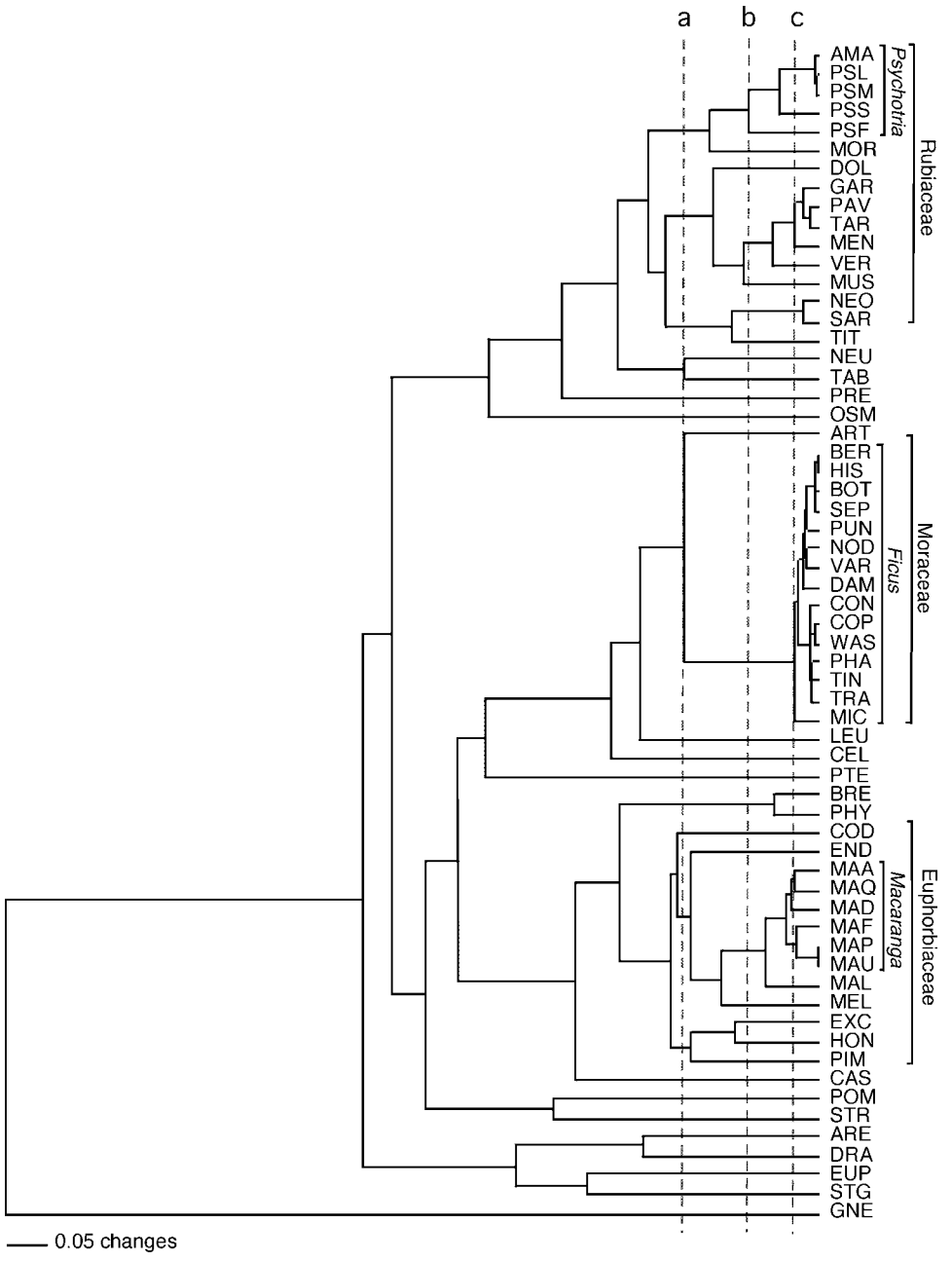

FIG. 2. Molecular divergence among 62 selected, woody host plant species in lowland tropical rain forest on the island of New Guinea (see Table 1 for species abbreviations). The ultrametric tree was derived from penalized-likelihood analysis. (a) Shallowest split between families, Loganiaceae and Apocynaceae, (b) deepest crown radiation of a genus, *Psychotria*, and (c) shallowest crown radiation of a genus, *Ficus*. Brackets mark the angiosperm families and genera that were the focus of herbivore sampling. Branch lengths as shown are proportional to the number of nucleotide changes per site under maximum likelihood. The scale bar indicates 0.05 substitutions per site.

distance between all pairs of n host plants sharing an herbivore. High values of these indices suggest clustering, whereas low values point to evenness (i.e., overdispersion). We tested whether these measures of phylogenetic dispersion of herbivore associations across the community phylogeny were significantly different from chance expectations. Under a null model of random association, we performed 1000 permutations of host associations to simulate a distribution of NRI and NTI for each herbivore species. A two-tailed test of significance evaluated the rank of observed values at $P = 0.05$. For example, a rank of <25 or >975 of 1000 permutations constituted significant overdispersion or clustering, respectively.

