

COMMUNITY AND PHYLOGENETIC STRUCTURE OF REPRODUCTIVE TRAITS OF WOODY SPECIES IN WET TROPICAL FORESTS

ROBIN L. CHAZDON,^{1,5} SONIA CAREAGA,² CAMPBELL WEBB,³ AND ORLANDO VARGAS⁴

¹Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043 USA

²Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Av. Liga Periférico-Insurgentes Sur 4903, Col. Jardines del Pedregal, Tlalpan 14010 México, D.F.

³Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511 USA

⁴Reserva Ecológica Bijagual de Sarapiquí, Apartado 35-3069, Puerto Viejo de Sarapiquí, Costa Rica

Abstract. We compare the distribution of reproductive traits in woody vegetation of 10 wet tropical forests in northeastern Costa Rica. Based on quantitative sampling of seedlings, saplings, and trees, we assess whether particular sexual systems, pollination syndromes, or seed-dispersal modes are associated with successional stage, prior selective logging, woody growth forms, or patterns of abundance or rarity. We further examine the phylogenetic structure of these traits in the regional woody flora, testing explicit hypotheses regarding phylogenetic clustering of reproductive traits and habitat distributions. Animal dispersal and insect pollination predominate across all forest types and size classes. In second-growth trees, relative abundance of species with explosive dispersal, hermaphroditic flowers, and insect pollination is higher, and relative abundance of species with animal dispersal and mammal pollination is lower, compared to old-growth and logged forests. Overall, dioecy and wind dispersal are more frequent than expected in canopy trees, and hermaphroditic flowers are more frequent than expected in shrubs. Reproductive traits, growth-form traits, and relative abundance patterns show significant clustering within the supertree phylogeny. Patterns of trait distribution across forest types are closely linked with patterns of floristic composition at the genus and family level. Species-level associations among reproductive traits and woody growth form can be explained by phylogenetic correlations. Wind dispersal and hummingbird pollination are significantly concentrated in clades with hermaphroditic flowers, whereas wind pollination is concentrated in clades with unisexual flowers. Legacies of both phylogenetic history and forest disturbance structure the distribution of reproductive traits within and among tropical wet forest communities.

Key words: Costa Rica; forest regeneration; logged forest; old-growth forest; phylogenetic conservatism; pollination; reproductive traits; second-growth forest; seed dispersal; sexual systems; wet tropical forest.

INTRODUCTION

Reproductive traits of tropical forest trees critically influence population- and community-level processes, such as stand dynamics, genetic diversity, and species interactions. Linking reproductive traits with species abundance patterns in tropical forests in different stages of succession provides a fundamental knowledge base for understanding forest regeneration processes and the essential roles that animals play as pollinators and seed dispersal agents (Corner 1949, Baker 1970, Howe and Smallwood 1982, Baker et al. 1983, Kress and Beach 1994, Wunderle 1997).

Because reproductive traits tend to be strongly phylogenetically conserved (Fox 1985), ecological patterns emerging from comparisons involving large numbers of species from many taxonomic groups may not reflect evolutionarily independent, species-level associations (Felsenstein 1985, Harvey and Pagel 1991,

Kelly and Purvis 1993, Silvertown and Dodd 1997). How does the phylogenetic structure of forest communities influence the distribution of reproductive traits? Here, we examine the distribution of reproductive traits in local communities of woody vegetation to determine whether particular sexual systems, pollination syndromes, or seed-dispersal modes are associated with successional stage, prior selective logging, woody growth forms, or patterns of abundance or rarity. We go beyond an assessment of ecological patterns to examine the phylogenetic structure of these traits in the regional woody flora, testing explicit hypotheses regarding phylogenetic clustering (phylogenetic conservatism) of reproductive traits and ecological traits, such as woody growth form and differential abundance in second-growth and old-growth stands. Our study is among the first to examine the influence of phylogenetic conservatism on the ecological distribution of reproductive traits of woody species in tropical forest communities (Ibarra-Manríquez et al. 2001).

Many studies have compared the frequency and abundance of reproductive traits across tropical forests

Manuscript received 6 May 2002; accepted 16 June 2002.
Corresponding Editor: L. F. Delph.

⁵ E-mail: chazdon@uconn.edu

(Frankie et al. 1974, Opler et al. 1980*b*, Gillespie 1999, van Dulmen 2001). In many cases, surveys are based on floras (Flores and Schemske 1984, Bullock 1985, Ibarra-Manríquez and Oyama 1992) and lack quantitative data on the relative abundance of species differing in reproductive traits (but see Zapata and Arroyo 1978). Most community studies examine only one or two reproductive traits (Kato 1996, Momose et al. 1998). Other studies are based on small sample sizes or have little or no replication among forest types (Zapata and Arroyo 1978). Studies including second-growth or degraded forests (Opler et al. 1980*a*, Gillespie 1999, Corlett 2001) are crucial, given the fact that these forest types are growing in area and importance in wet tropical regions throughout the world (Wadsworth 1997, Guariguata and Ostertag 2001). Selectively logged forests are the predominant type of forest cover in the Sarapiquí region of Costa Rica and are characterized by a mixture of species common to both second-growth and old-growth forests (Butterfield 1994, Guariguata and Dupuy 1997, Finegan and Camacho 1999).

Phylogenetic considerations provide unique insights in comparative ecological studies of functional traits (Ackerly 1999, Webb et al. 2002). Phylogenetic analysis of correlations between two or more traits among species reveals that correlations may be better explained by common ancestry than by adaptive causes acting independently on species' traits. Similarly, the phylogenetic assessment of site-trait correlations permits us to determine whether these correlations may be better explained by shared clade composition and phylogenetic conservatism than by independent selection for these traits in particular sites. Renner and Ricklefs (1995), in their survey of dioecy in flowering plants, found that the frequency of dioecy in a local flora reflects the particular pool of families occurring there as much as, or more than, environmental factors. Across many habitat types, seed mass is often a conservative trait between genera or families (Hodgson and Mackey 1986, Mazer 1989, Lord et al. 1995). Ibarra-Manríquez et al. (2001) showed a high degree of phylogenetic conservatism in seedling morphology in a lowland rain forest community in Mexico. Advances in molecular systematics now provide opportunities to test explicit hypotheses regarding evolutionary transitions in reproductive characters and to discern whether a given trait is more likely to evolve in branches of a clade distinguished by another trait (Donoghue 1989, Ackerly 1999, Prach and Pysek 1999, Weller and Sakai 1999, Weiblen et al. 2000).

We compiled data on reproductive traits from a variety of published sources and from personal observations and combined this information with vegetation inventory data for 10 forest stands in the same floristic and climatic zone of northeastern Costa Rica (Guariguata et al. 1997, Chazdon and Coe 1999, Nicotra et al. 1999). We first compare the incidence and relative

abundance of species with different reproductive traits among forest types, stem size classes, and woody growth forms, without taking phylogenetic relationships into account. To gain further insight into these patterns, we assess interactions among reproductive traits and compare the incidence of traits among common and rare tree species (singletons) in second-growth and old-growth stands. We then assess whether sexual systems, dispersal modes, pollination modes, and growth-form traits are associated phylogenetically in the pool of species that we examine (Donoghue 1989, Maddison 1990). Our analysis demonstrates that legacies of both phylogenetic history and land-use history structure the distribution of reproductive traits within and among tropical wet forest communities.

MATERIALS AND METHODS

Study areas and stand selection

Study areas were located in the Atlantic lowland rain forest of Sarapiquí, Costa Rica in the premontane wet forest life zone (Holdridge et al. 1975). Five sites were located within La Selva Biological Station, owned by the Organization for Tropical Studies (Table 1). This region is a mosaic of active pastures, small- and large-scale agriculture, second-growth forest, selectively logged forest, and old-growth forest in protected areas (Butterfield 1994). Land-use history of each stand was determined by a combination of historic records (Pierce 1992), aerial photographs, satellite images, and interviews with local residents, farm staff, and landowners (Table 1). Second-growth stands were cleared for pasture in the early- to mid-1970s, actively managed for 4–6 years, and subsequently abandoned in the late 1970s or early 1980s. Only a few remnant canopy trees were found in all second-growth stands (Guariguata et al. 1997). In the two selectively logged stands, all commercial tree species >70 cm dbh were removed 15–20 years before our study (Chazdon and Coe 1999). Species richness, floristics, seedling and sapling growth forms, and vegetation structure in six of these stands are described in further detail by Guariguata et al. (1997) and Chazdon et al. (1998). Nicotra et al. (1999) and Montgomery and Chazdon (2001) describe light heterogeneity, woody seedling regeneration, and forest structure in a subset of these stands.

Woody vegetation inventory

In each stand, woody vegetation was sampled in nested, contiguous quadrats along three roughly parallel transects 100–160 m in length. In 1993–1994, trees ≥ 5 cm dbh were sampled in 10×10 m quadrats (total area sampled per stand = 0.24–0.48 ha); saplings (stems > 1 m tall and < 5 cm dbh) were sampled in 5×5 m quadrats (total area sampled per stand = 0.135–0.24 ha); and seedlings (stems 20–100 cm tall) were sampled in 1×1 m quadrats (total area sampled per stand = 270–480 m²). Transects did not traverse

TABLE 1. Site characteristics of 10 forest stands in the Caribbean lowlands of Costa Rica.

