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Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica

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Abstract

Lianas can have a large impact on the diversity, structure, and dynamics of tropical forests, yet they remain essentially unknown even in some of the most intensely studied tropical forests, such as La Selva Biological Station in Costa Rica. We quantified the diversity, abundance, and mortality of lianas in primary and selectively logged forest at La Selva for over 3 years, from January 1999 until July 2002. We measured, identified, permanently marked, and mapped all lianas ≥ 1.3 m in length and 2 mm in diameter, whether climbing or free-standing, in nine, 24m \times 36 m (864 m²) plots. There were no significant differences in density, diversity, or mortality between primary forest and areas that were selectively logged approximately 50 years prior to our study. We found a mean density of 1493 lianas ha⁻¹ and a mean species richness of 23 species per 864 m² plot. Annual mortality was 9.4% over all size-classes, but was the highest for the smallest individuals (<2 cm in diameter). Annual mortality for larger individuals (≥ 5 cm) was much lower over the 3.5-year period (3.2% per

year) and the five most abundant species suffered no mortality in this size-class. In contrast to many lowland neotropical forests, where Bignoniaceae and Fabaceae are reported to be the dominant liana families, at La Selva we found that Sapindaceae was the most speciose family and Dilleniaceae the most abundant. *Moutabea aculeata* (Polygalaceae) was the most abundant species, constituting approximately 17% of the individuals and having the lowest mortality of all 60 species. The 10 most abundant species at La Selva accounted for more than 60% of all individuals. Compared to other lowland sites in the neotropics, including other wet forests, the abundance and diversity of lianas at La Selva are very low.

Keywords

Lianas, Species diversity, Demography, Tropical forest, La Selva, Costa Rica

1. Introduction

Lianas are an important component of tropical forests and are often cited as the most obvious physiognomic difference between temperate and tropical forests ([Croat, 1978](#), [Putz and Mooney, 1991](#), [Richards, 1996](#), [Schnitzer and Bongers, 2002](#)). Lianas commonly compose up to 25% of the woody individuals and species in tropical forests, although in some forests they can constitute as much as 44% of the species ([Gentry, 1991a](#), [Perez-Salicrup et al., 2001](#)). Lianas influence a number of important forest processes, including reducing tree growth and fecundity, increasing tree mortality, suppressing and altering gap-phase regeneration, and increasing canopy connectedness ([Putz, 1984a](#), [Stevens, 1987](#), [Putz and Mooney, 1991](#), [Perez-Salicrup and Barker, 2000](#), [Schnitzer et al., 2000](#), [Schnitzer and Carson, 2001](#)). For example, at La Selva Biological Station in Costa Rica, [Clark and Clark \(1990\)](#) found a significant negative correlation between the number of lianas in a tree's canopy and that tree's growth rate. Furthermore, they found that nearly 50% of those trees that were larger than 10 cm in diameter had lianas in their crowns. [Schnitzer et al. \(2000\)](#) demonstrated that when abundant, lianas could impede tree regeneration in canopy gaps to such an extent that they essentially arrest gap-phase regeneration.

Lianas also play a role at the ecosystem level by contributing to the carbon budget of tropical forests, representing as much as 10% of fresh aboveground biomass ([Putz, 1984a](#)). More importantly, when lianas become abundant they can reduce the amount of carbon sequestered by tropical forests (reviewed in [Schnitzer and Bongers, 2002](#)), which may have important ramifications for ecosystem function ([Laurance et al., 2001](#), [Phillips et al., 2002](#)). Consequently, lianas play a large role in many aspects of tropical forest dynamics, and their importance may be increasing with global change ([Phillips and Gentry, 1994](#), [Phillips et al., 2002](#)).

Although the study of lianas has increased dramatically in recent years (e.g., [DeWalt et al., 2000](#), [Gerwing and Farias, 2000](#), [Perez-Salicrup and Barker, 2000](#), [Schnitzer et al., 2000](#), [Horvitz and Koop, 2001](#), [Laurance et al., 2001](#), [Nabe-Nielsen, 2001](#), [Perez-Salicrup et al., 2001](#), [Schnitzer and Carson, 2001](#), [Burnham, 2002](#), [Phillips et al., 2002](#), [Schnitzer and Bongers, 2002](#)), the ecology of lianas in most forests is still poorly understood. For example, the forest at La Selva Biological Station in Costa Rica is one of the most intensely studied tropical sites in the world (see [McDade et al., 1994](#)), with more than 100 species of lianas, which account for an estimated 6% of the floral richness and 15% of the primary forest canopy foliage ([Hartshorn and Hammel, 1994](#), [Werner, 1985](#)). Yet aside from this cursory information, lianas remain essentially unstudied at La Selva ([Clark, 1994](#); but see [DeWalt and Chave, 2004](#)). [Hartshorn and Hammel \(1994\)](#) speculated that the number of liana species at La Selva may be on par with that of other forests, but that liana diversity only appears to be lower "because lianas are the growth-form most difficult to collect and still the most poorly known at La Selva". Furthermore, even basic information on liana communities, such as the relative abundance of species and their changes over time, remains largely unexplored. To fill this obvious gap in our understanding of the liana community, we established

permanent plots in both selectively logged and primary forests at La Selva and quantified the abundance, diversity, and mortality of lianas over a 3.5-year period.