TABLE 2. Numbers and percentages of insect herbivore species with significantly clustered (and overdispersed) patterns of host association across a community sample of 62 woody plant species from New Guinea lowland rain forest.

	Excluding singletons							
	NRI				NTI			
Taxon	NB	BL	PL	LF	NB	BL	PL	LF
Lepidoptera	76 (0)	65 (1)	61 (5)	61 (5)	68 (0)	58 (3)	60 (9)	60 (9)
Lepidoptera (%)	55 (0)	47 (1)	45 (4)	45 (4)	50 (0)	42 (2)	44 (6)	44 (6)
Coleoptera	30 (1)	43 (0)	46 (1)	46 (1)	26 (0)	27 (0)	24 (3)	24 (1)
Coleoptera (%)	30 (1)	43 (0)	46 (1)	46 (1)	26 (0)	27 (0)	24 (3)	24 (1)
Orthopteroids	12 (0)	14 (0)	9 (0)	9 (0)	8 (0)	4 (1)	4 (2)	4 (6)
Orthopteroids (%)	30 (0)	35 (0)	22 (0)	22 (0)	20 (0)	10 (2)	10 (5)	10 (15)
Total herbivores	118 (1)	122 (1)	116 (6)	116 (6)	102 (0)	89 (4)	88 (14)	88 (16)
Herbivores (%)	43 (1)	44 (1)	42 (2)	42 (2)	37 (0)	32 (1)	32 (5)	32 (6)

Notes: Two-tailed tests of phylogenetic dispersion assessed significance at $P = 0.05$ with ranks >975 (or <25) out of 1000 randomizations. Abbreviations: NRI = net relatedness index; NTI = nearest taxon index; NB = no. branch lengths (no. intervening nodes); BL = rescaled molecular branch lengths (nonultrametric); PL = rescaled ultrametric branch lengths (penalized likelihood); LF = rescaled ultrametric branch lengths (Langely-Fitch nonparametric rate smoothing).

We further examined the relationship of herbivore community similarity to the phylogenetic distance between hosts. We calculated community similarity as the percentage of the total number of herbivore species feeding on any pair of host species that were shared between the hosts (Novotny et al. 2002). We estimated phylogenetic distance from branch lengths based on DNA sequence divergence under penalized likelihood as implemented in r8s (Sanderson 2002). We used linear regression to analyze the direction and linear regression and Mantel tests to assess the significance of this relationship.

RESULTS

Community ecology

Among the 62 193 insects, including 464 caterpillar species reared to adults, 388 beetle species, and 109 orthopteroids, there were 281 species collected as single individuals (singletons). Singleton species were excluded from subsequent analyses, because it is impossible to assess host range when a species is known from only one feeding record (Novotny and Basset 2000). Apart from singletons, our sample also included 156 herbivore species that fed on a single plant species. Our analysis did not examine whether these species are truly monophagous or were simply sampled in insufficient numbers. Rather, we focused on the host phylogenetic distribution of associations for the remaining 524 herbivore species (55% of the total) that were found to feed on more than one plant species.

Community phylogeny

A phylogeny was obtained for the host plant community sample by grafting hypotheses of relationship for selected Euphorbiaceae (see Appendix). Rubiaceae (Novotny et al. 2002), and *Ficus* (Weiblen 2000) to an ordinal phylogeny based on multiple data sets (Angiosperm Phylogeny Group 2003). The phylogeny is shown in Fig. 1 with *rbc*L and ITS branch lengths rescaled in terms of *ndh*F substitutions. Nonparametric rate smoothing (Langely-Fitch) and penalized likelihood yielded highly similar ultrametric trees (Fig. 2). As expected, phylogenetic distances between congeneric species were lower than between confamilial genera and extaordinal families.

Phylogenetic dispersion

Each of 226 Lepidoptera, 212 Coleoptera, and 87 orthopteroid species observed on multiple hosts was tested for nonrandom patterns of association with respect to host plant phylogeny. Under a more stringent coding of host association that excluded all solitary feeding records, the 137 Lepidoptera, 99 Coleoptera, and 40 orthopteroid species encountered on multiple hosts (multiple times each) were also analyzed with respect to host phylogenetic dispersion. Results under four different branch length assumptions, two different indices of phylogenetic dispersion, and two feeding thresholds indicated that herbivores with nonrandom dispersion of associations feed on closely related hosts more often than on distantly related hosts (Table 2). In particular, 25–43% of the herbivore species we analyzed were significantly clustered on the host plant phylogeny compared to 0–6% that were overdispersed.