Site name, by forest type	Site abbrevi- ation	Location: latitude, longitude	Recent land-use history	No. years since disturbance
A) Second-growth forest				
Lindero Occidental	LOC	La Selva: 10°26' N; 84°01' W	cleared in 1971–1973; pasture for 6 years; regrowth cleared before pasture abandoned	15–17
Peje	PEJE	La Selva: 10°26' N; 84°02' W	cleared in 1972–1974; pasture for 5 years; regrowth cleared before pasture abandoned	15–17
La Martita	LAM	Chilamate: 10°27' N; 84°04' W	cleared in 1971–1972; pasture for 4–5 years, then abandoned	17–20
Cuatro Rios	CUA	La Virgen: 10°23' N; 84°08' W	clear-cut in mid 1970s for timber and burned; little or no grazing	15–20
Sendero Holdridge	SHO	La Selva: 10°25' N; 84°01' W	cleared in 1950s; pasture abandoned in 1967	25
B) Old-growth forest				
La Selva	PRI	La Selva: 10°25' N; 84°03' W	no apparent human disturbance	
Ramirez	RAM	Chilamate: 10°27' N; 84°04' W	no apparent human disturbance	
Cay Rica	CAY	El Roble: 10°26' N; 84°05' W	no apparent human disturbance	
C) Logged forest				
Intervenido	INT	La Selva: 10°25' N; 84°02' W	logged for more than 10 years until late 1970s; ~3–4 stumps/ha	15–17
Kelady	KEL	Pueblo Nuevo: 10°29' N; 84°09' W	logged for more than 10 years until early 1980s; ~8–9 stumps/ha	12–14

any steep slopes or known environmental gradients. Species were identified in the field by project staff assisted by an expert local naturalist; in questionable cases, specimens were collected, dried, and pressed, and were used to identify species by comparison with specimens in the La Selva Herbarium or the Costa Rican National Herbarium. Vegetation data were entered into a specimen-based, relational database (Colwell 1996) with growth form as a custom field and reproductive traits as auxiliary fields in the species table. Species and family names follow an updated list published by Robert L. Wilbur and collaborators (McDade et al. 1994) and posted on the OTS web site.⁶ Additional species information is available at the La Selva Digital Flora web site.⁷

Reproductive and growth-form traits

Data on dispersal modes, sexual systems, and pollination modes were compiled from a variety of published sources. Additional data were obtained from observations at La Selva Biological Station by the station naturalist (Orlando Vargas) or through personal communication with specialists. The full set of data and literature sources is provided in the Appendix. Sexual systems were defined based on studies by Bawa et al. (1985b), Kress and Beach (1994), and many other individual sources (Appendix). Species were classified as hermaphroditic, monoecious, or dioecious (Beach and Bawa 1980, Bawa and Beach 1983). Bawa et al.

(1985b) noted that dioecious species are difficult to distinguish from perfect-flowered hermaphroditic ones because stamens or pistils that are present may be non-functional, rendering the flowers unisexual. Thus, several species considered hermaphroditic here may, in fact, be cryptically dioecious.

Pollination modes were defined based on general categories of insect pollination, wind pollination, mammal pollination, and hummingbird pollination following Bawa et al. (1985a) and Kress and Beach (1994) and other sources listed in the Appendix. In many cases, specific insect pollinators could be identified from the literature, but because these details were not available for all species, these cases are all lumped together in one broad category. Species that are pollinated by mammals as well as insects (moths), such as *Pachira aquatica* (Bombaceae), were considered to be mammal pollinated; species pollinated by hummingbirds and insects, such as several species of *Inga* (Fabaceae), were considered to be hummingbird pollinated. This simplification does lead to a bias toward the more derived states of mammal and bird pollination and away from insect pollination, which is by far the most predominant pollination mode in the regional woody flora (see *Results*).

Primary seed-dispersal modes were defined as wind dispersal, animal dispersal, explosive dispersal, and gravity dispersal. Secondary seed dispersal is not considered here, as information is limited for most species. In cases in which more than one primary dispersal mode could apply within a species, the mode that predominates in the La Selva region was used. For ex-

⁶ URL: (<http://www.ots.duke.edu/en/laselva/species/vascular.shtml>)

⁷ URL: (<http://www.virtualherbarium.com/laselva/>)

ample, in our upland sites, *Pentaclethra macroloba* disperses through explosive dehiscence rather than through hydrochory (Williamson and Costa 2000).

Species were assigned to one of four woody growth forms: canopy tree, midstory tree, liana, or shrub. Palms (Arecaceae) were excluded from these categories because their distinctive growth form confounds analyses of reproductive traits in relation to phylogeny and growth form. Canopy trees include emergent species with crowns projecting above the canopy, as well as species attaining heights >15 m. Midstory trees are defined as species that do not exceed 15 m in height. Shrubs do not exceed 5 m in height and are often multiple stemmed.

*Relative abundance, common species,
and "overabundant" species*

We performed four sets of comparisons based on relative abundance data. First, within each of the 10 forest stands, we computed the incidence and relative abundance of species with different dispersal modes, sexual systems, and pollination modes for tree, sapling, and seedling size classes. Tree size classes included all individuals with a dbh ≥ 5 cm. Across forest types, mean relative abundance in replicate stands was computed and values were compared using nonparametric statistical tests (Kruskal-Wallis and Mann-Whitney). Second, in each of the eight old-growth and second-growth stands, common species were defined as those with a dbh ≥ 5 cm with five or more individuals in the 0.24–0.48 ha sample, whereas singletons were species represented by a single individual. These are not necessarily rare species, as noted by Pitman et al. (1999), but they are infrequent species within the sampled areas. Mann-Whitney tests were used to compare the incidence (percentage of species) of specific traits between common species and singletons within old-growth and second-growth stands.

Third, to determine which tree species were more abundant than expected in second-growth or old-growth stands, only individuals with a dbh ≥ 10 cm were included, eliminating midstory tree species and juveniles of canopy tree species. The total abundance of species in five second-growth sites and three old-growth sites was tabulated, and expected abundances, by species, were computed based on the relative abundance in all eight stands combined, as in a chi-squared test. This approach is similar to a test of habitat association. Those species with actual abundances exceeding expected abundance by a factor of 1.2 were considered to be "overabundant" in that forest type. This tabulation was also done separately for shrub species. In a fourth (more simplistic) comparison, we computed the relative abundance of these tree and shrub species within pooled old-growth and pooled second-growth stands. All species with a relative abundance >1% were considered to be common and all others were considered to be uncommon.

Phylogenetic reconstruction and character mapping

A hypothesis for the phylogenetic relationship of the 366 species was constructed using previously published phylogenetic studies. This process was automated by the Phylomatic database and assembly tools (Webb and Donoghue 2002). Phylomatic is based on a single higher plant supertree (Sanderson et al. 1998), or "tree of trees," that grows continuously as new phylogenies are attached and changes as major branches are rearranged as the result of new work. Full assembly rules for this supertree are given on the Phylomatic website (Webb and Donoghue 2002). In brief, the tree "backbone" is the most recent all-angiosperm, three-gene tree (Soltis et al. 2000), to which strict consensus trees are attached. An online program then translates the input list of taxa into a phylogeny for those taxa, attaching unrecognized species to a polytomous "genus" node and unrecognized genera to a polytomous "family" node. The supertree database used in this study was revision L20011010, containing 38 sources of data. The phylogeny used here thus represents a best hypothesis for the relationship of its taxa based on up to 38 other studies of a wide range of genes and morphology, with its terminal clades being strict consensus. A NEXUS version of our 366 taxa supertree is available online.⁸

We used MacClade version 4.0 (Maddison and Maddison 2000) to reconstruct the distribution of traits on the phylogeny of our pool of 366 species. In case of equivocal character tracings, we selected the option to show all most parsimonious states at each node (Maddison and Maddison 2000). Individual reproductive character states, woody life-form states, and abundance states (second-growth overabundance, old-growth overabundance, common species in second growth, common species in old growth) were coded as unordered, binary characters. Polytomies at the generic and species level were resolved randomly to create 10 trees. Individual character states were then traced (mapped) onto these phylogenetic trees. Isolating each character state as a binary character permits us to assess whether this trait is clustered in the phylogeny, but does not allow a determination of the sequences of change or the ancestral or derived character state.