2. Methods

2.1. Study site

La Selva Biological Station in Costa Rica is a 1500+ ha forested reserve, located at the confluence of the Sarapiquí and Puerto Viejo rivers (10°26'N, 83°59'W; [McDade and Hartshorn, 1994](#)). The primary forest at La Selva dominates the property, with more than 800 ha that have remained free of major human disturbance for at least 1100 years. Slightly more than 100 ha of what was once primary forest were selectively logged in the 1940s and 1950s ([Hartshorn and Hammel, 1994](#), [McDade and Hartshorn, 1994](#), R. Matlock, pers. commun.). The vegetation at La Selva is characterized as tropical wet forest in the Holdridge life zone system ([Holdridge et al., 1971](#)). The region receives approximately 4000 mm of rainfall per year, with no month receiving less than 100 mm ([McDade and Hartshorn, 1994](#)). The lava-derived ultisols are strongly acid and rich in organic matter ([Sollins et al., 1994](#)), resulting in relatively fertile soils compared to those found in many other tropical forests ([Powers and Lerdau, in review](#)). For more detailed information concerning the geology, climate, flora, and fauna of La Selva see [McDade et al. \(1994\)](#).

2.2. Sampling procedures and analysis

We set up nine, 24m×36 m permanent plots (864 m²) in December 1998. Six of these plots were in primary forest and three were in selectively logged forest. We randomly selected the plots along three north–south trails, each plot >50 m from a trail. We omitted extremely steep slopes and floodplains, and thus most of our plots were on relatively flat, upland sites on residual soils. Plots were on average 375 m apart (range 200–800 m). In January 1999, we measured all free-standing and climbing liana individuals (apparent genets) that were rooted within the plot and ≥0.2 cm in diameter and ≥1.3 m in length (from the roots). We identified all lianas to species, permanently marked them with aluminum tags, and measured their diameters 1.3 m along the stem from the roots. We also recorded the location of each liana on a detailed map of the plot in order to relocate individuals for subsequent measurements. In June and July 2002, we recensused the previously tagged lianas in each of the plots, but we did not measure new recruits. Gerardo Vega, a local taxonomist, verified all species identifications in the field using herbarium specimens at La Selva and Duke University. Voucher specimens are currently being collected and will be placed in the herbarium at La Selva. Nomenclature follows that found in [McDade et al. \(1994\)](#) and that used at the La Selva herbarium.

In our effort to understand the demography of the liana community at La Selva, we included in the census only truly independent lianas, i.e., those that were not connected above ground or obviously connected below ground to any other stem in the census. When a single liana individual had multiple vegetative offshoots connected to the main stem, we considered the multiple stems to be more analogous to the branches of a tree than independent individuals, and in this case we included only the largest diameter stem. We excluded all multiple vegetative offshoots of an apparent genet by following each stem down to the soil surface to verify that it was independently rooted. Once a liana stem became an independently rooted individual, however, we treated it as an apparent genet (methods follow those of [Gentry, 1982](#), [DeWalt et al., 2000](#), [Nabe-Nielsen, 2001](#), [Perez-Salicrup et al., 2001](#), [Schnitzer and Carson, 2001](#), [Burnham, 2002](#)). By excluding ramets connected to parent stems, we likely underestimated the abundance and basal area of liana stems. Indeed, in a study in a liana-rich primary forest in French Guiana, Schnitzer et al. (unpublished manuscript) reported that excluding ramets that were still connected to the parent stem underestimated liana abundance and basal area by 14 and 19%, respectively.

We compared average liana density, species richness, Fisher's log series α (Fisher's α), and mortality among plots in primary and selectively logged forests using *t*-tests. We included Fisher's α as an index of diversity because it varies less with sample size than does species richness and thus facilitates comparisons between study sites (Magurran, 1988, Leigh, 1999). Fisher's α , however, becomes unpredictable at very low stem densities; thus, we only calculated Fisher's α for each of the plots (Table 1) and for each of the size-classes with all the plots combined (Table 2). We calculated annual mortality by dividing the total mortality by the length of the study (41 months). We calculated the importance value of each species as the mean of that species' relative abundance and relative basal area in each plot (Hartshorn and Hammel, 1994). Because we did not climb into the canopy, we were unable to identify 11.7% of the individuals, even to morphospecies, so our estimates of diversity are somewhat conservative (Appendix A). We included the unidentified lianas in the analyses of density and basal area.