The incorporation of sequence divergence in branch length estimation had a dramatic impact on the detection of phylogenetic dispersion. In the case of nearest taxon index, for example, results under the assumption of equal branch lengths only agreed with those under molecular branch length assumptions in 65% of cases, three variations on the latter agreed in 93% of cases, and the two assumptions based on ultrametric trees agreed in all cases. Exclusion of feeding records represented by single observations also enhanced the detection of nonrandom associations with respect to host plant phylogeny. Without singletons, 32–37% of herbivore species rejected the null model of association

TABLE 2. Extended.

Including singletons							
NRI				NTI			
NB	BL	PL	LF	NB	BL	PL	LF
124 (0)	93 (0)	90 (4)	91 (4)	103 (0)	78 (7)	75 (13)	76 (13)
55 (0)	41 (0)	40 (2)	40 (2)	46 (0)	34 (3)	33 (6)	34 (6)
41 (6)	70 (0)	75 (3)	76 (3)	45 (0)	44 (0)	49 (1)	50 (1)
19 (3)	33 (0)	35 (1)	36 (1)	21 (0)	21 (0)	23 (0)	23 (0)
20 (1)	27 (0)	23 (0)	24 (1)	13 (0)	8 (3)	9 (2)	10 (2)
23 (1)	31 (0)	26 (0)	27 (1)	15 (0)	9 (3)	10 (2)	11 (2)
185 (7)	190 (0)	188 (7)	191 (8)	161 (0)	130 (10)	133 (16)	136 (16)
35 (1)	36 (0)	36 (1)	36 (2)	31 (0)	25 (2)	25 (3)	26 (3)

compared to 25–31% including singletons in the analysis, a trend that was upheld by each of three insect groups.

Community similarity and phylogenetic distance

Herbivore community similarity, defined as the fraction of the total herbivore species on two host species that are shared between the hosts (Novotny et al. 2002), was negatively associated with phylogenetic distance as estimated by rate-smoothed molecular divergence under penalized likelihood (Fig. 3). The regression of community similarity against phylogenetic distance was highly significant (ANOVA, $F_{1, 3842} = 1243.5$, $P < 0.0001$), and the correlation between these variables was also significant according to a Mantel test (Pearson's product-moment correlation, $r = 0.423$, $P < 0.01$). Declining community similarity with increasing phylogenetic distance between hosts indicates that herbivores tend to feed on closely related plants more often than on distantly related plants.

DISCUSSION

While it is tempting to trace ecological character evolution on community phylogenies, ancestral reconstructions of host associations in community samples often yield implausible inferences. Equally weighted parsimony for highly polyphagous species implies that these herbivores colonized the common ancestors of major angiosperm clades and were subsequently lost from some host lineages. Consider for example the ancestral association of *Rhinoscapha tricolor* under equally weighted parsimony (Fig. 4). It is highly unlikely that this particular polyphagous species was associated with the common ancestor of the angiosperms and the gymnosperm *Gnetum*. Ancestral state reconstructions are sensitive to taxon sampling (Cunningham et al. 1998, Cunningham 1999), and colonization or extinction patterns cannot necessarily be inferred from local assemblages because community phylogenies are incomplete by definition. This problem is not unique to the evolution of host associations, but also occurs whenever the included taxa might be a subset of an entire clade of extant taxa. This is why we applied indices of phylogenetic dispersion to examine the relationship between herbivore associations and host plant phylogeny.

Phylogenetic dispersion of host associations

Community phylogenies, null models, and measures of phylogenetic dispersion taken together increase the precision with which herbivore associations can be studied. Previous attempts to quantify host specificity, for example, have either relied on taxonomic ranks that are not commensurate with plant lineages or ignored the branch length information contained in molecular phylogenies (Symons and Beccaloni 1999, Novotny et al. 2002). Branch length assumptions influence our

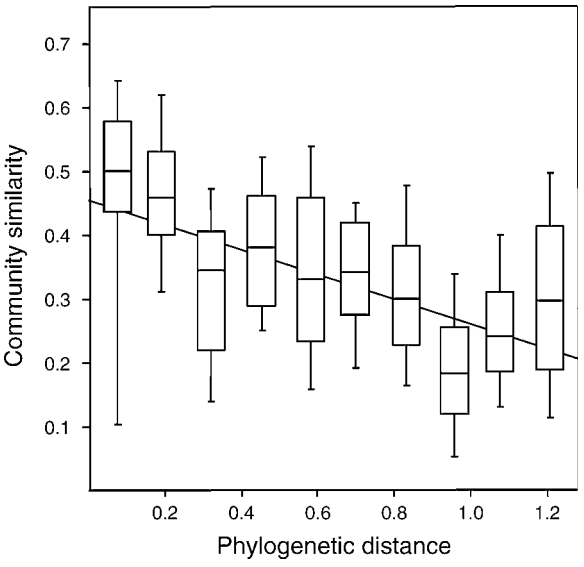

FIG. 3. Herbivore community similarity as a function of the phylogenetic distance between host plants. Similarity is the fraction of the total fauna on two hosts that is shared between the hosts. Phylogenetic distance was derived from the penalized-likelihood ultrametric phylogram shown in Fig. 2. Means, standard deviations, and ranges of community similarity are shown for selected distance intervals. The outgroup is excluded from the regression.