We used two methods to examine phylogenetic conservatism, or clustering of traits. The first method is based on the number of steps required for each character, which is the summed cost of all changes (gains and losses) in the most parsimonious ancestral state reconstruction (Maddison and Slatkin 1991). For each character state considered, we randomly reshuffled the states among the taxa 1000 times. Using character tracing, we compared the actual number of steps for each character with the number of steps in the 1000 trees based on randomly reshuffled character states. In this

⁸ URL: <http://www.phylodiversity.net/phylomatic/studies/chazdon.nex>

way, the degree of clustering of character states within the phylogeny can be assessed. In the case in which a full phylogeny (all extant taxa) is being examined, if 950 or more randomized trees have a greater number of steps than the actual tree, the character being traced can be viewed as having arisen independently significantly less often than would be expected by chance, given the distribution of traits among taxa. In this study, using a tree based on only 366 taxa, if the actual number of steps ranked within the lowest 50 of the 1000 "re-shuffled" trees, we considered that character to be significantly phylogenetically clustered. We performed these analyses using the original supertree, considering polytomies to represent simultaneous speciation events (hard polytomies). Although this is a conservative assumption, for the purpose of examining phylogenetic clustering among clades, it provides a reasonable way to standardize the tests.

Another component of phylogenetic conservatism not measured by the previous test is general phylogenetic proximity of taxa with the same trait, i.e., whether they are sister taxa or whether they are distantly related. To assess this proximity component of conservatism, we used a second method, which compares the phylogenetic distance (in units of intervening nodes) of taxa for all pairs that have the same (binary) trait values against the distance of taxa for all pairs with different trait values. This method is a variation on phylogenetic regression tests (Grafen 1989), and was implemented in the R statistics package (R Project 2001). A significantly shorter distance for taxa with the same trait values than for taxa with different trait values indicates that, overall, more similar taxa are more likely to be closely related. A greater than expected distance for taxa with the same trait values can occur either when there is real convergence, or when there is phylogenetic conservatism in small groups of widely separated taxa.

We used the concentrated-changes test in MacClade (Maddison 1990, Maddison and Maddison 2000) to examine whether observed associations among traits reflect phylogenetic correlations. This test examines whether gains in one character (character state changes) are concentrated more than would be expected at random in branches of the tree having a particular state in a second character. To perform this test, we randomly resolved polytomies, as previously described. The test was repeated using five randomly resolved trees.

Statistical analyses

We used nonparametric tests (Mann-Whitney and Kruskal-Wallis) to compare the incidence (percentage of species) and relative abundance (percentage of stems) for each reproductive trait among forest types and to compare the incidence of traits between common species and singletons. These tests were done using Statistica for Power Macintosh (StatSoft, Tulsa, Oklahoma, USA). A hierarchical log-linear test (SPSS

version 10.0) was used to assess significant interactions between reproductive traits and woody growth form. Four factors were included: woody growth form (four levels), seed dispersal (four levels), sexual system (three levels), and pollination system (four levels). Understory and canopy palms were excluded from this analysis because these growth forms are confounded with taxonomic group. We assessed the significance of all two-way and higher order interactions among growth form, dispersal mode, sexual system, and pollination mode using a fully saturated model.

When multiple tests are performed, as is the case here, Bonferroni or other corrections for multiple, post hoc comparisons should normally be applied to yield an experiment-wise α value of 0.05. However, because of the small number of replicate stands in our study ($n = 2, 3, \text{ and } 5$), this type of correction greatly increases the risk of Type II error, the acceptance of a false null hypothesis. Our approach here is to present uncorrected P levels for each individual test, acknowledging that many of these values fall short of global statistical significance. In effect, we are setting an experiment-wise alpha level higher than 0.05 in order to keep β , the probability of Type II error, at an acceptable level.

RESULTS

The original vegetation survey included a total of 459 species. Among those species that could be conclusively identified, we were able to obtain reproductive data for 366 species in 198 genera and 72 families. We identified dispersal mode for all species, sexual system for 350 species (95.63%), and pollination mode for 353 species (96.45%; Appendix). Ten families account for 207 (56.6%) of these species: Fabaceae (41 species), Rubiaceae (31), Melastomataceae (31), Arecaceae (24), Lauraceae (17), Piperaceae (17), Moraceae (13), Annonaceae (12), Sapindaceae (11), and Euphorbiaceae (10). Canopy trees and palms form the largest concentration of species (167 species, 45.6%), whereas 94 species are midstory trees (27.3%), 63 species are shrubs (17.2%), 24 species are lianas (6.6%), and 18 species are understory palms (4.9%).

Overall, 90.71% (332 species) of the woody species sampled have animal-dispersed seeds. Seed dispersal by wind occurs in 24 species (6.56%), and nine species (2.46%) have explosive seed dispersal. Only one species, a canopy tree, *Macrolobium costaricense*, has seeds dispersed by gravity or water. Most species (67.76%) are hermaphroditic. Overall, 18.31% of the species are dioecious and 9.56% are monoecious. Insect pollination is the most common mode of pollination overall, exhibited by 69.13% of the species. Twenty-four species (6.56%) are pollinated by hummingbirds and 13 species (3.55%) are pollinated by wind. Nine species (2.46%) in our sample are pollinated by mammals, predominantly bats. The Appendix contains a table of reproductive traits for the 366 species studied.



PLATE 1. (Left) Fruits of the jelly bean palm, *Synechanthus warscewiczianus*, in the understory of La Selva Biological Station. The jelly bean palm has a monoecious sexual system and the fruits are bird-dispersed and insect pollinated. (Middle) *Socratea exorrhiza*, a stilt palm common in old-growth forest, overlooking a sea of forest. *Socratea* is monoecious, pollinated by beetles, and the fruits are dispersed by birds and mammals. (Right) Flowering individual of *Asterogyne martiana*, an understory palm. It has a monoecious sexual system and the fruits are bird-dispersed and flowers are insect pollinated. Photographs by R. Chazdon.

Plate 1 shows examples of the wide variety of reproductive traits among the study species.

*Distribution of reproductive traits
across forest types and size classes*

Sexual systems.—At the level of species, different forest types and size classes are not associated with differences in the frequency of sexual systems ($P > 0.05$ for all tests; Table 2). Across stands, 57–69% of tree species ≥ 5 cm dbh and 59–65% of saplings and seedling species have hermaphroditic (bisexual) flowers (Table 2). Dioecious species compose 18–28% and monoecious species compose 8–15% of the tree, sapling, and seedling species sampled.

Relative abundance of tree species with different sexual systems does vary consistently with forest type and size class, however. Relative abundance of hermaphroditic trees in second-growth is higher (79.87%) than in logged (56.78%) or old-growth (54.66%) forests (Fig. 1; Kruskal-Wallis, $P = 0.032$). Second-growth forests show the lowest relative abundance of monoecious and dioecious species (Fig. 1; Kruskal-Wallis, $P = 0.022$ [monoecy] and $P = 0.033$ [dioecy]). Logged forests show the highest relative abundance of dioecious tree species (24–28%; Fig. 1). These differences persist for sapling size classes; hermaphroditic species averaged 62.53% of all stems in second-growth stands compared to 38.86% in old growth and 47.27% in logged stands (Kruskal-Wallis; $P = 0.050$). Across all forest types, the relative abundance of hermaphroditic species decreases, whereas monoecious species increase in abundance from tree to sapling size classes.

In old-growth forests, monoecious species compose 20.5% of the trees and 30.4% of the sapling stems (data are not shown). For seedling size classes, relative abundance of species with different sexual systems does not differ significantly with forest type (Kruskal-Wallis; $P > 0.05$; data are not shown).

Pollination modes.—Animal pollination is overwhelmingly the most common syndrome in all forest types, with insect pollination predominating (Table 2, Fig. 2). The pollination mode of 18–23% of the species of trees, saplings, and seedlings in old-growth forests is unknown, however (Table 2). The frequency of mammal pollination in trees is low, but varies with forest type, showing a lower frequency in second-growth forests (1.9%) than in logged (3.1%) or old-growth forests (4.3%; Kruskal-Wallis, $P = 0.031$). Insect pollination is more frequent among species of second-growth forest trees (69.82%) than in old-growth forests (63.87%; Mann-Whitney U test, $P = 0.053$). The frequency of pollination systems shows no significant variation across size classes (Table 2).

Relative abundance of insect-pollinated tree species differs across forest types and is highest (84.92% of all stems) in second-growth forests (Kruskal-Wallis, $P = 0.049$; Fig. 2). Although uncommon overall (1.46% of all stems sampled), mammal-pollinated trees, saplings, and seedlings are significantly less abundant (or absent altogether) in second-growth forests than in old-growth forests (Mann-Whitney U test: $P = 0.025$ for trees; $P = 0.052$ for saplings, and $P = 0.052$ for seedlings). Saplings and seedlings show no differences in

TABLE 2. Percentage of woody species (mean \pm 1 SD) in five second-growth, two selectively logged, and three old-growth forests exhibiting different sexual systems, pollination, and dispersal modes.