Table 1. Mean density, species richness, Fisher's α , and mortality of all climbing and standing lianas (apparent genets ≥ 0.2 cm DBH) for nine 24m \times 36 m (864 m²) plots in primary and selectively logged forests at La Selva^a

Plot location	Number of lianas (864 m ⁻²)	Number of lianas (ha ⁻¹)	Liana species richness (864 m ⁻²)	Fisher's α	% Mortality (per year)
CC 400	146	1690	25	8.69	9.62
CC 600	179	2072	23	7.02	12.26
CC 1400	114	1319	22	8.12	7.96
LOC 1550	108	1250	20	7.23	8.13
LOC 1950	109	1262	22	8.32	8.86
LOC 2150	121	1400	25	9.58	6.05
SSA 1300	147	1701	21	6.71	11.35
SSA 1500	100	1157	25	10.72	8.78
SSA 1950	137	1586	25	8.97	11.54
Plot means (\pm S.E.)	129 (8.5)	1493 (97.9)	23 (0.65)	8.37 (0.43)	9.39 (0.67)
Primary forest mean (S.E.)	130 (11.4)	1499 (132.3)	23 (0.79)	8.16 (0.39)	8.81 (0.84)
Logged forest mean (S.E.)	128 (14.3)	1481 (165.5)	24 (1.33)	8.80 (1.16)	10.56 (0.89)
<i>T</i> -test results: primary vs. selectively logged forests	<i>P</i> = 0.94	<i>P</i> = 0.94	<i>P</i> = 0.63	<i>P</i> = 0.65	<i>P</i> = 0.21

^aThe CC and LOC plots were located in the primary forest and the SSA plots were in the selectively logged forest. There were no significant differences between the primary and selectively logged forest for liana abundance, species richness, or mortality.

Table 2. Mean density, species richness, Fisher's α , and annual mortality of all lianas across a range of diameter size-classes^a

Liana size-class (cm)	Mean number of lianas (864 m ⁻²) (\pm S.E.)	Total number of lianas (0.78 ha ⁻¹)	Mean species richness (864 m ⁻²) (\pm S.E.)	Total species richness (0.78 ha ⁻¹)	Fisher's α (0.78 ha ⁻¹)	% Mortality (per year) (\pm S.E.)
0.2–1	61.6 (10.3)	555	16.2 (0.9)	46	11.9	13.3 (0.8)
1–2	29.4 (3.0)	265	12.7 (0.6)	42	14.1	7.2 (0.9)
2–3	15.1 (1.0)	136	8.9 (0.5)	30	11.9	4.0 (0.9)
3–4	8.3 (1.2)	75	5.9 (0.6)	18	7.5	8.2 (1.3)
4–5	5.3 (0.9)	48	3.3 (0.5)	13	5.9	3.0 (1.3)

5–6	3.0 (0.3)	24	2.5 (0.3)	11	7.9	3.2 (1.5)
6–7	2.3 (0.3)	14	2.3 (0.3)	8	7.8	0.0 (0.0)
7–8	2.1 (0.5)	15	1.9 (0.4)	6	3.7	2.1 (1.8)
8–9	1.8 (0.3)	11	1.5 (0.2)	7	8.3	2.4 (2.0)
9–10	1.0 (0.0)	4	1.0 (0.0)	4	–	7.3 (4.9)
10+	2.0 (0.4)	14	1.6 (0.4)	7	5.6	4.2 (3.7)
Plot mean	129 (8.5)	–	23 (0.7)	–	8.37 (0.4)	9.39 (0.7)
Total for all individuals	–	1161	–	60	13.4	9.39

aWe present the mean of all nine 24m×36m (864m²) plots as well as the total numbers based on all plots combined (0.78ha). Fisher's α is based on the total number of individuals in the census in order to increase the sample size. Fisher's α for the 9–10cm size-class was omitted from the analyses because the sample size ($n=4$) was too low for an accurate calculation.

3. Results

We found a total of 1161 free-standing and climbing lianas ≥ 0.2 cm diameter in the nine plots (0.78 ha), representing 60 species, 40 genera, and 28 families ([Appendix A](#)). The most diverse families in terms of the number of species were the Sapindaceae (7), Bignoniaceae (6), and Dilleniaceae (4). The Dilleniaceae was represented by 233 individuals, followed by Polygalaceae (198), Bignoniaceae (135), and Sapindaceae (118). The Polygalaceae, however, was represented by only one species, *Moutabea aculeata*, which was considerably more abundant than any other species of liana at La Selva. The overall density of lianas averaged 1493 individuals ha⁻¹ and ranged from 1157 to 2072 ha⁻¹ ([Table 1](#)). Species richness averaged 23 species per 864 m² plot and ranged from 20 to 25. Nevertheless, the species accumulation curve rose steeply for the first four plots and then began to level off, indicating that our sample size was sufficient to include the majority of species occurring at La Selva ([Fig. 1](#)). Fourteen species (23%) in this census were represented by only one individual.

