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ABSTRACT

The importance of lianas in tropical forest processes and diversity has recently been recognized, leading to an increase in studies on liana biomass, abundance, and physiology. In this study, liana species richness, grouped by family, and morphological characters of lianas are evaluated as a function of successional forest age in two neotropical forests: a dry seasonal forest and a moist seasonal forest in Costa Rica and Panama, respectively. Diversity, and morphology are compared between the dry (Costa Rica) and seasonally moister (Panama) forests. Vegetative characters examined include climbing mechanism, leaf organization, leaf margin and petiole length. Reproductive characters include diaspore type, diaspore and seed size, and seeds per fruit. Bignoniaceae, Sapindaceae and Fabaceae were the most species rich families at each site. Celastraceae was more species rich in the moist forest while Malpighiaceae was more species rich in the dry forest. The proportion of tendrilling lianas was similar in the dry (50%) and moist (48%) forest, and there were no significant changes of dominant climbing mechanism among species across forest age. The other vegetative characters did not vary significantly across forest age at either site and were not different between sites. Wind dispersal was more dominant for species in the dry forest (76%) than the moist forest (60%). The relative number of animal dispersed species increased with successional forest age in Panama, perhaps due to dispersers' response to changes in forest stand structure. Seed size did not vary significantly across forest age or between sites, most likely due to canopy gaps maintaining diversity in older forests. This study suggests that family level species richness and the morphology of liana communities may not respond strongly to forest age or to sites with variable seasonality in the neotropics, however evaluation using abundance data is in order.

INTRODUCTION

Lianas are woody climbing plants that play an important role in tropical forest dynamics but have often been neglected relative to other vascular plant habits (Gentry 1991a; Schnitzer & Bongers 2002; Schnitzer 2005). Lianas sequester carbon and contribute to overall forest productivity (Domingues et al. 2007), arrest gap regeneration (Schnitzer et al. 2000), compete with tree hosts (Malizia & Grau 2006; Toledo-Aceves & Swaine 2008; Llorens & Leishman 2008), and provide food and access between trees to arboreal animals (Emmons & Gentry 1983). While lianas are present and important in temperate forests, they are more abundant and diverse in tropical forests (Gentry 1991a; Schnitzer & Bongers 2002; Quigley 2003) where they can contribute 10-40% of the leaf area (Hegarty & Caballé 1991) and up to 25% of the woody stem abundance (Gentry 1991a).

The abundance of lianas is on the rise in neotropical forests (Phillips & Gentry 1994; Phillips et al. 2000; Wright et al. 2004, 2007) mainly due to human impacts and possibly increased global CO_2 levels (Mohan et al. 2006), increased temperatures (Wright 2007), and increased hunting (Wright et al. 2007). Lianas are often light-demanding and therefore have affinities for disturbed areas and secondary forests (Hegarty & Caballe, 1991; Laurance et al., 2001; Schnitzer & Carson 2001). Therefore, given their increasing dominance as a consequence of human disturbance, it is important to understand how lianas will respond to future changes in neotropical forests.

While studies of neotropical forest succession are common, until recently, few have included or focused on lianas (see DeWalt et al. 2000; Heinrich & Hurka 2004; Kalacska 2004; Madeira et al. 2008). DeWalt et al. (2000) examined liana diversity, density, and climbing mechanism across a chronosequence in a lowland tropical moist forest in Panama. Heinrich & Hurka (2004) examined diversity of the whole plant community across a chronosequence in a tropical dry forest in Guanacaste, Costa Rica.

Looking to climbing mechanism as an explanation for liana distribution patterns, as seen in DeWalt et al. (2000), is not a completely new idea. Since lianas are dependent on support structures, the means by which they climb has been of interest since observations made by Darwin (1867). Lianas climb via twining stems or branches, tendrils, scrambling (often with hooks/thorns), adventitious roots, or a combination of

these adaptations. This unique morphology and habit of lianas has been used to infer explanations for their distribution across forest ages (Gentry 1991a; Schnitzer 2005). A study by Putz (1984) suggests that twining lianas use larger diameter supports than tendril climbers, which supports initial observations made by Darwin (1867). DeWalt et al. (2000) found that the relative abundance of twining lianas increased with forest age, further supporting this idea because hosts of a larger diameter were more abundant in older stands (DeWalt et al. 2003).

Mean annual precipitation may also affect the distribution of certain climbing types. In the old world tropics of India, tendrillate lianas were more abundant in dry evergreen forests than wet evergreen forests (Parthasarathy et al. 2004), although little is known about the distribution of climbing mechanism in various forest types of the neotropics.

Diaspore, or the unit of dispersal for a plant (seed, fruit, or some segment of a fruit), is also important in understanding plant distribution patterns across successional forest ages. Opler (1980) suggested that animal dispersed seeds (zoochores) increase with forest age in successional forests, while wind dispersed seeds/fruits (anemochory) are more important in younger forests. Wind dispersal is more common among lianas relative to trees and shrubs (Gentry 1982; Howe & Smallwood 1982). For lianas, the importance of animal and wind dispersal (taking into account relative density and dominance) showed no trend across successional stand ages in Panama (DeWalt et al. 2003).

Precipitation may affect dominant diaspore type as well. Studies suggest that lianas of dry forests are predominantly dispersed by wind, while in wet forests animal dispersal is more important (Gentry 1982). However, Solorzano et al. (2002) found that abiotic dispersal (including wind) dominated in liana communities of both wet and dry tropical forests, with no difference in the importance of wind dispersal between the sites. Furthermore, the frequency of dispersal syndromes shows no significant trend across neotropical forests of increasing mean annual rainfall (Solorzano et al., 2002).

Vegetative characters examined in this study (leaf organization, leaf margin, petiole length) are expected to respond to environmental variables and forest stand structure. It has been proposed that compound leaves funtion as 'throw away branches,'

adapted to tolerate seasonal drought or rapid vertical growth (Givnish 1978), and are therefore assumed to be more common in relatively drier communities, including seasonally dry forests. Modern and paleoclimatic data suggests that species with serrate leaf margins are/were relatively more important in cooler areas (Wolfe 1979, 1993; Wilf 1997). Finally, light foraging ability may be dependent on petiole length. Plant species increase their petiole length in response to shading, which has been called 'shade avoidance' (Smith 1994; Smith & Whitelam 1997). Ballaré et al. (1997) suggests that the fitness of individual plants in high shade may be dependent on their light foraging abilities. If so, the changing light environment across a successional chronosequence could lead to changing petiole length among liana species.

Fruit characters (seed size and seeds per fruit) have been hypothesized to change with successional forest age. Among animal dispersed species, large single-seeded fruits should increase with forest age while small many-seeded fruits should decrease (McKey 1975). Furthermore, small gravity dispersed seeds are more important in early successional forests (Opler 1980). Little is known about the response of liana seed characteristics to mean annual rainfall.

In this study I examine two data sets of lianas from successional gradients in two seasonal Central American forests; one, a tropical dry forest, and the other, a tropical moist forest. Trends in diversity and morphological characters (climbing mechanism, leaf organization, leaf margin, petiole length, diaspore type, diaspore size, seed size, seeds per diaspore) are examined on a presence/absence basis across forest age and between the two sites. Questions addressed are:

1) Does liana species richness and/or morphology change with forest age at either site?
2) Does liana species richness and/or morphology differ between a moist and dry neotropical forest?
3) What are the implications of the observed trends for forest management and conservation in the neotropics?