Trait, by size class	Second growth	Logged	Old growth	<i>P</i>
A) Sexual system				
Monoecious				
Trees	10.03 \pm 1.64	9.46 \pm 3.17	8.55 \pm 0.57	0.700
Saplings	11.46 \pm 2.56	10.86 \pm 0.55	12.00 \pm 1.11	0.696
Seedlings	11.11 \pm 1.38	12.20 \pm 1.53	13.45 \pm 1.23	0.086
Hermaphroditic				
Trees	64.38 \pm 3.73	58.10 \pm 0.93	61.30 \pm 3.88	0.131
Saplings	64.14 \pm 1.89	64.17 \pm 0.30	59.89 \pm 1.34	0.055
Seedlings	60.72 \pm 4.02	61.17 \pm 2.53	59.22 \pm 0.33	0.696
Dioecious				
Trees	23.32 \pm 3.50	26.18 \pm 0.58	23.35 \pm 4.40	0.733
Saplings	21.31 \pm 1.32	21.07 \pm 0.62	22.88 \pm 1.76	0.280
Seedlings	24.02 \pm 1.88	22.12 \pm 1.46	21.73 \pm 1.18	0.278
B) Pollination mode				
Insect				
Trees	69.82 \pm 3.51	67.03 \pm 1.49	63.87 \pm 2.70	0.122
Saplings	72.90 \pm 4.44	71.49 \pm 4.09	69.08 \pm 2.81	0.760
Seedlings	73.97 \pm 4.16	70.03 \pm 1.80	71.46 \pm 1.11	0.244
Hummingbird				
Trees	9.69 \pm 2.88	7.35 \pm 1.64	6.76 \pm 1.35	0.280
Saplings	5.74 \pm 1.06	5.72 \pm 0.13	6.37 \pm 1.22	0.833
Seedlings	7.86 \pm 1.82	7.29 \pm 1.47	7.40 \pm 0.63	0.753
Wind				
Trees	3.90 \pm 0.83	5.22 \pm 1.36	5.08 \pm 1.91	0.393
Saplings	3.31 \pm 0.77	3.87 \pm 1.93	3.64 \pm 1.77	0.993
Seedlings	3.59 \pm 1.65	4.74 \pm 1.17	3.70 \pm 0.31	0.306
Mammal				
Trees	1.92 \pm 0.55	3.14 \pm 0.07	4.32 \pm 1.19	0.031
Saplings	2.26 \pm 0.89	3.00 \pm 0.70	2.60 \pm 0.49	0.516
Seedlings	1.48 \pm 0.48	2.10 \pm 0.35	2.13 \pm 0.38	0.139
Unknown				
Trees	14.67 \pm 3.92	17.26 \pm 1.84	19.98 \pm 2.30	
Saplings	15.48 \pm 4.27	15.93 \pm 1.32	18.31 \pm 2.01	
Seedlings	13.11 \pm 3.78	15.86 \pm 4.09	15.31 \pm 0.86	
C) Primary seed dispersal mode				
Wind				
Trees	8.95 \pm 2.65	4.70 \pm 0.64	5.73 \pm 2.50	0.131
Saplings	4.49 \pm 2.11	4.49 \pm 1.05	4.77 \pm 1.27	0.932
Seedlings	4.72 \pm 2.77	3.06 \pm 0.09	3.47 \pm 1.68	0.516
Explosive				
Trees	5.59 \pm 0.70	4.19 \pm 0.09	3.60 \pm 0.83	0.032
Saplings	3.08 \pm 1.30	3.31 \pm 0.25	2.42 \pm 0.48	0.233
Seedlings	4.13 \pm 0.83	2.95 \pm 0.24	3.40 \pm 0.66	0.112
Animal				
Trees	85.81 \pm 3.39	91.11 \pm 0.54	90.33 \pm 1.94	0.055
Saplings	92.43 \pm 2.65	91.89 \pm 0.86	92.60 \pm 1.81	0.993
Seedlings	89.97 \pm 4.29	93.64 \pm 0.16	93.14 \pm 2.03	0.395

Notes: In each forest type, samples include trees (\geq 5 cm dbh), saplings (1 m tall to 5 cm dbh), and seedlings (20–100 cm tall). *P* levels are based on a comparison of forest types using Kruskal-Wallis tests.

relative abundance of other pollination modes across forest types (Fig. 2).

Dispersal modes.—Animal dispersal strongly predominates among trees, saplings, and seedlings in all forest types (Table 2, Fig. 3). For trees \geq 5 cm dbh, the

incidence of animal dispersal among species varies significantly across forest types (Kruskal-Wallis, *P* = 0.054; Table 2). Old-growth forest trees have a higher frequency of animal dispersal (90.33% of species) than do second-growth forests (85.81%; Mann-Whitney *U*

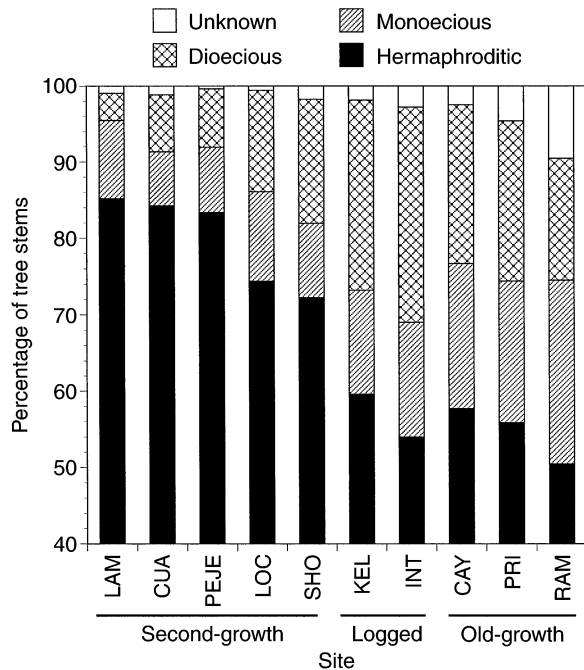


FIG. 1. Relative abundance of sexual systems (percentage of tree stems ≥ 5 cm dbh) within 10 wet tropical forest stands varying in land-use history.

test; $P = 0.051$), but the frequency of animal-dispersed seedlings and saplings does not vary significantly with forest type (Table 2). The incidence of explosive seed dispersal among species also differs across forest types (Kruskal-Wallis, $P = 0.032$), with a higher frequency in second growth (5.59%) than in old growth (3.60%). In second-growth forests, the frequency of animal dispersal increases, whereas wind dispersal decreases from tree size classes to sapling and seedling size classes (Table 2).

Relative abundance of wind-dispersed species does not vary significantly among forest types (Kruskal-Wallis, $P > 0.10$). On average, species with explosive dispersal are more abundant than species with animal dispersal (Table 2, Fig. 3). In two second-growth forests, explosive dispersal occurs in only 5–7% of the species but in 22–24% of the trees. In all forest types, the relative abundance of animal-dispersed species increases from tree size classes (75.06% on average) to sapling (87.11%) and seedling (78.52%) size classes, whereas the relative abundance of explosive and wind-dispersed species decreases (Fig. 3).

Traits of common vs. rare tree species

In old-growth stands, common tree species have a higher incidence of monoecy and a lower incidence of animal dispersal, wind pollination, and hermaphroditic flowers than singleton species (Fig. 4; Mann-Whitney U test, $P = 0.046$ – 0.049). As in old-growth stands, second-growth forests also show a higher incidence of animal dispersal among singletons than among com-

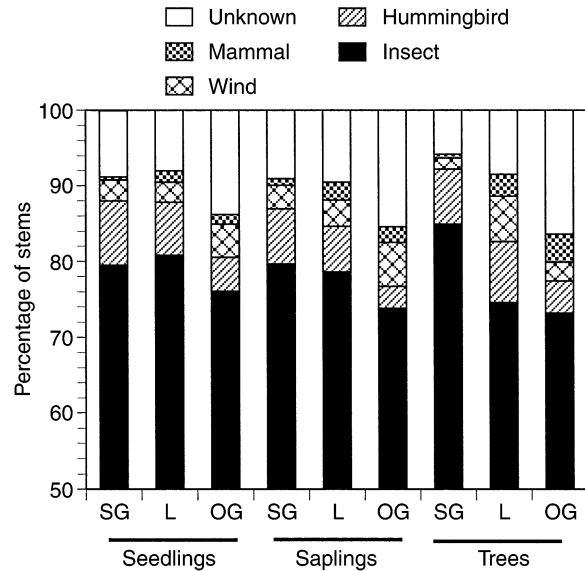


FIG. 2. Relative abundance of pollination syndromes for trees, saplings, and seedlings in second-growth (SG), logged (L), and old-growth (OG) forests. Size classes are described in *Materials and Methods, Woody vegetation inventory*.

mon species (Fig. 4; Mann-Whitney U test, $P = 0.016$). Insect pollination is more frequent in common species than in singletons in second-growth forest (Fig. 4; Mann-Whitney U test, $P = 0.047$).