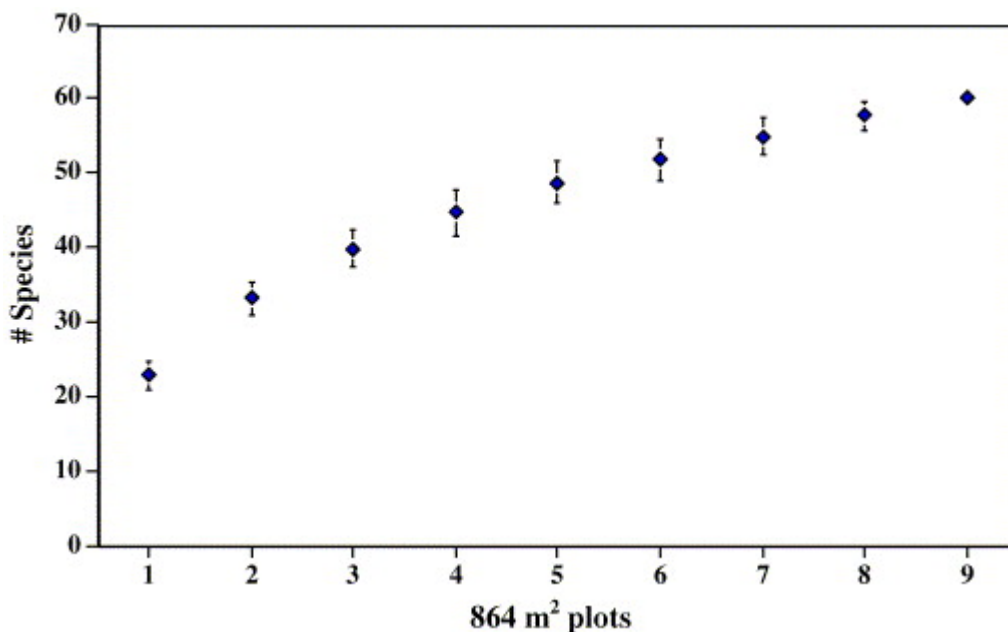


Fig. 1. Liana species accumulation curve based on nine 864 m² plots at La Selva Biological Station. Each point represents the mean number of species found with the addition of each additional plot. Plot order was randomly selected 100 times using the software EstimateS ([Colwell, 2000](#)). Error bars represent ± 1 S.D.

Liana density, species diversity (species richness and Fisher's α), and mortality did not differ significantly between primary and selectively logged forest (Table 1); consequently, we treated all nine plots as replicates for subsequent analyses. Liana density and species richness decreased predictably with increasing size-class, but Fisher's α remained relatively constant among the lower size-classes (Table 2). Fisher's α for the size-classes was nearly identical to the mean Fisher's α of the plots (8.44 ± 1.0 vs. 8.37 ± 0.4 , respectively; Table 2). Approximately 26% of liana individuals in the census died during the 3.5-year measurement interval, indicating a mean annual mortality of 9.4% (Table 2). Most mortality was concentrated in the smallest size-classes and there was very little mortality for individuals ≥ 5 cm diameter (Fig. 2; Table 2). Indeed, no individuals ≥ 5.0 cm diameter for the five most abundant species died during the study period. *M. aculeata*, the most abundant species in the census, suffered relatively little mortality over all the size-classes and had the lowest mortality of all 60 species.

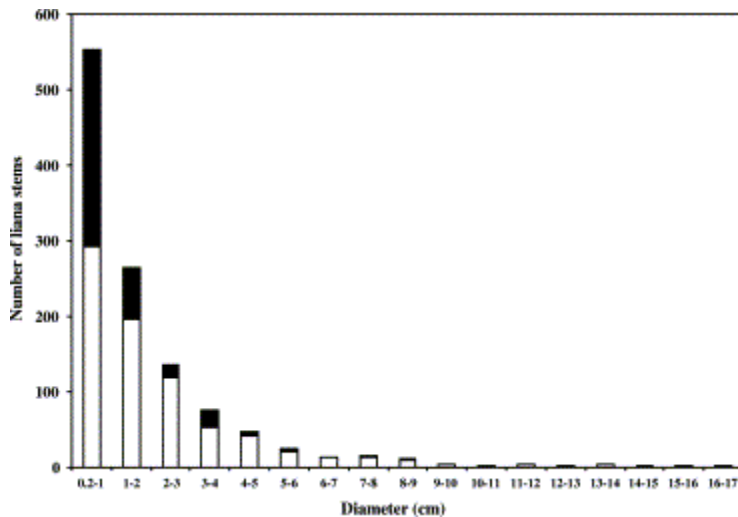


Fig. 2. Size distribution of all lianas in the nine 24m x 36 m plots (0.78 ha) at La Selva Biological Station, Costa Rica. The bottom, unshaded portion of the bar represents the living individuals and the top, shaded portion represents the individuals that died during the 41-month study period.