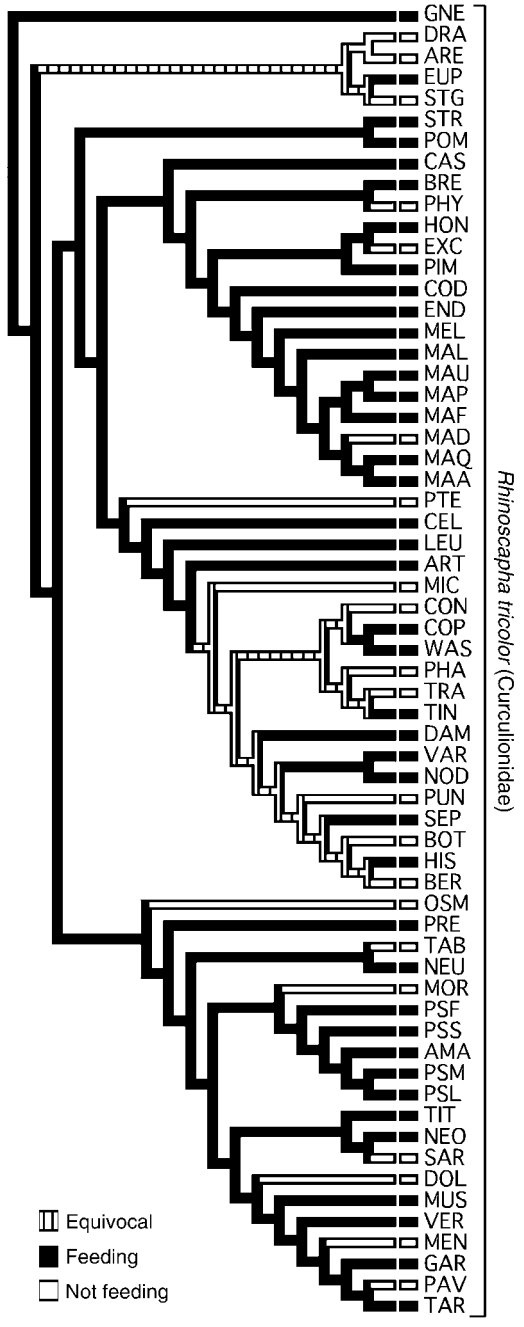

FIG. 4. Erroneous inference of ancestral host use in community samples under equally weighted parsimony. *Rhinoscapha tricolor* is a polyphagous generalist that parsimony suggests had an implausible, ancient association with the common ancestor of *Gnetum* and flowering plants. See Table 1 for species abbreviations.

power to detect patterns of phylogenetic dispersion in at least one important way. Failure to consider the extent of molecular divergence between hosts will underestimate the extent of herbivore clustering (or overdispersion) given that closely related hosts and extremely divergent hosts with the same number of intervening nodes in the community phylogeny are assumed to be equidistant when they are not. Branch lengths scaled to molecular divergence distinguish between these cases and enhance the power to detect significant patterns in host use (Table 2). Ultrametric molecular branch lengths approximate relative ages of lineages, and thus the length of time for ecological associations or adaptations to arise. We found that a large proportion of herbivores feed on closely related plants, including congeneric species and confamilial genera, and that a small number of herbivores feed on more divergent hosts than expected by chance. The former pattern is expected in cases of herbivore specialization (Jaenike 1990, Futuyma et al. 1993) and the latter pattern when herbivores are tracking convergent chemical, morphological, or ecological host traits (Becerra 1997).

The incorporation of molecular branch lengths in a community phylogeny assembled from multiple genes poses interesting methodological challenges that invite further exploration. Communities are usually composed of heterogeneous taxa, some very closely related and others distantly so. Grafting of multiple phylogenies based on different genes could be necessary when no single gene resolves phylogenetic relationships at all taxonomic levels in the community sample. This was the case in our sample, where ITS sequences were employed to resolve relationships among *Ficus,* but this region could not be aligned across plant families. Rescaling of branch lengths from different gene regions based on the ratio of absolute character differences between taxon pairs represents one possible solution among many. An improvement on our method would be to correct for multiple substitutions in a model-based maximum-likelihood framework when rescaling branch lengths across grafted phylogenies.