Common tree species in second-growth stands have a higher incidence of hermaphroditic flowers ($P = 0.03$) and insect pollination ($P = 0.03$) compared to common trees in old-growth stands. Rare species do not differ in the incidence of any reproductive traits

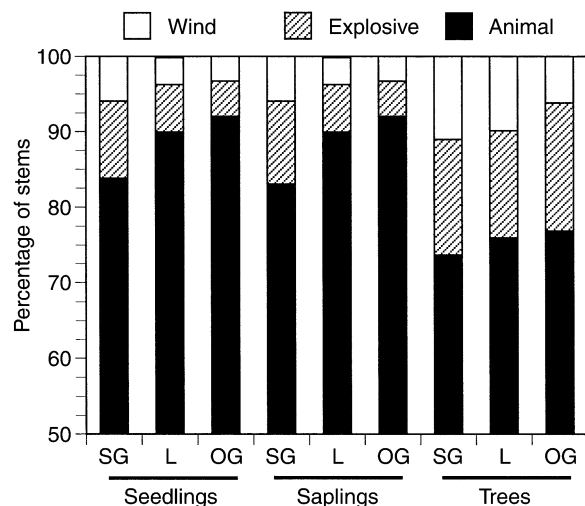


FIG. 3. Relative abundance of seed dispersal syndromes of trees, saplings, and seedlings in second-growth (SG; $n = 5$), logged (L; $n = 2$), and old-growth (OG; $n = 3$) forests. Size classes are described in *Materials and Methods, Woody vegetation inventory*.

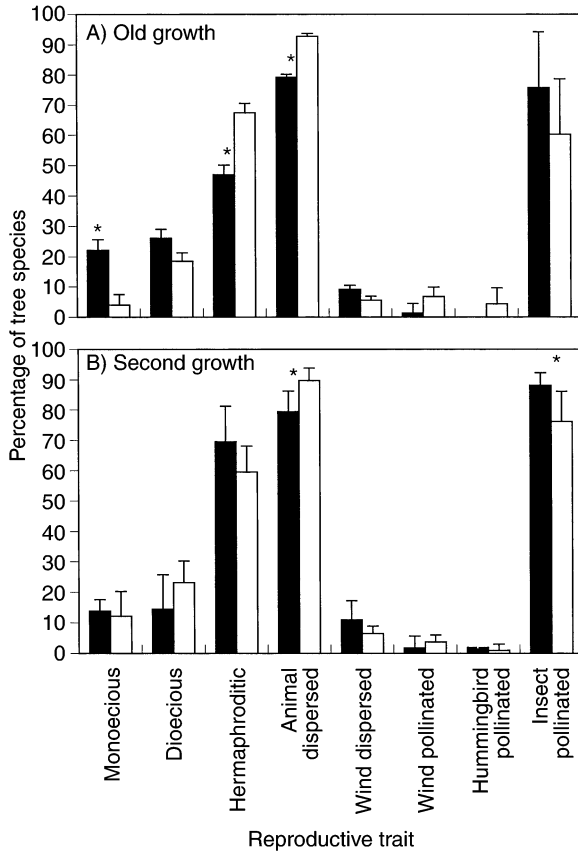


FIG. 4. Percentage (mean + 1 SD) of common (filled bars) and singleton (open bars) tree species ≥ 5 cm dbh with particular reproductive traits in (A) three old-growth stands and (B) five second-growth stands. Species with five or more individuals in a 0.27–0.48 ha sample are considered common, whereas species represented by a single individual are singletons. Within each forest type, comparisons between relative abundances of common species and singletons with $P < 0.05$ are denoted by an asterisk.

between second-growth and old-growth stands ($P > 0.05$).

Distribution of reproductive traits across woody growth forms

Woody growth form shows a highly significant interaction with sexual system (likelihood ratio $\chi^2 = 30.18$, $df = 9$, $P = 0.0004$). Dioecy is more frequent than expected among canopy tree species (Fig. 5). Monoecy is less frequent than expected in shrubs and midstory trees and more frequent than expected in canopy trees (Fig. 5). Hermaphroditic flowers are more frequent than expected in shrubs (Fig. 5). Pollination system shows no significant interaction with woody growth form ($P = 1.0$). The only exclusive relationship revealed is that all 20 species of lianas are pollinated by insects.

Woody growth form also shows significant interactions with seed-dispersal mode (likelihood ratio $\chi^2 =$

27.58, $df = 9$, $P = 0.011$). Wind dispersal is more frequent than expected in canopy trees and lianas and is absent in shrub species (Fig. 5).

Associations among reproductive traits

Sexual system and seed-dispersal mode show a significant two-way interaction (likelihood ratio $\chi^2 = 33.85$; $df = 9$; $P = 0.0001$). Explosive dispersal is more frequent than expected among monoecious species (Fig. 6). Wind dispersal is lacking among dioecious species and is more frequent than expected among hermaphroditic species (Fig. 6). In fact, all of the 23 wind-dispersed species have hermaphroditic flowers. Finally, all of the 67 dioecious species have animal-dispersed seeds, but this is not significantly more frequent than expected, given the high frequency of animal dispersal overall (Fig. 6).

Sexual systems and pollination mode also show a highly significant two-way interaction (likelihood ratio $\chi^2 = 41.05$, $df = 12$, $P < 0.0001$). Most notably, dioecy is more frequent than expected among wind-pollinated species, whereas hermaphroditic species are more frequent than expected among hummingbird-pollinated species (Fig. 6). All of the 24 hummingbird-pollinated species are hermaphroditic. There are no significant associations between pollination mode and dispersal mode, nor are any higher level interactions significant ($P = 1.0$ for $k = 3$ and $k = 4$).

Associations between abundance and forest type

Among the 260 species included in the forest association analysis, 78 species are more abundant than

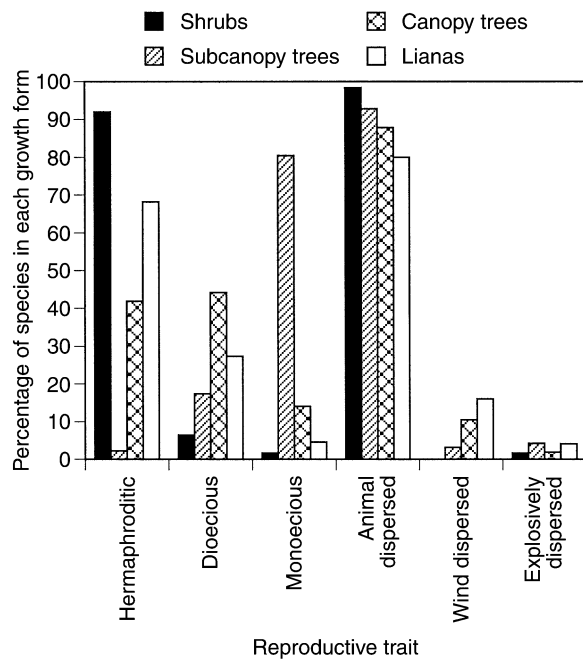


FIG. 5. The percentage of species in each of five woody growth forms associated with particular reproductive traits.

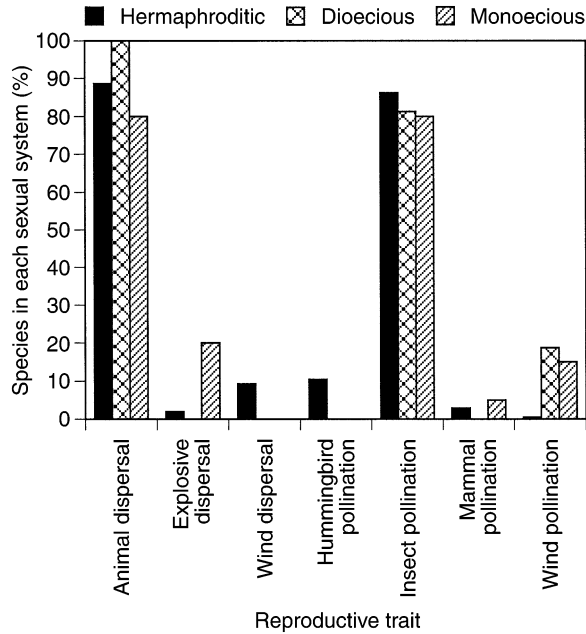


FIG. 6. The percentage of species in three sexual systems associated with particular seed dispersal and pollination traits.

expected in second-growth forests, whereas 132 species are more abundant than expected in old-growth. Fifty species show no association between abundance and forest type. In the pooled old-growth and second-growth stands, common species of trees ≥ 10 cm dbh compose 72.3% of stems in second-growth stands (15 species), but only 58.6% of stems in old-growth stands (23 species). Thus, second-growth stands are dominated by fewer species of trees than old-growth stands. For shrubs, common species compose 92.7% of stems in second growth (24 species) and 92.1% of stems in old growth (22 species).

Phylogenetic reconstruction

The phylogeny for the 366 species produced by Phylomatic is dominated by taxa in the Eurosoid I clade (112 species, Fig. 7; see APG [1998]). Other major clades are the Ranalean (basal woody angiosperms; 58 species), monocots (27 species), Myrtalean (34 species), Eurosoid II (46 species), and Euasterids (76 species). A complete list of species and families is found in the Appendix. As described in *Methods*, the super-tree produced by Phylomatic contains a large number of polytomies at the genus and family level. Character mapping reveals that animal dispersal and insect pollination are ancestral character states in this phylogenetic tree. The ancestral sexual system is equivocal.