Using the current knowledge on liana biology, a number of predictions can be made. The proportions of twining species, species with serrate leaf margins, long petioles, animal dispersed seeds, large seeds, and few-seeded fruits, are expected to

increase with stand age as a function of changes in stand structure and environmental variables, namely light availability. On the other hand, the proportions of hooking species, scrambling species, wind dispersed species, and many-seeded fruits may decrease with stand age due to changes in stand structure that may favor other traits.

Some characters may vary between the dry and moist site. Wind dispersed species are expected to be more important at Guanacaste than BCNM due to its drier climate. Moreover, tendrilling species should comprise a higher percentage of the liana flora at Guanacaste as a function of the presence of smaller support structures. Phylogenetic constraint on some characters is expected to play a role in their proportional distributions across stand ages and between sites. For example, if a family has only one type of diaspore, and that family is equally dominant in all stand ages or at each site, little variation is expected in that diaspore type.

METHODS

STUDY SITES

Barro Colorado Nature Monument (BCNM), Panama: BCNM is comprised of Barro Colorado Island (BCI) and adjacent mainland peninsulas in central Panama. Mean annual precipitation at BCNM is $\geq$2600mm, with a pronounced wet season between May and December (Windsor 1990). Mean annual temperature is 27°C, ranging from an average high (28°C) in the early wet season to an average low (26.7°C) in the late wet season (Windsor 1990). Many canopy trees lose their leaves during the dry season. BCNM is classified as a tropical moist forest (Holdridge 1967).

Modern human alteration of forests at BCNM dates back to the mid-1800s with the establishment of roads and railways. Canal construction in the early 1900s led to cattle grazing and fruit and vegetable cultivation in the area. Banana plantations dominated the land from the 1920s to the late 1930s. BCI was declared a preserve in 1923 but slash and burn agriculture was prevalent on the peninsulas until BCNM was established in 1979 (Denslow & Guzman, 2000). I obtained a liana species list of Barro Colorado Nature Monument (BCNM) from DeWalt et al. (2000). Saara DeWalt also provided me with forest age-specific liana lists.

Santa Rosa, Guanacaste, Costa Rica: Sector Santa Rosa is in Northeastern Costa Rica. The study site will be referred to as Guanacaste. Mean annual precipitation at Guanacaste is 1503mm but is highly variable from year to year (Janzen 1993). There is distinct seasonality with a dry season between December and April. During the dry season, monthly average maximum temperature ranges from 31°C to 36°C, while in the wet season it ranges from 27°C to 33°C (Heinrich & Hurka, 2004). The study site at Guanacaste is considered a tropical dry forest (Holdridge, 1976).

Human impact in Sector Santa Rosa, Guanacaste, dates to the establishment of the Hacienda Santa Rosa in the late 1500s, which was divided amongst many owners for various agricultural purposes (Heinrich & Hurka 2004). At the time of data collection in the field, the study site was a patchwork of abandoned farms and ranches left fallow and given protected status (Heinrich & Hurka, 2004). I obtained liana species lists from the Sector Santa Rosa of the Area de Conservación Guanacaste in northwestern Costa Rica from Heinrich and Hurka (2004).

CHOICE OF STUDY SITES

BCNM and Guancaste are about 400 miles apart. The sites were chosen based on available reports of species diversity across a successional gradient with the inclusion of (Heinrich & Hurka 2004) or focus on (DeWalt et al. 2000) lianas, and identification of lianas to the species level. Climatic differences between sites influenced study site choice. While Guanacaste and BCNM both have a pronounced dry season, they vary in total mean annual rainfall and are classified differently according to Holdridge's Life Zone concept. BCNM is a tropical wet forest, while Guanacaste is a tropical dry forest. Liana diversity and morphology can therefore be compared on the basis of variable precipitation between sites.

DATA COLLECTION IN THE FIELD

BCNM: DeWalt et al. (2000) censused lianas (≥ 0.5cm diameter; ≥1.3m height) in secondary forest stands of approximately 20, 40, 70, and 100 years old. Old growth stands, suspected to be older than 500 years, were also censused. Their study sampled two stands per forest age (10 stands total). In 9 of 10 stands, two parallel 160m transects

at least 20m apart were established inside the forest edge. One 20 year-old stand only allowed for one transect. Lianas were censused in eight, 5m x 10m quadrats along each transect. Lianas were identified at the Smithsonian Tropical Research Institute Herbarium. Voucher specimens had been disposed of by the time of analysis for the current study.

Guanacaste: Heinrich and Hurka (2004) censused lianas of all size classes in successional stages of 0, 1, 3, 5, 10, 15, 20, 30, and 50 years after human disturbance. Plots of 20m x 50m were established in two sites of each successional age. Lianas were identified to species, and vouchers are deposited at the Santa Rosa, Costa Rica and University of Osnabrueck (Germany) herbaria.

DATA COLLECTION FROM HERBARIA AND LITERATURE

I updated species names from original data sets using TROPICOS database of the Missouri Botanical Gardens and personal communication with Nancy Henshold at The Field Museum of Natural History. For taxonomic name changes in the family Malpighiaceae, I consulted with specialist William R. Anderson.

I collected data on morphological characteristics and dispersal syndromes of species primarily from herbarium specimens at The University of Michigan Herbarium (Ann Arbor, MI) and The Field Museum of Natural History (Chicago, IL). Characters included: climbing mechanism, petiole length, leaf margin, leaf organization, diaspore type, diaspore size, seed size, and seeds per fruit. I chose these characters based on suspected trends across forest age and each character's availability on herbarium specimens. In total, I collected data from 434 herbarium specimens and 129 species (Appendices 1 & 2).

DeWalt et al. (2000) previously categorized climbing mechanism for each species as stem twiner, branch twiner, and tendril climber based on field observation and literature. For this study, climbing type was reevaluated using a modified set of character states based generally on Hegarty (1991). My character states included twining, tendrilling, hooking, and scrambling. Twining species included both apical twining species, those twining with the main stem, and branch twining, those that twine with leaf-bearing branches. All species with modified, determinant, helical structures (shoots,

leaves, leaflets), specialized for climbing were considered tendrilling. Hooking species included those species that climb with recurved spines or stipules. Species with simple spines were not necessarily classified as hooking species if they utilized twining or tendrilling as the primary means of climbing. Finally, species with no apparent climbing mechanism listed above were categorized as scrambling. No root climbers were present in either flora so this climbing mechanism was not included.

In addition to herbarium observations, I scored diaspore character states using Croat (1977) and the Smithsonian Tropical Research Institute's Website (http://www.stri.org/). I categorized diaspore type based on five different character states (Table 1). I based diaspore character states roughly on Solorzano et al. (2002), with the addition of Hydrochory.

Table 1: Liana diaspore characters based on following descriptions

Diaspore Category	Character State Description
Pterochore	wind dispersed with papery wing
Pogonochore	wind dispersed with plume
Zoochore	animal dispersed with fleshy fruit and/or arillate seed
Barochore	self dispersed with heavy seed falling near parent
Hydrochore	water dispersed

I measured diaspore (length in cm) and seed size (length in mm) from at least one herbarium specimen with mature fruits. For most species I measured three diaspores and three seeds from three different specimens of that species. These measurements were averaged to account for intraspecific variation in diaspore and seed size. I categorized diaspore and seed sizes into bins of increasing size. Petiole measurement (cm) was made and categorized similarly. Petioles were measured from point of insertion on the stem (node) to the base of the lamina for simple leaves, and from node to base of first petiolule for compound leaves. For size class bins of measured characters, see Table 2.