We do not know the extent to which the phylogenetic dispersion of herbivores in our samples is representative of herbivore community structure on the complete local plant community or tropical rain forests in general. The scope of our sampling universe is incomplete for even the local community. Fifteen figs, 13 Rubiaceae, 13 Euphorbiaceae, and 21 other angiosperms hardly encompass the woody vegetation of a study area that contains hundreds of flowering plant species. The selection of study plants was made to replicate the taxonomic ranks of family and genus, and is at best a highly skewed sample in terms of local abundance and distribution. At least one way to avoid artifacts due to taxonomic unevenness is to restrict analyses to single representatives of given taxonomic ranks, such as families, but this is not satisfactory owing to the phylogenetic nonequivalence of taxa at any single rank. Age estimates of family clades in a recent study of angiosperms range from <25 Ma to >150 Ma (Davies et al. 2004). The problem of taxonomic unevenness could be addressed by including all members of a local community, provided that the boundaries of the community can be defined. We intend to explore these

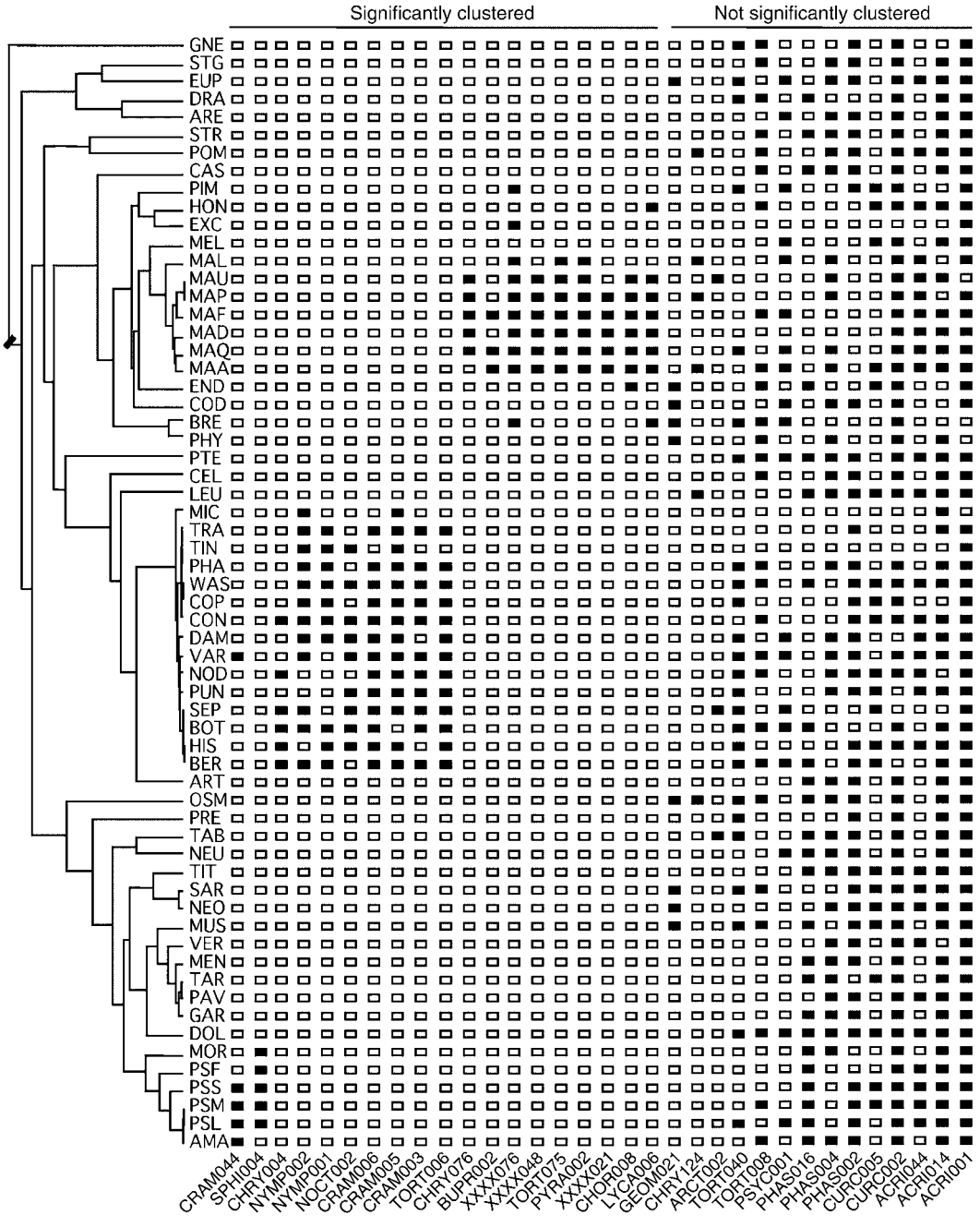

FIG. 5. Phylogenetic dispersion of host range in 30 herbivore species arbitrarily selected from the community sample to illustrate the extremes of variation. Herbivores are grouped into nonsignificantly clustered species including polyphagous generalists, and significantly clustered species including oligophagous specialists feeding on *Macaranga*, *Ficus*, or *Psychotria*. Branch lengths of the host community phylogeny are proportional to molecular divergence as in Fig. 4, except for the truncated root indicated by a slash. Host species codes are defined in Table 1, and herbivore species codes are defined in Table 3. As in Fig. 4, solid boxes indicate herbivore presence and open boxes indicate herbivore absence.

issues in the future through the complete enumeration of vegetation in specific areas of forest (Novotny et al. 2004*a*). At the very least, it is encouraging that the relationship between herbivore community similarity and host phylogenetic distance was strengthened by the expansion of our sample from 51 host species in Novotny et al. (2002) to 62 in the present study, and through the incorporation of branch length information.