Phylogenetic clustering of reproductive traits, growth form, and forest distributions

Based on the number of steps of character-state change in trees with randomized character states, all of the reproductive traits examined show highly sig-

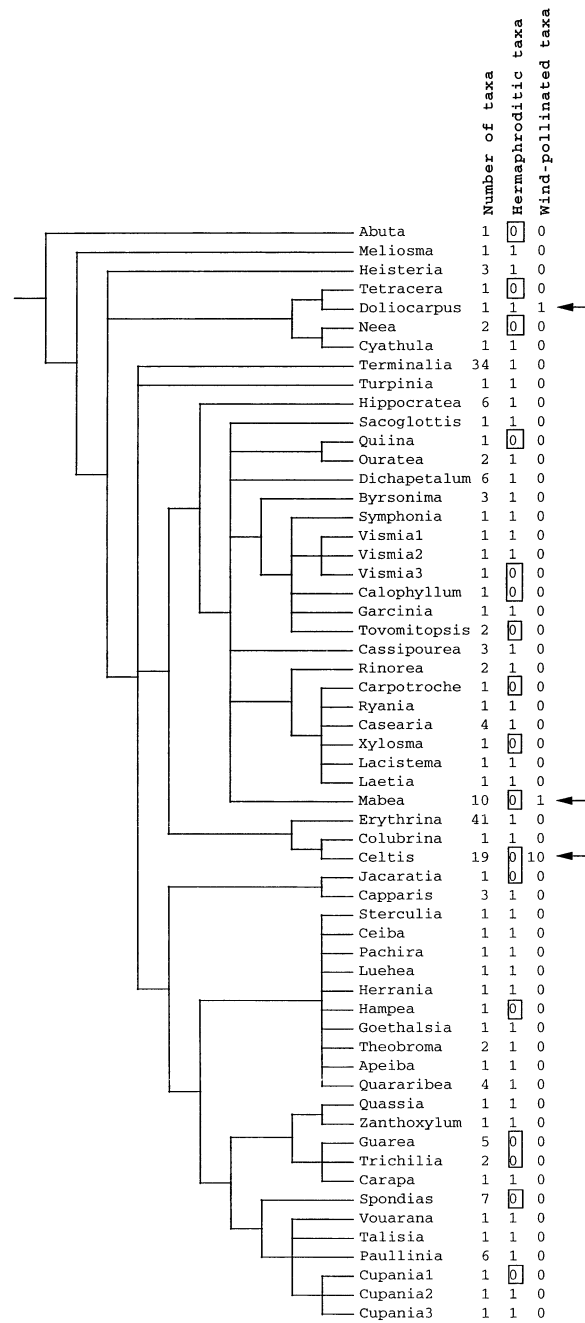


FIG. 7. An example of trait correlation, using hermaphroditism and wind pollination. Only the eurosoid clade of 112 species, part of the full tree, is shown. Each terminal clade has been collapsed so that all the taxa in the clade share the same character state (1, hermaphrodite flowers; 0, flowers not hermaphrodite). The number of taxa in each terminal clade is indicated. Each clade is labeled using the name of a single member genus. The number of taxa in each clade with wind dispersal is then given. Note that all but one occurrence of wind pollination are in clades lacking hermaphroditic flowers, a consistent pattern throughout the whole phylogeny, producing a strong overall trait correlation.

TABLE 3. Results of tests for greater trait conservatism in the supertree phylogeny than expected under random distribution of character states among terminal taxa.

Trait examined	Method 1			Method 2	
	Observed no. steps	Range of steps in 1000 randomizations	Rank of observed relative to randomized	F value for ANOVA	Significance
Reproductive traits					
Animal dispersal	28	29–34	1	inc	inc
Wind dispersal	18	19–23	1	inc	inc
Explosive dispersal	7	7–9	1	inc	inc
Hermaphroditic	24	48–69	1	503.1	***
Dioecy	31	57–66	1	426.9	***
Monoecy	14	31–36	1	30.30	***
Insect pollination	29	38–48	1	inc	inc
Hummingbird pollination	13	20–23	1	inc	inc
Wind pollination	7	10–12	1	83.79	***
Woody growth form					
Canopy tree	73	124–154	1	387.5	***
Understory shrub	33	56–64	1	85.66	***
Liana	14	20–24	1	inc	inc
Ecological distribution					
Common, second growth	36	33–39	33	inc	inc
Common, old growth	37	36–43	3	6.029	*
Overabundant, second growth	71	63–78	218	inc	inc
Overabundant, old growth	77	81–112	1	0.2526	NS

Notes: Method 1 tested the observed number of steps of character state change. Method 2 tested the difference in mean phylogenetic distance (number of intervening nodes) between all pairs of taxa with the same trait and all pairs with different traits (treatment $df = 1$). Cases in which the mean phylogenetic distance was greater than expected for taxa pairs with the same trait value are labeled “inc,” an inconclusive result that can indicate real convergence or phylogenetic conservatism in small groups of widely separated taxa.

* $P = 0.05$; ** $P = 0.01$; *** $P = 0.001$.

nificant nonrandom distributions within the phylogenetic tree, confirming the conservative nature of trait evolution within the woody taxa represented in this regional flora. For each dispersal, sexual system, or pollination character tested, the number of steps for the actual trees is ranked lower than any of the 1000 trees with randomly shuffled character states (Table 3). Over half of the wind-dispersed species are restricted to three families (Fabaceae, Bignoniaceae, and Rubiaceae), whereas explosively dispersed species are restricted to four families (Euphorbiaceae, Annonaceae, Fabaceae, and Rhamnaceae). Dioecious species are concentrated in nine plant families (Moraceae, Meliaceae, Burseraceae, Cecropiaceae, Euphorbiaceae, Siparunaceae, Myristicaceae, Smilacaceae, and Clusiaceae), whereas monoecious species are concentrated in three plant families (Arecaceae, Euphorbiaceae, and Moraceae). Wind pollination is concentrated in two families (Moraceae and Cecropiaceae), whereas hummingbird pollination is concentrated in three families (Fabaceae, Rubiaceae, and Capparidaceae) and mammal (bat) pollination is concentrated in the Bombacaceae.

Canopy trees, understory shrubs, and lianas also show significant clustering within the phylogeny, suggesting that woody growth form is a highly phylogenetically conserved character (Table 3). Nearly half of the canopy tree species occur in only six families (Fabaceae, Lauraceae, Moraceae, Euphorbiaceae, Meliaceae, and Flacourtiaceae), whereas 76% of the shrub

species occur in three families (Melastomataceae, Piperaceae, and Rubiaceae). Over half of the liana species occur in three families (Sapindaceae, Smilacaceae, and Fabaceae).

Forest distributions also show some tendency to be restricted within certain phylogenetic groups (Table 3). Tree and shrub species that are common in old-growth stands are significantly clustered within the phylogeny. The 44 species common in old-growth stands are from only 18 families; for trees ≥ 10 cm dbh, species are concentrated within the families Arecaceae, Burseraceae, Flacourtiaceae, and Rubiaceae. Common tree and shrub species in second-growth forests are also significantly clustered (Table 3). In second-growth forests, the Fabaceae, Tiliaceae, Flacourtiaceae, Annonaceae, and Arecaceae contain a larger number of common canopy and midstory tree species than other families, and Piperaceae, Melastomataceae, and Rubiaceae are the dominant families of common shrub species. Tree and shrub species with higher than expected abundance in old growth (“overabundant” species) also show significant clustering within the phylogeny. In contrast, “overabundant” species in second-growth stands are not significantly clustered within the phylogeny (Table 3). These species might as well be selected at random from the phylogeny.

Our second test of phylogenetic trait conservatism is based on comparisons of differences in phylogenetic distance (number of intervening nodes) between all

pairs of taxa with the same trait and all pairs with different traits. This test is highly significant for sexual system traits ($P < 0.001$) and for wind pollination ($P < 0.001$), but the result is inconclusive for dispersal traits (Table 3). Canopy tree and understory shrub growth forms also show highly significant phylogenetic correlations in the supertree phylogeny ($P < 0.001$; Table 3). Only one abundance trait shows a phylogenetic correlation using this method. Tree and shrub species common in old-growth forest show smaller summed phylogenetic distances than those species that are not common ($P < 0.05$; Table 3).

Patterns of correlated character evolution

Correlations between two traits can reflect shared evolutionary history or ecological convergence. To distinguish between these processes, we used the concentrated-changes test of Maddison (1990), which tests whether phylogenetic changes in one character are more likely than the random expectation to be associated with changes in another character within a selected clade. We found several cases of correlated evolution. Wind dispersal is significantly concentrated in clades with hermaphroditic flowers ($P = 0.0-0.002$). Explosive dispersal is significantly concentrated in monoecious clades ($P = 0.0$). Wind pollination is significantly concentrated in clades with unisexual flowers ($P = 0.0-0.002$; Fig. 7). Hummingbird pollination is significantly concentrated in clades with hermaphroditic flowers ($P = 0.014-0.022$). Dioecy is not significantly concentrated in clades with animal-dispersed seeds ($P = 0.052-0.124$).