I collected data on number of seeds per fruit from herbaria, from Croat (1977), and from species descriptions in the literature. I classified leaf(let) margin as entire or serrate, and leaf arrangement as simple or compound based on herbarium observation.

Table 2: Bins for character states measured from herbarium specimens

FEATURE					
BINS		Diaspore (cm)	Seed (mm)	Seeds/ Fruit	Petiole (cm)
	0	0-1	0-5	1	0-2
	1	1-2	5-10	2-5	2-4
	2	2-3	10-15	6-10	4-6
	3	3-4	15-20	11-20	6-8
	4	4-5	>20	>20	8-10
	5	5-6	--	--	>10
	6	6-7	--	--	--

DeWalt et al. (2000) and Heinrich and Hurka (2004) identified some liana species only to the generic level. In order to use these species in analyses, I examined at least six determined species of a given genus at herbaria. If climbing mechanism, diaspore, seeds per fruit, leaf margin, or leaf organization was consistent across all species examined, an undetermined species within that genus was assigned those values. No seed size, diaspore size, or petiole length measurements were made for these undetermined species.

ANALYSIS

To determine the correlations between morphological characters and forest age, I regressed the proportion of liana species with each character state on the log transformed stand age using SPSS 16.0. The number of species in dominant families was also regressed on stand age. Old growth forests at BCNM were assumed to be 500 years old (DeWalt et al., 2000). While regression analyses were performed on SPSS 16.0, all graphs were created using Microsoft Excel 2008. Stand ages 0-5 years at Guanacaste were omitted from all regression analyses due to low liana diversity, and resulting skewed character state proportions.

The average length for measured characters (petiole length, diaspore size, seed size) was calculated for the whole liana flora at each site. Averages were then compared between sites using an independent-samples T-test. For categorical data (climbing mechanism, leaf margin, leaf organization, diaspore, and bin for seeds per fruit) a chi-

square test for homogeneity was run to determine if the distributions of character states differed between sites. These analyses allowed for an examination of differences in liana morphology between the tropical dry and tropical moist forest.

RESULTS

LIANA DIVERSITY

Including all stand ages, 90 liana species were recorded at BCNM while at Guanacaste 50 species were found. For a complete list of liana species with categorization of morphological characters, see Appendices 1 and 2. Species diversity was distributed similarly among plant families at BCNM and Guanacaste. Four families comprised 59% and 62% of liana diversity at BCNM and Guanacaste, respectively (Fig. 1). Bignoniaceae was the most diverse family at both sites and Sapindaceae and Fabaceae were among the top four most diverse families at both sites. Malpighiaceae was important at Guanacaste (2rd) but less so at BCNM (5th, equal with Dilleniaceae). Celastraceae was more important at BCNM (4th) than at Guanacaste (1 sp.).

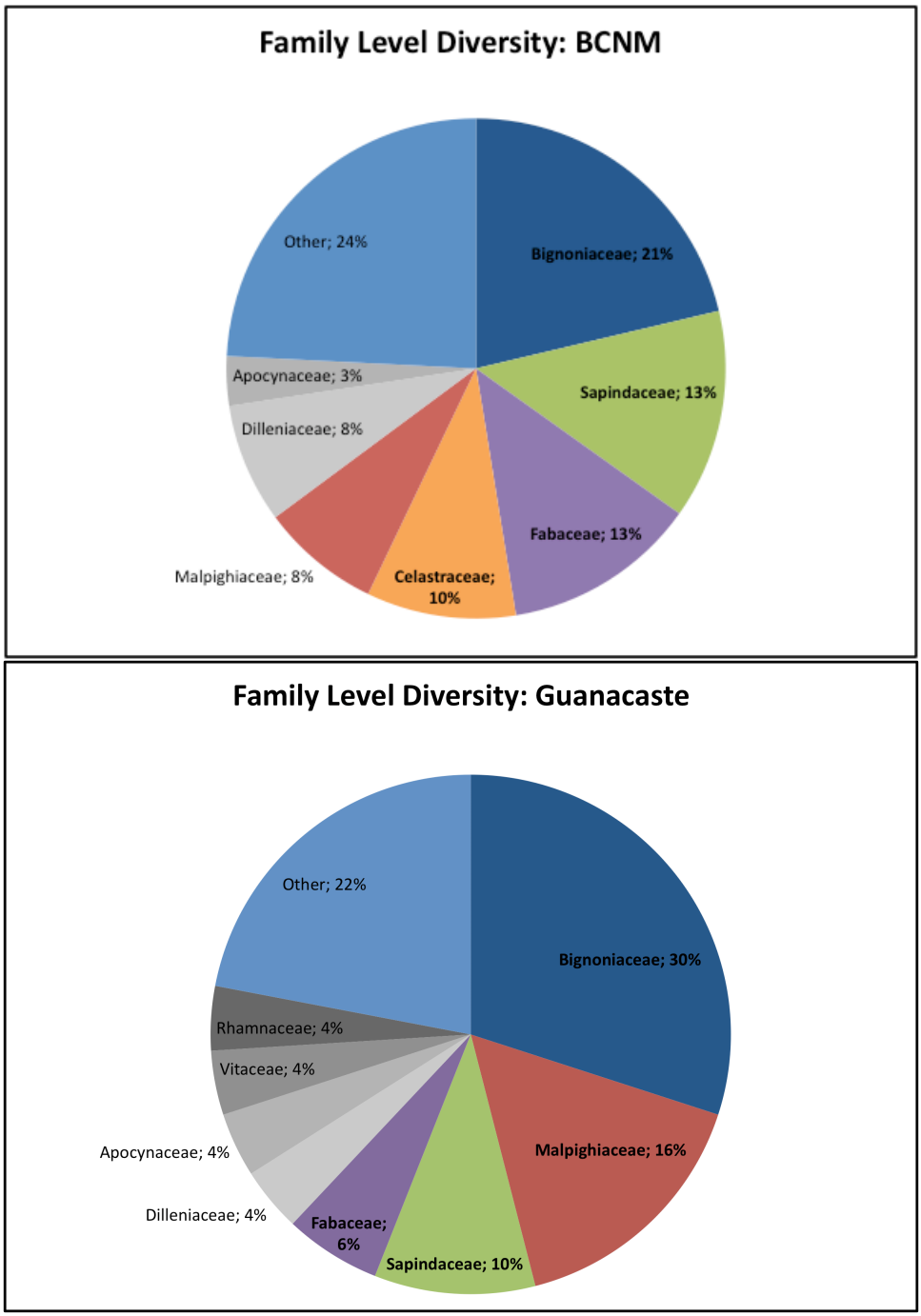

Figure 1: Most species rich families. Top four families in bold type. All forest ages included for BCNM and Guanacaste.

At BCNM, liana species richness was highest in 40 year-old stands with 49 species and lowest in 100 year-old stands with 31 species (DeWalt et al. 2000). Sixteen species were ubiquitous across all forest ages. Ubiquity was defined as a species' presence in all stand ages. If a species was recorded in all ages except 70, it was

considered ubiquitous. These species were probably present in 70-year old stands but not accounted for in the sample quadrats. Four of seven Dilleniaceae species at BCNM were ubiquitous. Twenty-two species were restricted to young forest stands (≤40 years) while 12 were restricted to old forests (≥70 years). All Apocynaceae (3 spp.) recorded at BCNM were restricted to young sites. Only one Euphorbiaceae, *Omphalea diandra*, was recorded, and it was restricted to one old growth site. Of the dominant families (Fig. 1), only Fabaceae species diversity showed a significant decreasing trend across forest age (Fig. 2).