It is remarkable that a full quarter of the variance of herbivore community similarity can be explained by the phylogenetic relationships among hosts ($r^2 = 0.244$) when we consider the variability that environmental and

TABLE 3. Herbivore species from Fig. 5 arranged alphabetically by morphospecies code.

Code	Order	Family	Species	*N*	*H*	NRI	NTI
ACRI001	Orthopteroid	Pyrgomorphidae	*Desmopterella biroi* (Bolivar, 1905)	2215	58	−0.36	−0.74
ACRI014	Orthopteroid	Acrididae	*Valanga papuasica* (Finot, 1907)	273	49	1.09	0.55
ACRI044	Orthopteroid	Eumastacidae	*Paramnesicles buergersi* Bolivar, 1930	111	29	1.28	1.94
ARCT002	Lepidoptera	Arctiidae	*Darantasia caerulescens* Druce, 1899	3	3	−0.54	−0.89
BUPR002	Coleoptera	Buprestidae	*Habroloma* sp.	20	3	3.34	2.33
CHOR008	Lepidoptera	Choreutidae	*Brenthia salaconia* Meyrick, 1910	389	7	5.60	2.38
CHRY004	Coleoptera	Chrysomelidae	genus indeterminate	125	6	6.60	2.60
CHRY076	Coleoptera	Chrysomelidae	*Deretrichia* sp.	16	5	5.01	2.45
CHRY124	Coleoptera	Chrysomelidae	*Deretrichia* sp.	16	6	0.55	−0.26
CRAM003	Lepidoptera	Crambidae	*Glyphodes margaritaria* (Clerck) 1794	318	11	9.04	3.22
CRAM005	Lepidoptera	Crambidae	*Talanga deliciosa* (Butler) 1887	856	14	10.02	3.37
CRAM006	Lepidoptera	Crambidae	*Talanga sexpunctalis* (Moore) 1877	329	13	9.50	3.21
CRAM044	Lepidoptera	Crambidae	"*Coelorhycidia*" nr. *purpurea* Hampson, 1907	234	5	2.65	1.51
CURC002	Coleoptera	Curculionidae	*Apirocalus ebrius* Faust, 1892	2349	54	−1.31	−1.38
CURC005	Coleoptera	Curculionidae	*Alcidodes elegans* (Guerin) 1838	141	22	1.94	2.51
GEOM021	Lepidoptera	Geometridae	*Cleora repetita* Butler, 1882	12	9	0.11	0.21
LYCA006	Lepidoptera	Lycaenidae	*Philiris helena* Snellen, 1887	121	8	5.54	2.00
NOCT002	Lepidoptera	Noctuidae	*Asota heliconia* Linnaeus, 1758	257	9	7.70	2.94
NYMP001	Lepidoptera	Nymphalidae	*Euploea leucosticos* Gmelin, 1788	108	11	8.12	3.04
NYMP002	Lepidoptera	Nymphalidae	*Cyrestis acilia* Godart, 1819	156	12	9.52	3.32
PHAS002	Orthopteroid	Heteronemiidae	*Neopromachus vepres* (Brunner von Wattenwyl) 1907	211	41	−0.15	−1.43
PHAS004	Orthopteroid	Phasmatidae	*Dimorphodes prostasis* Redtenbacher, 1908	98	35	0.06	−0.74
PHAS016	Orthopteroid	Phasmatidae	*Eurycantha insularis* Lucas, 1869	38	25	1.65	−0.68
PSYC001	Lepidoptera	Psychidae	*Eumeta variegata* Snellen, 1879	33	19	0.72	0.12
PYRA002	Lepidoptera	Pyralidae	*Orthaga melanoperalis* Hampson, 1906	246	7	5.99	2.55
SPHI004	Lepidoptera	Sphingidae	*Macroglossum melas* Rothschild & Jordan, 1930	167	5	4.32	2.11
TORT006	Lepidoptera	Choreutidae	*Choreutis lutescens* (Felder and Rogenhofer) 1875	332	13	9.50	3.21
TORT008	Lepidoptera	Tortricidae	*Adoxophyes templana* complex	482	29	−1.54	−1.65
TORT040	Lepidoptera	Tortricidae	*Homona mermerodes* Meyrick, 1910	815	25	−0.1	−1.53
TORT075	Lepidoptera	Thyrididae	*Mellea ramifera* Warren, 1897	56	7	5.99	2.55
XXXX021	Lepidoptera	Pyralidae	*Unadophanes trissomita* Turner, 1913	301	5	4.97	2.35
XXXX048	Lepidoptera	Gelechiidae	*Dichomeris ochreoviridella* (Pagenstecher) 1900	394	6	5.79	2.48
XXXX076	Lepidoptera	Gelechiidae	*Dichomeris* sp. nr. *resignata* Meyrick, 1929	324	10	6.01	1.88