DISCUSSION

Our results show that successional stage and previous logging influence the relative abundance of tree species with different sexual systems and pollination modes (Figs. 1-3), but have relatively little or no effect on the frequency of these traits among species (Table 2). Our approach further reveals that all of the reproductive traits examined are highly phylogenetically structured. Thus, the distribution of reproductive traits within these tropical forest communities and observed associations among traits strongly reflect clade composition and phylogenetic conservatism. The species-level traits considered here are clearly not "independent" of their phylogenetic history. The 24 species with wind-dispersed seeds are clearly not a random subset of species that independently evolved wind dispersal (Figs. 5 and 6). Functional groups within these plant communities, at least with respect to these reproductive and growth-form traits, have a strong historical (phylogenetic) bias. Recognizing this bias (or legacy) enhances our understanding of geographic variation, effects of regional land-use, and evolutionary constraints on trait associations (Webb et al. 2002).

Distribution of reproductive traits among forest stands

Among species and individuals, animal dispersal, hermaphroditic flowers, and insect pollination predominate across all forest types and size classes. These results confirm those of other studies in lowland wet forests of Costa Rica and wet tropical forests in other Neotropical regions (Frankie et al. 1974, Gentry 1982, Bawa 1990, Ibarra-Manríquez and Oyama 1992, Kress and Beach 1994). Opler et al. (1980b) reported animal-dispersed fruits in 90% of trees and 91% of treelets/shrubs in the mature forest at La Selva. Surveys by Bawa et al. (1985b) reported that 65.5% of species were hermaphroditic (including 12 heterostylous species), 11.4% were monoecious, and 23.1% were dioecious. Within four different plots totaling 12.4 ha in old-growth forest at La Selva, 47% of the individual trees ≥ 10 cm dbh were hermaphroditic, 31.1% were monoecious, and 21.9% were dioecious (Lieberman and Lieberman 1994). For trees and treelets studied at La Selva by Bawa et al. (1985a), the highest frequency were pollinated by medium-sized to large bees (27.5% of species), followed by moths (15.9%), small diverse insects (15.8%), and small bees (14%). Overall, 90.3% of the species in their survey were insect pollinated. In a lowland dipterocarp forest in Lambir, Sarawak, Malaysia, Momose et al. (1998) found the largest number of species to be pollinated by social bees (32%), followed by beetle-pollinated species (20%). Plant species pollinated by animals that move long distances, specifically mammals, lepidopterans, and birds, are less frequent in Lambir than in La Selva (Momose et al. 1998).

Revealed within this general pattern are several key differences between forests with different land-use histories. For tree species, second-growth forests in this region differ from mature forests in their lower frequency of animal dispersal and higher frequency of explosive dispersal (Table 2). In terms of relative abundance, second-growth forests show a higher fraction of hermaphroditic species and a lower frequency of monoecious species (Fig. 1). Second-growth forests also show the highest relative abundance of insect-pollinated tree species (Fig. 2). Second-growth forests in this region are dominated by a relatively small number of tree species compared to old-growth and logged forests (Guariguata et al. 1997). Most of these dominant second-growth species are hermaphroditic and insect pollinated, and several are wind dispersed, e.g., *Vochysia ferruginea* (Vochysiaceae) and *Goethalsia meiantha* (Tiliaceae), or explosively dispersed, e.g., *Pentaclethra maculosa* (Fabaceae) and *Croton schiedeana* (Euphorbiaceae; Fig. 4). Although few data are available for comparison, a study in 30-year-old second-growth forest in Costa Rica shows that 70% of the tree species ≥ 10 cm dbh are animal dispersed, whereas the

majority of individuals in this size class (52%) are wind dispersed (Finegan and Delgado 2000).

Because of the trait conservatism inherent in this pool of 366 woody species, patterns of trait distribution across forest types are closely linked with patterns of floristic composition at the genus and family level. In second-growth stands, the four families with the largest number of common canopy and midstory tree species (Fabaceae, Annonaceae, Flacourtiaceae, and Tiliaceae) are all strictly hermaphroditic. In selectively logged stands, dioecious species in wind-pollinated Cecropiaceae and Moraceae reach high abundance. The relative abundance of canopy and subcanopy palms, all of which are monoecious, is considerably lower in second-growth forests (6–10%) than in old-growth or logged forests (13–19%; also see Lieberman and Lieberman 1994). These factors largely explain the high relative abundance of hermaphroditic species in second-growth forests and the higher relative abundance of monoecious and dioecious species in old-growth and logged forests (Fig. 1). The understory shrub layer is dominated by species in the Melastomataceae and Piperaceae, which are exclusively hermaphroditic.

A shift in our focus from the species level to the family level also provides an evolutionary context for geographic comparisons of functional groups in tropical forests. Dominant woody genera and families in wet tropical forests throughout Central America and South America appear to be drawn from the same pool (Gentry 1982, 1990, Pitman et al. 2001). The Fabaceae, Rubiaceae, Moraceae, Piperaceae, Lauraceae, and Arecaceae are particularly rich in dominant species in lowland wet Neotropical forests (Gentry 1990, Hartshorn and Hammel 1994, Pitman et al. 2001). The similar floristic structure among these wet forests explains broad similarities in the predominance of mammal and bird dispersal as well as the prevalence of woody species with small, inconspicuous flowers visited by a wide range of insect pollinators, as noted by Gentry (1982). Floristic differences among wet tropical forests in different continents can also explain variation in the incidence of reproductive traits, although few community-level studies are available for comparison. For example, levels of dioecy in rain forests of southern Nigeria (40% of the tree species and 38% of the trees) are considerably higher than in our study area and in the Neotropics overall (Jones 1955, Bawa and Opler 1975). The families Ebenaceae and Meliaceae dominate in the Nigerian forest and both families consist almost entirely of dioecious taxa (Bawa and Opler 1975).

Species that are common (>1% relative abundance) in second-growth and old-growth forest are also concentrated in particular families. In the present study, 20 species are common in both types of forest; among these are two canopy tree species, *Pentaclethra macroloba* (Fabaceae) and *Casearia arborea* (Flacourtiaceae), and two canopy palm species, *Euterpe pre-*

toria and *Socratea exorrhiza*. The remaining 16 species are all shrubs, concentrated in the Melastomataceae, Piperaceae, and Siparunaceae. Thus, it is likely that that shrub habitat association strongly influences the apparent phylogenetic conservatism of common species. In a study of successional habitats in Central Europe, Prach and Pysek (1999) also found that dominant species were strongly overrepresented in a small number of families (Poaceae, Asteraceae, Chenopodiaceae, and Rosaceae).

Floristic composition differs substantially between second-growth and old-growth forest (Guariguata et al. 1997). In this study, we found 144 tree species and 40 shrub species in old growth and 111 tree species and 53 shrub species in second growth. Tree species richness in old-growth stands is higher than in second-growth stands (Guariguata et al. 1997), but species richness of saplings and shrubs is quite similar between the two forest types (Chazdon et al. 1998). In many cases, “overabundance” is due to the presence of a species in one forest type and its absence in another; 88 of the tree and shrub species that are overabundant in old growth are absent from second growth and 69 of the tree and shrub species that are overabundant in second growth are absent from old growth. The finding that species overabundant in second growth are randomly distributed throughout the phylogeny (Table 3) suggests that the ability to establish and survive in young, successional forests is not strongly associated with phylogenetically conserved traits. On the other hand, species that are more abundant in old growth than second growth are clustered phylogenetically ($P = 0.05$; Table 3). For trees and shrubs that are common in old-growth forest, there is a significantly lower than expected mean phylogenetic distance (Table 3). Thus, phylogenetically conserved traits appear to be more important for woody plant distribution in mature or late-successional tropical forests than in younger successional forests. One such trait may be large seed size, as we will discuss (Hammond and Brown 1995).

Phylogenetic conservatism of traits within the supertree

Our study revealed that all reproductive traits and woody growth form traits are significantly clustered within certain clades rather than exhibiting a random distribution across the phylogeny. Thus, the molecular-based phylogenetic hypothesis used here supports the principle of classical plant taxonomy that reproductive characters are highly conserved at the family level. Sexual systems and canopy tree and shrub growth form are probably derived traits that are conserved at deep levels within the supertree phylogeny. Other trait states exhibit significant phylogenetic clustering at the tips of the phylogenetic branches, but no overall concentration in one major branch of the phylogeny (Table 3). This pattern could arise if the trait states were probably ancestral (e.g., animal dispersal and insect polli-

nation), or because they have evolved multiple times, more recently (e.g., wind dispersal, explosive dispersal, and hummingbird pollination).

As is now well recognized, the sampling of taxa for which a phylogeny is reconstructed strongly influences the inferences about patterns of character evolution (Felsenstein 1985, Maddison 1990, Ackerly 2000). Even a full phylogeny of all extant taxa can mislead ancestral character reconstruction, if extinction was not random with respect to different character traits. Our sample of taxa is strongly biased (woody, Neotropical representatives from the whole angiosperm clade); hence, we cannot make statements about "global" patterns of trait conservatism and correlated evolution. However, it is nonetheless valid to describe phylogenetic patterns within this particular subset of all taxa. Indeed, the "local" distributions of traits in this subset are exactly the ones that are relevant to the questions of community assembly and composition addressed in this paper, because this set of species forms our best estimate of the available pool of species present in the region.