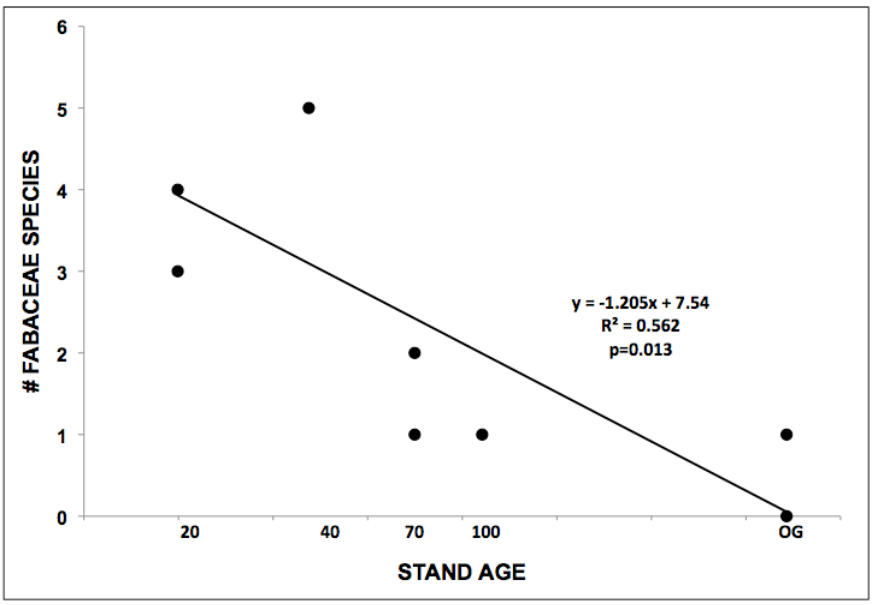

Figure 2: Fabaceae species richness decreases with increasing forest age at BCNM. Both sampled sites in 40-year old stands and both sites in 100-year old stands recorded the same number of species so only one point is depicted on the graph for these ages.

Fifty liana species were recorded at Guanacaste. Species richness was highest in 15-year old stands with 30 species, and lowest in one-year old stands with only two species. Across stand ages 15-50 years, eight species were ubiquitous. Of these eight species, three were in the family Sapindaceae. No species were ubiquitous across all ages. None of the 4 dominant families (Fig. 1) showed significant trends in species richness across stand age (data not shown).

Guanacaste and BCNM shared 14 species. Of the shared species, seven were in the family Bignoniaceae and three were in Malpighiaceae. *Serjania mexicana* (Sapindaceae) was ubiquitous across all ages at BCNM and from stand ages 10-50 at

Guanacaste. At Guanacaste there were 33 species that were not recorded at BCNM. The number of shared species between sites may be skewed due to undetermined species. For example, 10 Bignoniaceae were undetermined at BCNM, and may in fact be shared species with Guanacaste.

MORPHOLOGICAL CHARACTERS

Climbing Mechanism

Tendrilling was the most common climbing strategy at BCNM (48.2%) followed by twining (40%). Hooking (10.6%) and scrambling (0. 1%) were uncommon. At Guanacaste, 50% of the species were tendrilling, also followed by twining (38%). Scrambling (10%) and hooking (2%) were less important. The proportional distributions of observed climbing mechanisms did not differ between site (Tab. 3)

At BCNM the proportion of hooking climbers decreased significantly across stand age (R^2=0.291, B=-0.02±0.011 p=0.031). Proportions of all other climbing types (twining, tendriling, scrambling) showed no correlation with stand age (data not shown). At Guanacaste the proportion of twining lianas appeared to increase with forest age (Fig. 3), however the relationship was insignificant. Conversely, the proportion of tendrilling lianas showed an insignificant decreasing trend with forest age (Fig. 3).

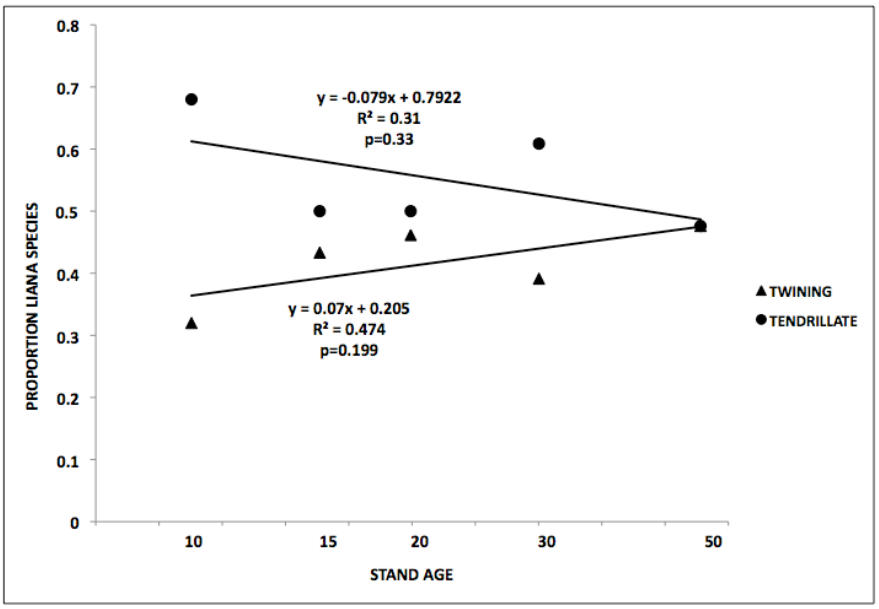

Figure 3: Proportion of twining species increase, while proportion of tendrilling species decrease across stand age at Guanacaste. Relationships are not significant.

Leaf organization, leaf(let) margin and petiole length

Leaf organization (proportion simple vs. compound), leaf margin (proportion entire vs. serrate) and petiole length did not change significantly across stand age at BCNM or at Guanacaste (data not shown). There was no significant difference in leaf organization, leaf(let) margin, or petiole length between sites (Tab. 3).

Diaspore Type

Pterochores dominated at BCNM with 55.8% of the liana species dispersing their seed (or fruit) with a wing. Zoochores (34.9%) were second most important followed by barochores (4.7%) and pogonochores (3.4%). One hydrochore (1.2%) was recorded. Lianas with pterochores (66%) were more dominant at Guanacaste than at BCNM. Pterochores were followed by sarcochores (20%), pogonochores (8%), and barochores (4%) at Guanacaste. One hydrochore (2%) was recorded. Proportional distribution of diaspore types did not differ between sites (Tab.3).

Dominant diaspore type was not predictable using stand age at BCNM. Removal of Old Growth stands from the linear regression analysis, however, produces a positive, significant correlation between proportion of lianas with sarcochores and age of forest (Fig. 4). Diaspore type was not correlated with stand age at Guanacaste (data not shown).