The five most common species (*M. aculeata*, *Davilla nitida*, *Paragonia pyramidata*, *Paullinia echinocarpa*, *Doliocarpus dentatus*) accounted for nearly 45% of all individuals in the census, while the 10 most common species accounted for over 60% of the individuals (Table 3). *M. aculeata* was by far the dominant species in terms of abundance, constituting an average 17.5% of the individuals and 14.8% of the total basal area per plot (Table 3). This species was present in each of the nine plots, averaging $255 (\pm 47 \text{ S.E.})$ individuals per plot. The relative abundance of *M. aculeata*, however, was highly variable, ranging from 2.2 to 30.6% of the liana stems per plot. The second most common liana, *D. nitida* averaged only $118 (\pm 61 \text{ S.E.})$ individuals per plot, but composed a greater percentage of total basal area than did *M. aculeata* (15.7 vs. 14.8%, respectively; Table 3).

Table 3. The most abundant liana species (apparent genets including both climbing and standing individuals ≥ 0.2 cm DBH) according to density and basal area (BA), arranged in order of decreasing abundance^a

Species	Total number of lianas (0.78 ha ⁻¹)	Mean number of lianas (ha ⁻¹) (\pm S.E.)	Mean relative abundance (\pm S.E.)	Mean BA (cm ²) of lianas (ha ⁻¹) (\pm S.E.)	Mean relative BA (\pm S.E.)	Importance value
<i>M. aculeata</i>	198	255 (47)	17.1 (3.1)	1175 (253)	14.8 (3.7)	16.1
<i>D. nitida</i>	92	118 (61)	7.1 (2.9)	1530 (614)	15.7 (6.0)	11.4
<i>P. pyramidata</i>	85	109 (23)	7.7 (1.8)	207 (56)	2.3 (0.7)	5.0
<i>D. dentatus</i>	70	90 (41)	5.6 (2.4)	1064 (345)	12.0 (4.5)	8.8

<i>P. granatensis</i>	70	90 (25)	6.2 (1.7)	581 (230)	6.1 (2.1)	6.2
<i>H. scandens</i>	49	63 (20)	4.8 (1.6)	381 (120)	4.6 (1.4)	4.7
<i>Forsteronia</i> sp.	45	58 (26)	3.8 (1.6)	94 (67)	0.9 (0.6)	2.3
<i>M. hyacinthina</i>	40	51 (14)	3.3 (0.7)	441 (165)	4.7 (1.7)	4.0
<i>S. domingensis</i>	38	49 (14)	3.7 (1.2)	30 (12)	0.3 (0.1)	2.0
<i>D. coriaceus</i>	36	46 (14)	3.0 (0.8)	467 (278)	5.4 (3.1)	4.2
<i>Davilla</i> sp.	35	45 (44)	2.2 (2.1)	370 (357)	3.0 (2.9)	2.6
<i>P. fuscescens</i>	24	31 (12)	2.2 (1.0)	288 (138)	2.6 (1.2)	2.4
<i>P. pinnata</i>	20	26 (11)	1.6 (0.7)	364 (203)	4.1 (2.2)	2.9
Subtotal top 10 species	723	930	62.7	6661	73.0	65.9
Total for all individuals	1161	1493	100.0	9027	100.0	100.0

aMean relative abundance and basal area were calculated by dividing the abundance or basal of the focal species per plot by the abundance or basal area of all the individuals in the plot, respectively, and then taking the average of the plots. We calculated importance values as the average of mean relative density and relative basal area.

We found an average abundance of 340 liana individuals ≥ 2.5 cm diameter ha^{-1} , a common size-class cut-off point in other liana studies (e.g., [Gentry, 1982](#), [Gentry, 1991a](#), [Gentry, 1991b](#)). The 10 most abundant species ≥ 2.5 cm diameter accounted for approximately 75% of the total stem density and basal area ([Table 4](#)). Only 36 species (57%), however, were present in this larger size-class. *M. aculeata* retained its dominance in this size-class (87 stems), and *D. nitida* again had the highest overall basal area (1485 cm^2 ; [Table 4](#)).