Notes: The total number of individuals (*N*) and the total number of host species (*H*), including solitary feeding records, are indicated. Net relatedness (NRI) and nearest taxon (NTI) indices are reported as calculated under the penalized-likelihood tree (Fig. 2).

population demographical heterogeneity must inevitably contribute to samples of herbivore associations from any site over any period of time. A recent community phylogenetic analysis of host use by beetles in Panamanian rain forest revealed the same pattern (Ødegaard et al. 2005). These findings provide quantitative support for long-standing theory (Ehrlich and Raven 1964, Strong et al. 1984, Schoonhoven et al. 1998). There are at least two explanations for the decline in herbivore similarity with increasing phylogenetic distance between hosts. The first has to do with the phylogenetic conservatism of host choice as manifest in the tendency for herbivore offspring to feed on the same host lineages as their parents. Second, it is possible that host choice is influenced by the conservatism of chemical, morphological, ecological, and physiological plant traits affecting herbivore performance. Power to detect phylogenetic conservatism in community samples could be improved by considering species abundance and increasing the universe of sampled hosts. Nonetheless, species presence/absence and a limited sample of the local plant community indicated a relatively strong influence of host relatedness on herbivore community composition.

Tests of host specificity

Community phylogenies and null models provide a quantitative test of significance for host specificity at the clade level. Examples of specialists on *Macaranga*, *Ficus*, and *Psychotria* that rejected null models of host association are shown in Fig. 5 and Table 3, along with nonspecialists that failed to reject null models. These examples were chosen to illustrate extreme cases and to reinforce the point that a quantitative definition of host specificity based on phylogenetic dispersion is more practical and powerful than definitions based on arbitrary taxonomic ranks. When singleton records were excluded from analyses, more host clade specialists were detected in all herbivore assemblages (Table 2). This result is not surprising given that herbivores tend to have a highly skewed distribution of abundance across the host range. The average herbivore species in New Guinea secondary forest, for example, has >90% of individuals aggregated on a single host species and feeds on one to three host species (Novotny et al. 2004*b*). Singletons representing rare or anomalous feeding events are likely to increase error rates in analyses such as ours that ignore abundance distributions and simply treat the associations as present or absent.

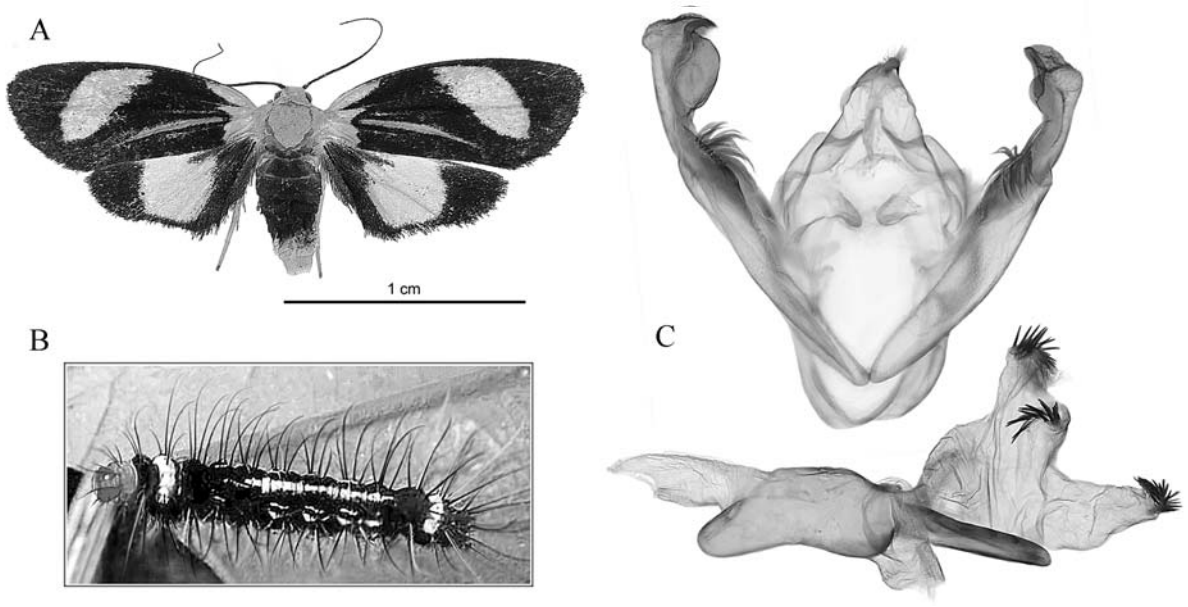

PLATE 1. *Darantasia caerulescens* Druce (Lepidoptera: Arctiidae): (A) Adult, (B) larva, and (C) male genitalia, with aedoeagus separated and vesica inflated. Genitalia, illustrated here for the first time, allow differentiation from similar-looking species. The caterpillars of this moth fed on three distantly related plant species (Fig. 5). Photo and dissection credit: Karolyn Darrow.