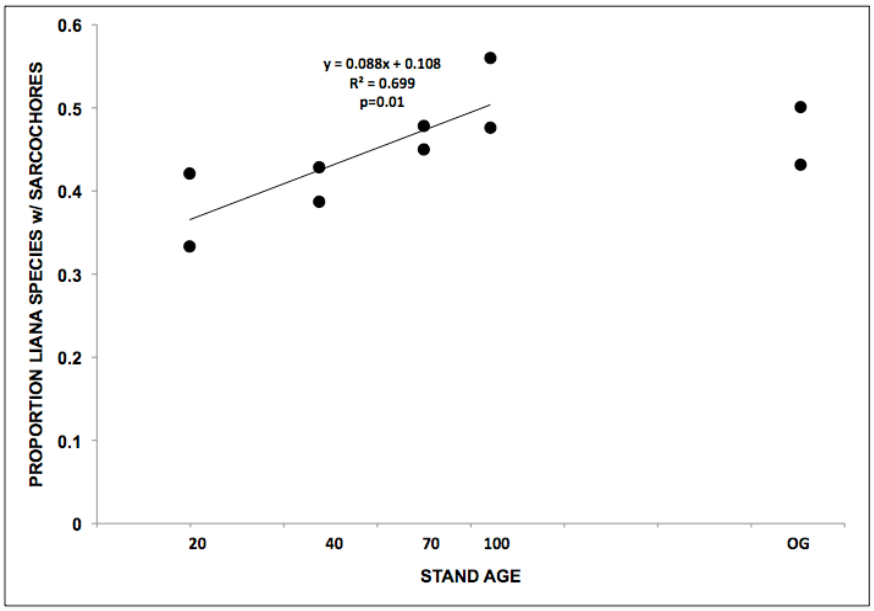

Figure 4: Proportion of species with animal dispersal across log transformed stand age at BCNM. Regression analysis is presented only across successional stand age; old growth age is removed from the analysis. Proportion sarcochorous species increases across successional stand age.

Diaspore and seed size

Diaspore size did not show a significant linear relationship with forest age at BCNM or Guanacaste. The proportion of liana species with large seeds (≥15 mm) was correlated with increasing forest age at Guanacaste, but the relationship was not significant (Fig. 5). Seed size showed no correlation with forest age at BCNM.

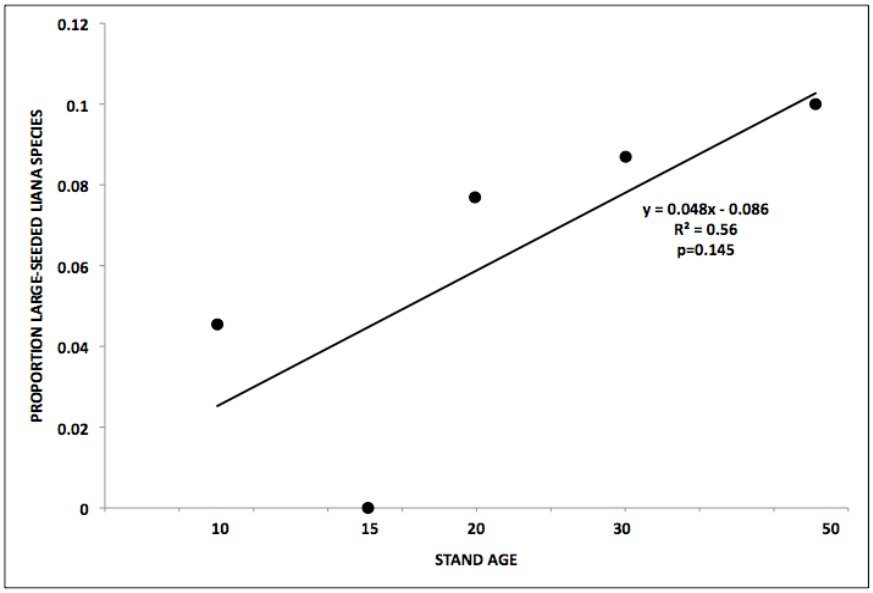

Figure 5: Proportion of lianas with large seeds (≥15mm; class 5 & 6) increases with log transformed stand age at Guanacaste.

Mean seed size of the whole liana flora at BCNM was 11.3mm (N=65, SD=9.3) and was 8.5mm (N=48, SD=6.3) for the liana species at Guanacaste, but these means were not significantly different (Tab. 3). Mean diaspore size at BCNM was 3.1cm (N=65, SD=2.4) and at Guanacaste mean diaspore size was 2.7cm (N=48, SD=1.8), and the difference was statistically significant at 95% confidence level(Tab. 3, p=0.029).

The proportion of lianas with many seeded (>20) fruits showed an insignificant decrease across stand age at both BCNM (R^2=0.11, B= -0.018±0.018, p=0.35) and Guanacaste (R^2=0.329, B= -0.072±0.06, p=0.312). The proportion of species with many seeded fruits (>20) was 25% at BCNM and 36% at Guanacaste.

Table 3: Proportion of categorical character states (climbing mechanism, diaspore type, many seeded fruits, leaf organization, leaf margin), and averages of measured character states (petiole length, diaspore size, seed size) for BCNM and Guanacaste. Significance for T-tests (marked by +) and Chi-square test for homogeneity (marked by ^) at p<0.05 level. P-value reported if significant.

Character	**BCNM**	**Guanacaste**	**T-Test or Chi-Square Results**
Climbing Mechanism			distributions different? ^ **n.s.**
% Tendrilling species	(41/85) 48.2%	(25/50) 50%	--
% Twining species	(34/85) 40%	(22/50) 44%	--
% Hooking species	(9/85) 10.5%	(1/50) 2%	--
% Scrambling speces	(1/85) 1.2%	(2/50) 4%	--
% Species Leaves Simple	(42/86) 48.8%	(25/50) 50%	^**n.s.**
% Species Leaves Entire	(69/85) 81.2%	(38/49) 77.6%	^**n.s.**
Average Petiole Length	3.7cm (n=65)	3.4 cm (N=48)	+**n.s.**
Diaspore			distributions different? ^**n.s.**
% Pogonochore species	(3/86) 3.4%	(4/50) 8%	--
% Pterochore species	(48/86) 55.8%	(33/50) 66%	--
% Zoochore species	(30/86) 34.9%	(10/50) 20%	--
% Barochore species	(4/86) 4.7%	(2/50) 4%	--
% Hydrochore species	(1/86) 1.2%	(0/50) 2%	--
Average Diaspore Size	3.1cm (N=65)	2.7cm (N=48)	+p=0.029
Average Seed Size	11.3mm (N=65)	8.5mm (N=48)	+n.s.
Average Bin for Seeds/Fruit	1.66	1.94	bin distribution different? ^ **n.s.**

DISCUSSION

DIVERSITY

Four dominant families comprised ~60% of liana species richness at the neotropical dry (Guanacaste) and neotropical moist (BCNM) forests. Bignoniaceae was the most species rich family at each site, while Sapindaceae and Fabaceae were important at both (Fig. 1). The observed family hierarchy for lianas was not surprising. Pitman et al. (2002) found that there is a predictable set of relatively few dominant tree species in Amazonian forests of Peru and Ecuador. Some families, genera, and species should reappear in hierarchies at different areas, much like the results in this study. About ten families, including Bignoniaceae and Fabaceae, are consistently dominant in lowland neotropical forests (Gentry 1988; Macía 2005). Furthermore it is not surprising that Bignoniaceae comprised such a large portion of species richness at each site (22% at BCNM and 30% at Guanacaste), because Bignoniaceae includes a large number of

climbing species (Woodson et al. 1973). Bignoniaceae climbers are generally most abundant in neotropical forests with a strong dry season (Gentry 1995). Bignoniaceae was the most species rich liana family in four of seven dry tropical forest sites in Central America, including Santa Rosa (Gillespie et al. 2000) and at two sites in Mexico (Solorzano et al. 2002). While this study did not take into account species abundance, it suggests strong oligarchic dominance at the family level for lianas in two seasonal forests in Central America. While not proven in this study, results suggest that high species richness at the family level may be related to high family abundance and dominance.