Table 4. Most abundant liana species (apparent genets including both climbing and standing individuals ≥ 2.5 cm DBH) according to density and basal area (BA), arranged in order of decreasing abundance^a

Species	Total number of lianas (0.78 ha^{-1})	Mean number of lianas (ha^{-1}) (\pm S.E.)	Mean relative abundance (\pm S.E.)	Mean BA (cm^2) of lianas (ha^{-1}) (\pm S.E.)	Mean relative BA (\pm S.E.)	Importance value
<i>M. aculeata</i>	47	87 (19)	18.2 (4.1)	877 (220)	13.5 (3.9)	17.5
<i>D. nitida</i>	25	46 (15)	9.4 (3.1)	1485 (615)	17.4 (6.9)	14.4
<i>D. dentatus</i>	22	41 (12)	9.1 (2.9)	1015 (332)	13.5 (5.3)	12.0
<i>P. granatensis</i>	22	41 (15)	7.7 (2.5)	503 (227)	5.9 (2.2)	7.7
<i>M. hyacinthina</i>	21	39 (11)	7.8 (2.4)	396 (153)	4.8 (1.9)	6.8
<i>H. scandens</i>	20	37 (13)	7.5 (2.6)	326 (103)	4.5 (1.4)	6.6
<i>P. fuscescens</i>	13	24 (13)	4.4 (2.0)	263 (135)	2.6 (1.3)	3.8
<i>P. pyramidata</i>	10	19 (6)	3.9 (1.4)	141 (50)	1.8 (0.7)	3.0
<i>P. pinnata</i>	9	17 (8)	3.8 (2.1)	338 (197)	4.4 (2.5)	4.4
<i>D. coriaceus</i>	6	11 (7)	2.5 (1.6)	427 (278)	5.5 (3.5)	4.1
<i>Davilla</i> sp.	3	6 (4)	1.0 (0.8)	354 (341)	3.1 (3.0)	2.1
Subtotal top 10 species	195	251	74.2	5984	75.2	74.0
Total for all individuals	264	340	100.0	7874	100.0	100.0

aMean relative abundance and basal area were calculated by dividing the abundance or basal of the focal species per plot by the abundance or basal area of all the individuals in the plot, respectively, and then taking the average of the plots. We calculated importance values as the average of mean relative density and relative basal area.

4. Discussion

Previous surveys of the flora of La Selva recorded 107 species of lianas, including one gymnosperm (*Gnetum*), one aroid (*Heteropsis*), one palm (*Desmoncus*), and one bamboo (*Elytostachys*) ([Hartshorn and Hammel, 1994](#)). These authors reported that Bignoniaceae and Fabaceae were the most speciose families for lianas at La Selva and for much of the lowland neotropics (see also [Gentry, 1982](#), [Gentry, 1991a](#)). Data to support this view were based largely on 0.1 ha samples of lianas ≥ 2.5 cm in diameter ([Gentry, 1982](#)). Restricting our data set to 0.1 ha areas and including only lianas ≥ 2.5 cm diameter, the species richness of Bignoniaceae dropped to third, behind Sapindaceae and Dilleniaceae, and the abundance of Bignoniaceae also remained third. The Fabaceae were poorly represented regardless of size-class, in both number of species (3) and individuals (12; [Appendix A](#)). Consequently, we suggest that the Bignoniaceae and particularly the Fabaceae families may be much less important in the La Selva liana community than had been previously thought. Interestingly, our census found all four species of Dilleniaceae known to occur at La Selva to be relatively common ([Table 3](#), [Table 4](#); [Appendix A](#)). The abundance of bird-dispersed Dilleniaceae over mostly wind-dispersed Bignoniaceae should not be surprising, however, considering the greater importance of animal dispersal for lianas in wetter forests ([Gentry, 1982](#), [Gentry, 1991b](#)).

The “king” of the liana community at La Selva (sensu [Burnham, 2002](#)) was clearly *M. aculeata* (Polygalaceae), constituting 17% of all individuals. Other studies have also reported strong dominance in the local liana community, but none have been as abundant as *M. aculeata* ([DeWalt et al., 2000](#), [Nabe-Nielsen, 2001](#), [Burnham, 2002](#)). For example, [DeWalt et al. \(2000\)](#) found that *Maripa panamensis* (Convolvulaceae) composed approximately 11% of the liana stems and was found in all stands in secondary and primary forests in Panama. Similarly, in Ecuador, [Burnham \(2002\)](#) reported that the most dominant liana, *Machaerium cuspidatum* (Fabaceae), represented approximately 11% of the liana stems (see also [Nabe-Nielsen, 2001](#)). The most common tree at La Selva, *Pentaclethra maculosa*, has a relative density of 12% among trees in primary forest ([Hartshorn and Hammel, 1994](#)). The importance value of *P. maculosa* was higher (17–23%), due to its extremely high relative basal area ([Hartshorn and Hammel, 1994](#)). *M. aculeata* is comparable in its importance to the liana community (16.1 and 17.5% for lianas ≥ 0.2 and 2.5 diameter, respectively) to that of *P. maculosa* to the tree community ([Table 3](#), [Table 4](#)). The success of *M. aculeata* may be attributed to its relatively low rate of mortality, especially at the smaller size-classes. We are currently testing this hypothesis at La Selva, paying particular attention to the common species. Several species of liana at La Selva (*P. pyramidata*, *Forsteronia* sp., *Smilax domingensis*) had relatively high mean densities, while contributing very little to basal area due to their relatively small stems ([Table 3](#), [Table 4](#)). The relative density of *P. pyramidata*, for example, dropped by 50% when stems < 2.5 cm diameter were excluded and, unlike the other common lianas, it suffered *higher* mortality above 2.5 cm diameter.