Phylogenetic conservatism and trait associations

Our results reveal many statistically significant, species-level associations among pollination mode, sexual system, dispersal mode, and woody growth form (Fig. 5). As noted by Kress and Beach (1994), wind dispersal is more frequent in canopy trees and less frequent than expected in understory shrubs (Fig. 5). Frankie et al. (1974) found that 83% of wind-dispersed trees in their survey of wet and dry tropical forests are canopy species. Howe and Smallwood (1982) also noted that most wind-dispersed plants of temperate and tropical forests are canopy trees or lianas. In our study, dioecy is more frequent than expected in canopy trees and less frequent than expected in understory shrubs, which are strongly hermaphroditic (Fig. 5). Bullock (1985) and Flores and Schemske (1984) noted similar trends in the flora of a Mexican dry forest and the flora of Puerto Rico and the Virgin Islands, respectively.

Many of these species-level ecological associations can be explained by phylogenetic correlations. For example, the association between explosive dispersal and monoecy reflects a significant concentration of taxa with explosive dispersal within monoecious clades. The significant association between the shrub growth form and hermaphroditic flowers reflects the predominance of three families, Melastomataceae, Piperaceae, and Rubiaceae, which are composed almost exclusively of hermaphroditic species in the regional flora (Appendix). The higher than expected frequency of dioecy among wind-pollinated species can be explained by the finding that wind pollination (primarily in the families Moraceae and Cecropiaceae here) is concentrated in clades with unisexual flowers (Fig. 7). Several other studies have also identified a significant association between wind pollination and unisexual flowers (Kress

and Beach 1984, Flores and Schemske 1984, Fox 1985, Bullock 1994, Renner and Ricklefs 1995, Sakai et al. 1995, Anderson et al. 2001). If dioecy or monoecy evolved first, followed by wind pollination, the concentrated changes test indicates that evolution of wind pollination occurred more readily in unisexual clades than in hermaphroditic clades. We do not really know, however, which trait evolved first (for more discussion of this topic, see Charlesworth [1993]).

Although all of the 63 dioecious species in our data set have animal-dispersed seeds, we did not find a significant association between dioecy and animal dispersal, nor did we find evidence for correlated evolution, assuming that animal dispersal evolved first (Givnish 1980, Donoghue 1989). Bawa (1980) found a significant association between dioecy and animal dispersal for 317 species at La Selva, and Flores and Schemske (1984) found these traits to be significantly associated for the entire flora of Puerto Rico and the Virgin Islands (2037 species). Dioecy has also been found to be associated with the woody habit (Bawa 1980, Givnish 1980, Flores and Schemske 1984, Fox 1985, Muenchow 1987, Renner and Ricklefs 1995). Our result is not too surprising, therefore, considering that woody species predominate in tropical plant families.

The species-level association between hummingbird pollination and hermaphroditic flowers also represents a correlated evolutionary change. This association extends to all hummingbird-pollinated species at La Selva, including herbaceous species (Kress and Beach 1994), and appears to be a general phenomenon throughout the New World (R. K. Colwell, *personal communication*). Renner and Ricklefs (1995) found a negative association of unisexual flowers with bird pollination and with vertebrate pollination in general. Among 750 genera of bird- and bat-pollinated angiosperm species, only two were found to contain dioecious taxa (Renner and Ricklefs 1995). The near absence of bird and bat pollination among dioecious taxa may be linked to floral adaptations required for pollination by large-bodied vertebrates, such as the production of large quantities of nectar and pollen (Renner and Ricklefs 1995).

Reproductive traits in relation to forest regeneration and land-use change

Our results highlight the importance of animal vectors for seeds and pollen in wet Neotropical forests (Baker 1970, Terborgh 1986, Bawa 1990). The maintenance of species richness and genetic diversity of populations in regenerating forests, logged diversity, and fragmented forests, as well as in intact areas of mature forest, critically depends on populations of insect and vertebrates required for pollination and seed dispersal (Gorchov et al. 1993). In a study of seed arrival in a Neotropical pasture in northeastern Costa Rica, Slocum and Horvitz (2000) found that animal-dispersed seeds

were far more abundant than wind- or explosively dispersed seeds. Dispersal modes are often associated with different seed sizes (Hammond and Brown 1995, Westoby et al. 1997, ter Steege and Hammond 2001), seedling morphology (Ibarra-Manríquez et al. 2001), and seedling survival in shade (Leishman and Westoby 1994, Metcalfe and Grubb 1995, Paz et al. 1999). Opler et al. (1977) found that species with wind-dispersed seeds composed nearly 100% of all plants that established during the first three months of succession following clear-cutting at La Selva. Over time, this fraction decreased, while the percentage of fleshy-fruited species increased asymptotically. Within three years, the frequency of animal-dispersed species reached 80%, similar to values in mature forest (Frankie et al. 1974). In a Mexican rain forest, non-animal dispersal (wind, explosive, and gravity) was predominantly associated with smaller seeds, epigeal seedlings, and leafy cotyledons, whereas animal dispersal was predominantly associated with larger seed mass, hypogeal germination, and reserve cotyledons (Ibarra-Manríquez et al. 2001). The increased relative abundance of animal-dispersed species and the decreased relative abundance of wind-dispersed species in seedling and sapling size classes compared to trees therefore may reflect the survival advantage of animal-dispersed seeds in the shaded understory of these forests (Fig. 3).

Large fractions of rain forest trees, shrubs, and lianas require animal vectors for pollination, and many species require specialized pollinators (Bawa et al. 1985a, Renner and Feil 1993, Kress and Beach 1994). Mammal-pollinated species are rare overall, but even more rare in second growth (despite our simplifying bias in identifying bat- and moth-pollinated species as mammal-pollinated). In a study of woody vegetation in seven Central American dry forest fragments, Gillespie (1999) found that the proportion of dioecious species was positively correlated with reserve size and forest cover, and the proportion of mammal-dispersed plants was positively correlated with forest cover. Meave and Kellman (1994) also found that dioecious and mammal-dispersed plants are rare in small, natural fragments of riparian tropical forest. Land-use changes, particularly those that result in loss of forest cover, decreased size of fragments, and increased isolation of forest fragments, are likely to have significant impacts on the distribution of many tropical forest species (Corlett 2001). Dioecious species may be more vulnerable than monoecious and hermaphroditic species, however. Heilbut et al. (2001) propose that the maintenance of dioecy among hermaphroditic competitors requires a substantial increase in relative fitness and/or a larger dispersal advantage of dioecious seeds. In old-growth forest at La Selva, dioecious tree species have a higher median density than monoecious or hermaphroditic species (Lieberman and Lieberman 1994), but this was not found to be the case in upper Amazonia (Pitman et al. 2001).

CONCLUSION

The spectrum of reproductive traits observed in today's tropics reflects two legacies: the legacy of phylogeny and the legacy of forest disturbance. Both legacies strongly impact the distribution of the reproductive traits of woody species. We have shown here that many reproductive traits are highly structured phylogenetically within forest communities of northeastern Costa Rica. Thus, knowledge of forest floristic composition, particularly at the genus and family level, offers critical insight into the likely frequency of sexual systems, pollination modes, and dispersal syndromes. Geographic similarities in dominant genera and families are likely to be associated with a similar ecological spectrum of reproductive traits. Changing patterns of species relative abundance associated with forest succession and disturbance produce a second legacy that is particularly evident in the current generation of tree species. Woody saplings and seedlings in second-growth forests are similar in their spectrum of reproductive traits to saplings and seedlings of old-growth forests, offering the potential for long-term recovery of species and reproductive traits characteristic of mature forests in this region.

ACKNOWLEDGMENTS

We dedicate this paper to the memory of Herbert G. Baker, whose lifetime of research focused on ecological and evolutionary aspects of the reproductive biology of plants. We thank Manuel Guariguata, Juan Manuel Dupuy, Carolina Gonzales Dupuy, Marcos Molina, Jeanette Paniagua, and Carlos Castillo for their work in field data collection and database management. The Organization for Tropical Studies and the staff of La Selva Biological station provided essential logistic and scientific support. Juan Nuñez Farfan, Robert Dunn, and Robert Colwell made useful comments on the manuscript. We thank Paul Lewis for his advice on tests of phylogenetic correlation. This research was supported by NSF grant DEB-9208931, a grant from the Andrew W. Mellon Foundation, and a Fulbright Senior Scholar Award to R. Chazdon. C. Webb was supported by the Donnelley Environmental Fellowship of the Yale Institute for Biospheric Studies. We thank Lynda Delph, George Weiblen, and one anonymous reviewer for their constructive comments on an earlier version of this manuscript.

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APPENDIX

A table of reproductive traits for 366 species in 10 wet tropical forests is available in ESA's Electronic Data Archive: *Ecological Archives* M073-004-A1.