Excluding singletons and considering molecular branch lengths, the NRI and NTI differed as expected, considering that NTI quantifies dispersion near the tips of the phylogeny whereas NRI measures overall dispersion. According to NRI, Lepidoptera was proportionally the most specialized fauna, with 42–44% of species significantly clustered with respect to host plant phylogeny, compared with 24–27% of coleopterans and 10% of orthopteroids. By contrast grasshoppers and relatives showed the highest proportion of overdispersed species (2–15%), compared with Lepidoptera (2–6%) and Coleoptera (0–3%). We attribute these differences to variation among feeding guilds. We expected Lepidoptera to show the greatest overall degree of host specificity, due to the fact that caterpillars feeding on foliage were reared from larvae to adults and host specificity is manifest at the larval stage. Coleoptera, on the other hand, were tested for feeding only as adults and potentially feed on a more restricted set of hosts as larvae. Root-, stem-, and wood-boring beetle larvae are expected to exhibit greater host specialization than adult stages, because the impact of plant chemistry on insect development is strongest in the early life stages (Mattson et al. 1988). The nonholometabolous assemblage of grasshoppers and relatives, feeding as nymphs and adults, are widely regarded as polyphagous (Chapman and Sword 1997) and therefore expected to show less phylogenetic clustering and greater overdispersion than the other assemblages. Orthopteroid nymphs are more mobile than caterpillars, enhancing opportunities to graze on multiple hosts and presumably selection for greater breadth of diet (Chapman and Sword 1997).

Clustering of similar plant traits in close relatives due to phylogenetic conservatism (Cavender-Bares et al. 2004) provides a simple explanation for the extreme patterns of clade specialization observed in many herbivore species. We believe that herbivore tracking of phylogenetically conserved plant traits is a more plausible explanation than co-cladogensis for patterns of association in many plant-herbivore interactions. Predation and parasitism might also indirectly promote specialization in phytophagous insect communities (Bernays and Graham 1988). Attack rates of caterpillar parasitoids in temperate forests, for example, vary among host plant species, and this variation has the potential to influence the evolution of herbivore host range (Lill et al. 2002). Apart from patterns of clade specialization, we also detected a small number of cases of phylogenetic overdispersion (3–6% of all herbivores) that could have a biological explanation.

Significant overdispersion is expected for herbivores feeding on distantly related hosts when hosts share a set of convergent traits that are palatable to particular herbivores (Cavender-Bares and Wilczek 2003). Convergence in plant traits can result from adaptive evolution (Agrawal and Fishbein 2006) or habitat specialization (Fine et al. 2006). For example, *Ficus tinctoria* (Moraceae) and *Excoecaria agallocha* (Euphorbiaceae) share an extreme environment and a unique set of herbivores along the seacoast. The identification of convergent ecophysiological, morphological, and chemical traits in distantly related hosts sharing similar herbivores might point to factors that limit the evolution of host range. Where trait convergence enables similar insects to feed on highly diverged plant lineages, we expect significant

herbivore clustering in more than one place on the plant phylogeny, causing the nearest taxon index to be significantly high when the net relatedness index is not.

Conclusions

This study of herbivore associations illustrates how the integration of community ecology and phylogeny can detect patterns of host specialization. A community phylogeny with molecular branch lengths and null models identified patterns of phylogenetic clustering in the associations of insect herbivores feeding on a sample of tropical rain forest vegetation in New Guinea. Quantitative, community phylogenetic studies such as ours show a general tendency for insects to feed on closely related hosts (Ødegaard et al. 2005). As predicted, we found greater phylogenetic structure in caterpillar associations than in herbivorous beetles or orthopteroids. Quantifying the phylogenetic dispersion of host associations has advantages over approaches that ignore phylogenetic distance or assume the equivalence of taxa of the same rank. Indices of phylogenetic dispersion provide a quantitative definition of host specificity that can be compared among studies, solving a problem that has plagued herbivore community ecology from the very beginning. The approach provides not only a standard for the identification of specialists, but also holds promise for the study of host shifts and the identification of alternative hosts.

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APPENDIX

A description of Euphorbiaceae phylogeny (*Ecological Archives* E087-111-A1).