Liana mortality was fairly high among all species, averaging 9.4% per plot per year over the 3.5-year period. Because of the paucity of long-term studies on liana communities, however, there are few data for comparison with other sites. In a 9-year study on the growth and mortality of 15 species of lianas on Barro Colorado Island, Panama (BCI; $n=189$), [Putz \(1990\)](#) reported a much lower rate of annual genet mortality at 0.27% for lianas > 0.44 cm diameter. The majority of the mortality in our study was primarily in the smallest size-class ([Fig. 2](#), [Table 2](#)), which is consistent with studies of other woody plants ([Clark, 1994](#)). Mortality dropped to almost 3.2% when lianas reached a size of 4 cm in diameter ([Fig. 2](#), [Table 2](#)). Consequently, the extremely high rate of liana

mortality in our study was likely due to our inclusion of the very small size-classes. It is also possible that mortality was unusually high between 1999 and 2002 due to the 1998 ENSO event, inflating our per year estimates. We are continuing to monitor the lianas at La Selva to improve our estimates of annual liana mortality, recruitment, and growth.

The lack of statistical differences in liana abundance, diversity, and mortality between primary and selectively logged forests was not surprising, considering that the selectively logged portions were not harvested for more than 50 years. This is ample time to assume the physiognomy of a primary forest, especially considering the logging was probably light. Indeed, on Barro Colorado Nature Monument, in Panama, [DeWalt et al. \(2000\)](#) reported that the number of lianas in forests that were 70 and 100 years old was indistinguishable from that of primary forests (>500 years old). At Pasoh Forest Reserve in Peninsular Malaysia, [Gardette \(1996\)](#) found similar liana density and species richness in previously primary forest that was selectively logged 40 years earlier and had the lianas cut prior to logging.

4.1. Comparisons with other neotropical forest sites

Liana communities can be extremely variable throughout the tropics ([Putz, 1984a](#), [Gentry, 1991a](#), [DeWalt et al., 2000](#), [Gerwing and Farias, 2000](#), [Schnitzer et al., 2000](#), [Nabe-Nielsen, 2001](#), [Perez-Salicrup et al., 2001](#), [Burnham, 2002](#), [Schnitzer and Bongers, 2002](#)). The highest diversity of lianas recorded in any comparable study comes from Yasuní National Park in Ecuador, where 311 species (≥ 1 cm diameter) were found in a total of twelve 0.2 ha plots ([Burnham, 2002](#)). Liana density at Yasuní (1812 individuals ha^{-1}), was more than twice as high as our estimate of 816 lianas ha^{-1} (≥ 1 cm diameter) for La Selva ([Table 2](#)). Considerably higher density and diversity of lianas were also found in the eastern Brazilian Amazon, where 78 morphospecies (> 2 m tall) were found in a sample area totaling only 0.30 ha ([Gerwing and Farias, 2000](#)). One of the most liana-dense tropical forests ever reported, in the Bolivian Amazon, had an average of 2471 lianas ha^{-1} (≥ 2 cm diameter) and an estimate of 51 species ha^{-1} ([Pérez-Salicrup et al., 2001](#)). The abundance of lianas at this site in Bolivia was more than five times higher than the comparable size-classes (≥ 2 cm) at La Selva ([Table 2](#)).

Restricting our comparisons to other tropical wet forests revealed that La Selva is extremely depauperate in liana abundance and diversity. We compared our liana abundance data for individuals ≥ 2.5 cm in diameter to the comparable size-class of lianas (excluding hemiepiphytes and stranglers) in 15 wet neotropical forests (>3500 mm rainfall per year) listed in [Gentry \(1991a\)](#). We found that these other wet lowland neotropical forests apparently had, on average, nearly 80% more lianas than did La Selva ([Gentry, 1991a](#)). Specifically, the mean number of lianas ≥ 2.5 cm in diameter in these wet neotropical forests averaged 605 ha^{-1} (± 49.6 S.E., $n=15$) compared with the 340 ha^{-1} that we found at La Selva ([Table 4](#)). [DeWalt and Chave \(2004\)](#) found only 210 lianas ha^{-1} (≥ 2.5 cm diameter) at La Selva, nearly 40% less than in our study and three times fewer than that of [Gentry \(1991a\)](#).