The four dominant families are not completely congruent between the sites. Malpighiaceae is more important at Guanacaste while Celastraceae is more important at BCNM. Reasons for this are not explored in this study. According to Pitman (2002) there are no 'magical traits' that result in dominance of a group of plants in a given area. Perhaps, ecological factors such as lower rainfall at Guanacaste led to a different oligarchy. Malpighiaceae, like Bignoniaceae climbers, may be well adapted to the dry season conditions of Guanacaste. This statement however should be tested with the inclusion of aseasonal wet tropical forests in analyses.

The most species rich four families at Guanacaste (Bignoniaceae, Malpighiaceae, Sapindaceae, Fabaceae) are also the most species rich families in a lowland rain forest and a seasonally deciduous forest in Mexico (Solorzano et al. 2002). Dominance by species of Malpighiaceae makes the liana flora of Guanacaste more similar to these Mexican sites than to BCNM. On the other hand, the differing oligarchies between sites in this study may be unimportant as there were 7 Malpighiaceae species at each, just showing that Guanacaste was relatively less speciose in lianas than BCNM.

Eleven of the 16 ubiquitous species at BCNM were in the top 20 most common lianas listed for BCI (Putz, 1984). Their ubiquity was therefore not surprising. Over half of the Dilleniaceae species at BCNM were ubiquitous, three of which were in the genus *Doliocarpus*. All *Doliocarpus* in this study have small arillate seeds that are bird dispersed. Arillate seeds are usually dispersed by a variety of birds (Howe & Smallwood 1982), which may be a highly effective mode of dispersal leading to ubiquity. On the other hand, there was no observed dominance of one diaspore type among the ubiquitous species: seven were pterochores and nine were zoochores. This may be explained by the

fact that the ability to be ubiquitous may be related to high dispersal efficiency regardless of dispersal syndrome. Variation within a syndrome (mass, size, shape etc.) has been shown to influence dispersal distance (Nathan et al. 2001).

Another explanation for ubiquity may be the ability of a species to germinate and survive under varying environmental conditions that are characteristic of different stand ages. Water is a major limiting factor for composition (Gentry 1988) and distribution (Holmgren & Poorter 2007) of tree species as well as liana abundance (Schnitzer 2005) in lowland tropical forests. Markesteijn and Poorter (2009) found that tree species of moist forests have increased light foraging ability while drought tolerant species employ a suite of strategies such as deep rooting and deciduousness. Shade and drought tolerance were found to be associated with different traits, so a 'mixed strategy' may lead to ubiquity in this study or even to a wide distribution in general. Lianas have been noted for drought tolerance due to deep root systems and efficient conduction (Schnitzer, 2005). Lianas accumulate more biomass, as well as allocate resources differently under high light environments relative to lower light (Toledo-Aceves & Swaine 2008). Sanches and Valio (2008) suggest that lianas are physiologically intermediate between shade-tolerant and light demanding species. A liana with a 'mixed strategy' of shade and drought tolerance may be able to succeed in all forest ages. The tradeoffs between the two strategies however may be too large for this 'mixed strategy' to be likely.

All three Apocynaceae species at BCNM were restricted to young forest stands. These species were also the only pogonochores at BCNM suggesting that their plumed seeds are not easily dispersed into older forests. McKey (1975) also predicted that many-seeded fruits with small seeds would be more characteristic of early successional stages. Apocynaceae fruits bear many small seeds and thus seem to fit McKey's prediction. Conversely, *Omphalea diandra*, was recorded in only one old growth site. *Omphalea diandra* had the largest diaspore (10cm, Fig. 6C) and seed (5cm, Fig. 6D) of all lianas at BCNM. McKey (1975) suggested that plants with large, few seeded fruits (like that of *O. diandra*) are 'high quality' and should be found more often in older forests. Howe & Estabrook (1977) suggest that fruits with greater mass attract a smaller dispersal guild than fruits of a smaller mass, leading to greater disperser specialization of larger fruited species. Mammals may in fact disperse *O. diandra* (Croat 1977) and perhaps its

disperser resides in older forests. Another explanation for *O. diandra*'s restriction may be that it is one of the few lianas that is leafless for only a short time (Croat 1977). Maintenance of leaves in the dry season may make it a competitive species sine it can photosynthesize during the dry season while other plants lose their leaves.

Fabaceae species richness decreased with forest age while other important families at BCNM (Bignoniaceae, Sapindaceae, Celastraceae) showed no trend. This correlation was mainly due to the loss of *Machaerium* and *Bauhinia* species with increasing stand age. Five of eight *Machaerium* species were identified only to genus, (given morphospecies status by DeWalt). If these morphospecies were in fact just variations of one of the three identified *Machaerium* species, the correlation may be spurious. In other words, Fabaceae diversity may have been inflated in some forest ages due to misidentification.

MORPHOLOGICAL CHARACTERS

Climbing Mechanism

Tendrilling and twining were the most common climbing mechanisms among lianas at both Guanacaste and BCNM. This result is consistent with other studies on a pantropical scale (DeWalt et al. 2000; Parthasarathy et al. 2004; Campanello et al. 2007). Parthasarathy et al. (2004) showed that tendrillate lianas were more important in terms of abundance and diversity in dry forests than wet forests in India. While tendrilling species were expected to be more important at Guanacaste since it is drier, the proportion of tendrilling species was nearly equal at the dry and moist neotropical sites examined (Table 3). These results do not coincide with Parthasarathy's. Parthasarathy's (2004) study system however was different from this study in two important ways, which may account for the disparity. The dry and wet Indian forests were evergreen whereas forests in this study were deciduous, and the family oligarchy of climber diversity is different in the Old World Tropics. Parthasarathy et al. (2004) found Vitaceae, Papilionaceae (Fabaceae), and Apocynaceae to be the most species rich families.

DeWalt (2000) used the same BCNM data set used in this study but evaluated abundance rather than presence/absence of species and found that twining *individuals* were dominant. Using the climbing mechanism classification from the current study

(lumping apical and branch twiners), over 78% of the individuals were twining. In contrast, I found the proportion of tendrilling *species* to be highest. Considering both types of data (abundance and presence/absence) may tell an important story. While tendrilling species make up a large proportion of the liana flora at BCNM, the twining species are much more abundant, suggesting that, while tendrilling lianas may be more diverse, twining may be more successful at BCNM.

The significant decrease in hooking species with stand age at BCNM may again be explained by the decrease in Fabaceae (in particular, *Machaerium*) diversity. I categorized *Machaerium* species as hooking because of their production of leafless shoots, bearing only recurved spines that function in climbing (R. Burnham, pers. comm.). Just as Fabaceae diversity may be skewed due to possible misidentification (discussed in 'Diversity' section), the decreasing proportion of hooking species with age may be skewed. Nonetheless, it was predicted that scrambling and hooking species would be more prevalent in younger stand ages and this trend was observed for hooking. The proposed mechanism for the trend is that dense, smaller vegetation in younger forests provides better support for hooking species than the larger-stemmed, less dense vegetation characteristic of older forests.

The categorization of climbing mechanism for *Machaerium* highlights an issue in defining climbing mechanism. While *Machaerium* species were considered hooking in this study, they could be considered scrambling due to their recurved spines or even tendrilling, since the hooked short shoots often curl (once or twice) around a supporting branch. This brings to light problems with variability of climbing mechanism categorization among studies, since many climbers use multiple mechanisms (Putz 1984). Because liana studies are becoming more common, a standard protocol for liana sampling has been created (Gerwing et al. 2006), yet climbing mechanism categorization was not a part of the protocol. Work towards a standard categorization for climbing mechanism is in order so that liana studies may be more easily compared.

The anticipated decrease in the proportion of tendrillate lianas with an increased proportion of twining lianas across forest age was shown at Guanacaste, but the correlations were insignificant. From 10 to 50 year old stands, the proportion of twining lianas went from 30% to 50% while the proportion of tendrilling lianas went from 70% to

50% (Fig. 3). Within the Santa Rosa Sector of Guanacaste, trees of larger DBH increase with stand age (Kalacska 2004), indicating that larger supports are relatively more important in older forests. Large trees (≥65cm DBH) were absent or rare in younger forests but were abundant in old forests at BCNM (DeWalt et al., 2003). Other studies show similar findings of larger DBH classes in older forests (Lewis et al. 2004; Saldarriaga et al. 1988). Twining lianas utilize larger support structures than tendrillate lianas (Putz, 1984), so if larger supports are more abundant in older forests at Guanacaste, this may explain the trend of an increasing proportion of twining lianas with stand age.

Leaf organization, leaf margin and petiole length

The remaining vegetative characters examined did not show correlations with forest age at BCNM or Guanacaste. Leaf organization and leaf margin are, for the most part, phylogenetically constrained at the family level (i.e., all Bignoniaceae climbers are compound and all Sapindaceae climbers have serrate leaflets). While stand ages may differ in some environmental variables (light, soil moisture etc.) and in structure, the source flora for each age is fundamentally the same. Phylogenetic constraint, coupled with a similar source flora and little change in family representation across age (except Fabaceae at BCNM), probably account for the lack in trends for leaf organization and leaf(let) margin with stand age. Phylogenetic constraint is again the most likely reason for no variation in vegetative traits between the moist and dry sites (Tab. 3) since three dominant families were shared at both sites (Fig. 1). Furthermore, Celastraceae (dominant at BCNM but not Guanacaste) and Malpighiaceae (dominant at Guanacaste but not BCNM) both have entire, simple leaves.

Diaspore type and fruit characteristics

Wind as the major seed dispersal mechanism for lianas at BCNM and Guanacaste was consistent with prior studies in the neotropics (Gentry 1982; Solorzano et al., 2002). The proportion of wind-dispersed lianas (pterochores + pogonochores) was higher at Guanacaste (74%) than at BCNM (~59%). Wind dispersal is more common among lianas in drier neotropical and old world tropical forests (Gentry 1982; Parthasarathy et al.

2004). However, Solorzano et al. (2002) found no difference in the proportion of wind-dispersed lianas in a dry and wet forest in Mexico. The trend of wind-dispersal being more dominant in drier sites may therefore be site specific.

Dominant dispersal syndrome did not change with forest age at BCNM or Guanacaste. The proportion of zoochores, however, increased significantly across successional stand ages at BCNM (Fig. 4) when old growth stands were removed from analysis. This suggests that the animal dispersal among lianas becomes more important with increasing successional forest age at BCNM. This may be a result of the variation of frugivore abundance across the chronosequence because dispersal of zoochores is highly affected by disperser behavior (Gorchov et al. 1993; Murray 1988). The majority of zoochorous lianas in this study are dispersed by birds (http://www.stri.org). In northeastern tropical India, both bird abundance and species richness increased with successional age (Raman et al. 1998). While some bird species respond to anthropogenic disturbance positively and others respond negatively (Gomes et al. 2008), many utilize natural and manmade canopy gaps in the neotropics (Wunderle et al. 2005; Zurita & Zuleta 2007). DeWalt et al. (2003) found more course woody debris in older successional forests at BCNM suggesting more treefall gap that bird populations may be exploiting. These factors may allow zoochorous liana species to be dispersed into older successional forests.

Another possible explanation for the observed trend is that seed size may be correlated with diaspore type. A post hoc independent samples t-test was performed to see if the average seed size of wind and animal dispersed seeds was different at BCNM. Mean seed size for zoochores was 11.9mm while mean seed size for wind dispersal units was 10.1mm. There was no significant difference in seed size based on diaspore type so seed size is not a factor contributing to the observed trend of increasing zoochores. In evaluating the trend of increasing zoochorous liana species with successional age, it is important to remember that old growth stands were removed from analysis, which may negate the trend's proposed mechanism of increasing frugivore usage of older forests.

While seed size did not change with forest age at BCNM, Guanacaste showed a trend (insignificant) of an increasing proportion of large-seeded lianas with stand age (Fig. 5). The trend should be evaluated with caution since proportions of large seeded

species were still very low in the oldest (50 year) forests: ~10%. Treefall gaps in older forests are very important to neotropical forest dynamics (Hartshorn 1980; Dupey & Chazdon 2008) but were not considered when predicting that seed size would increase with forest age. Within gaps, both large and small-seeded pioneer species successfully germinate, so gaps may possess sufficient light resources for pioneers to succeed regardless of seed size (Daws et al. 2008). Furthermore, the relationship between seed size and dispersal distance was not considered. Regardless of dispersal agent, seed size will affect the distance a seed can travel and therefore its abundance in the soil (Dalling et al. 1997). Small seeded lianas may be able to disperse across all forest ages and into gaps, therefore becoming important across the chronosequence.

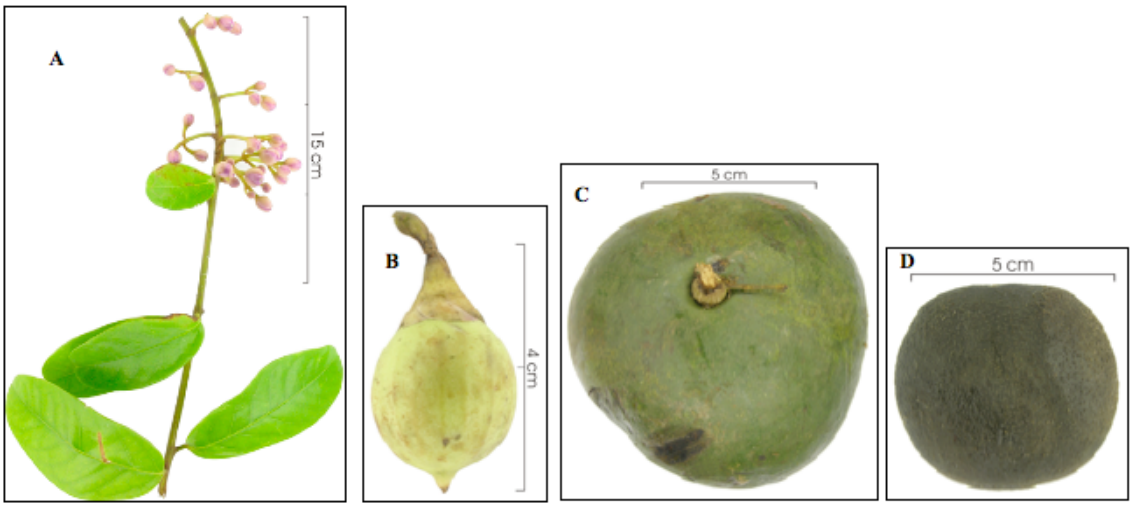

Figure 6: A. The dominant liana at BCNM, *Maripa panamensis*. **B**. *M. panamensis* fruit. **C**. Fruit of *Omphalea diandra*, a liana restricted to old growth at BCNM. **D**. *O. diandra* seed. All images from http://www.stri.org.

Conclusions and implication for conservation

Anthropogenic impacts on tropical forests worldwide are increasing on both a local and global scale (i.e., CO_2 increase; Wright 2005), and lianas are important players in forest ecosystem processes in the neotropics (Heijden & Phillips 2008). Our understanding of liana response to human disturbance and succession is therefore essential for proper forest management and conservation efforts. This study provides insight on liana response to forest age in two Central American forests. Findings from this study suggest topics for future research and can be utilized in forest management and conservation.

Family diversity at both sites mirrors previous studies, and stand age has little effect on the diversity of dominant families. Disturbance can increase liana abundance (Putz 1984; Schnitzer & Carson 2001) and liana species richness is greatest in intermediate successional stages (DeWalt et al. 2000), but at the higher taxonomic level of family, dominant climbing groups may not respond strongly to disturbance. Where there are lianas, there will always be Bignoniaceae, Fabaceae, and Sapindaceae species. Relative oligarchic dominance however is site-specific and may be correlated with water availability. With increased disturbance in neotropical forests, some liana species may become more abundant, but family level diversity in a mosaic of different forest ages may remain rather constant.

Ubiquity across stand age was common at BCNM, however restriction of some species to old or young stands occurred. Many narrowly-restricted species were found in younger forests at BCNM. Given this, liana diversity may decrease within protected areas as they are left to proceed through secondary succession and begin to resemble older forests. Treefall gaps are, and will be, important in maintaining those 'young forest' species. Ubiquitous species on the other hand, may be present regardless of successional age, environmental conditions, and forest structure. Within protected areas, maintenance of moderate disturbance in patches will allow for the greatest diversity of lianas—the ubiquitous will thrive and the more restricted species will be maintained. Some lianas (i.e. *Omphalea diandra* and Apocynaceae species) may even have the potential to be used as indicators of forest age or level of disturbance.

Tendrilling liana species dominated the species lists at both sites. In contrast, a prior study (DeWalt 2000) found that twining species were more important based on abundance at BCNM. Are twiners more successful at BCNM? *Maripa panamensis* (Convolvulaceae, Fig. 6A), a stem twining species, is the dominant liana at BCNM accounting for 10% of liana stems (DeWalt et al. 2000). So, twining as a climbing strategy may be more competitive than other climbing habits, or perhaps *M. panamensis* is dominant for another reason. Putz (1984) suggests that *M. panamensis* flattens its stem to increase friction against its host. This would allow for a more efficient climb to the canopy, suggesting that within species of a similar climbing habit, some are better than others. Given this, climbing habits of lianas may be currently lumped into oversimplified

categories. Furthermore, looking to fruit characters, Croat (1977) notes that fruits of *M. panamensis* (Fig. 6B) are often 'torn apart by animals' before dehiscing. Perhaps its fruits are favored by dispersers and *M. panamensis* is therefore dominant. In Yasuní, Ecuador, *Machaerium cuspidatum* (Fabaceae) is the most abundant liana, also accounting for 10% of the liana stems (Burnham, 2002), and its vigor may be due to vegetative propagation.

Hienrich and Hurka (2004) do not report abundance data of the censused species, however other species lists were evaluated to look for a dominant climber at Guanacaste. Data collected by Paul Foster in 1999 (unpublished) show that, within Santa Rosa National Park, Guanacaste, *Forsteronia spicata* (Apocynaceae) was the most abundant liana (combining data from four 50m transects). *Forsteronia spicata* accounted for 22% of the liana stems censused as well as 22% of the total liana basal area. Gillespie (2000) found that within Santa Rosa, *Arrabidaea mollissima* and *Pithecocentium crucigerum* (both Bignoniaceae) each contributed 15% of the total liana stems. It is apparent that within Santa Rosa, the dominant species varies by specific locality of data collection. On a larger scale of dry forests in the vicinity of Guanacaste, including seven sites from Northern Costa Rica and Nicaragua, an unknown Bignoniaceae climber contributed 11.3% of the total stems while *Machaerium kegellii* (Fabaceae) contributed to 9.3% of liana stems (Gillespie, 2000).

The dominant liana(s) at both BCNM (DeWalt 2000), Yasuní (Burnham 2002), and seven dry forests in Costa Rica and Nicaragua (Gillespie 2000) comprised a similar percentage of stems despite there being a greater number of species (311) at Yasuní (Burnham, 2002). Foster (unpublished) found the most intense dominance by *Forsteronia spicata* in Santa Rosa. It is important to note that censusing techniques varied in each study, most likely leading to differences in observed dominance patterns. The majority of studies however suggest that a dominant liana, accounting for ~10% of all stems, may be common across neotropical sites. Increased liana censusing with a standard technique would shed light upon whether this similar pattern of dominance is in fact legitimate. The dominant species discussed above have varying climbing mechanisms (twining, hooking, tendrilling) and diaspore types (zoochore, pogonochore, pterochore). This suggests that variation within these character states (like the flattened

twining stem of *M. panamensis*), rather than the character states themselves, may lead to increased competitive ability.

Although statistically insignificant, Guanacaste showed a decreasing trend in the proportion of tendrillate climbers and an increasing proportion of twining species, which is most likely due to changes in stand structure with forest age. Leaf characteristics (leaf organization, leaf margin, petiole length) however remained constant perhaps due to phylogenetic constraint on these characters and a similar source population for all stand ages. Between the moist and dry site, vegetative characters were not different (Tab. 3) due to general consistency of dominant families at each site. Throughout the study, the phylogenetic constraint on most characters played a major role in analyses. A change in the proportion of a given character state is almost always associated with a change in the species composition from one forest age to another.

Wind dispersal was most important at each site, but was relatively more important at the drier site (Tab. 3). This supports studies by Gentry (1982). Across successional ages at BCNM, the proportion of animal dispersed lianas increased. While mechanisms for this trend are not explored in this study, it may be due to animal dispersers being more common in older forests, especially birds. This illustrates the possible interaction of stand age and animal dispersers, and the consequent effect on plant distribution. As protected areas are left fallow within a matrix of land used by humans, dispersers may seek refuge in older, protected forest stands. This may greatly influence plant distributions—a plant species cannot be maintained where its disperser does not occur. Seed size was consistent across stand age at both sites, potentially caused by gaps in older forests mimicking early successional forests. Gaps may not only be important in maintaining liana diversity in older forests, but also affect the liana seed bank in older forests as well. The species found to be restricted to older forests in this study may be the species that persist as gaps close.

Given the similar family oligarchy between the dry and moist site, it was not surprising that the morphology of the liana communities was so similar between sites. (Tab. 3). This suggests that, within liana-rich families, liana species may have evolved to tolerate a wide range of habitat conditions regardless of the morphological traits evaluated here. Physiological studies on lianas under different conditions, controlling for

phylogeny, will develop a better understanding of this idea. This is not to say that liana species diversity does not matter or that all lianas can serve in a variety of habitats. It is clear that different forest types of the neotropics differ with regards to liana species richness, abundance, and the dominant climber. Gerwing (2004) showed that different lianas employ different growth strategies in response to light and successional stage. Perhaps looking to physiology, in combination with morphology, is the most essential next step towards explaining liana distributions.

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