Why lianas are less abundant at La Selva than in other wet lowland neotropical forests is unknown. [DeWalt and Chave \(2004\)](#) suggested that the abundance and basal area of lianas only appears to be lower at La Selva than in other wet lowland neotropical forests surveyed by [Gentry \(1991a\)](#) (transect data set available online from Missouri Botanical Garden), because Gentry may have overestimated liana abundance throughout the tropics by using many long, thin transects (10, 2m \times 50 m). Indeed, long, thin transects have been found to overestimate woody plant abundance compared to square plots ([Condit et al., 1996](#), [Leigh, 1999](#); Schnitzer et al., unpublished manuscript), although the exact cause for this phenomenon remains unknown. Nevertheless, Gentry (cited in [DeWalt and Chave, 2004](#)) used identical methods to census many forests throughout the neotropics and still reported 17% fewer lianas at La Selva (500 lianas ≥ 2.5 cm diameter ha^{-1}) than the average liana abundance in other lowland tropical wet forests (605 ha^{-1} ; [Gentry, 1991a](#)).

Lianas may be more abundant in seasonally dry forests than in wet forests ([Gentry, 1991a](#)). The mechanisms responsible for this pattern are still unclear, although here we present three potential hypotheses. (1) The presence of palms. It is possible that lianas do not regenerate well under the dense shade cast by palms, which are abundant in wet forests such as La Selva ([Hartshorn and Hammel, 1994](#)). [Putz \(1984b\)](#) suggested that palms were adept at shedding lianas, which may also be a factor in the paucity of lianas in forests with high palm abundance. (2) The presence of epiphytes. [Hartshorn and Hammel \(1994\)](#) suggested that the high abundance of epiphytes and stranglers in wet forests may displace lianas. (3) Competition for soil moisture. Lianas may compete better in seasonal forests, where soil moisture is lacking for part of the year because lianas can readily access water throughout the dry season ([Restom and Nepstad, 2001](#), [Schnitzer and Bongers, 2002](#), [Restom and Nepstad, 2003](#); Schnitzer, unpublished manuscript). These three hypotheses are not mutually exclusive and further studies are necessary to understand the mechanisms responsible for the distribution of lianas throughout the tropics.

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Appendix A.

Complete list of climbing and standing lianas (apparent genets ≥ 0.2 cm DBH) identified over the total 0.78 ha area (nine 24m \times 36 m plots), including the number of lianas, their relative density, density per hectare, and percent annual mortality.

Family	Species	Number of lianas (0.78 ha ⁻¹)	Relative density (%)	Liana density (ha ⁻¹)	Percent mortality (per year)
Acanthaceae	<i>Mendoncia gracilis</i>	5	0.4	6.4	17.56
Acanthaceae	<i>Mendoncia retusa</i>	1	0.1	1.3	29.27
Acanthaceae	<i>Mendoncia tonduzii</i>	2	0.2	2.6	0.00
Apocynaceae	<i>Forsteronia</i> sp.	45	3.9	57.9	12.36
Apocynaceae	<i>Odontadenia cognata</i>	9	0.8	11.6	16.26
Apocynaceae	<i>Odontadenia macrantha</i>	4	0.3	5.1	0.00
Araceae	<i>Heteropsis</i> sp.	1	0.1	1.3	29.27
Areaceae	<i>Desmoncus costaricensis</i>	5	0.4	6.4	11.71
Aristolochiaceae	<i>Aristolochia constricta</i>	20	1.7	25.7	5.85
Bignoniaceae	<i>Anemopaegma crysoleucum</i>	3	0.3	3.9	19.51
Bignoniaceae	<i>Anemopaegma orbiculatum</i>	2	0.2	2.6	0.00

Bignoniaceae	<i>Anemopaegma reticulatum</i>	1	0.1	1.3	0.00
Bignoniaceae	<i>Callychlamis latifolia</i>	4	0.3	5.1	7.32
Bignoniaceae	<i>Mussatia hyacinthina</i>	40	3.4	51.4	4.39
Bignoniaceae	<i>P. pyramidata</i>	85	7.3	109.3	8.95
Compositae (Asteraceae)	<i>Mikania leiostachya</i>	1	0.1	1.3	0.00
Compositae (Asteraceae)	<i>Piptocarpha poeppigiana</i>	4	0.3	5.1	7.32
Connaraceae	<i>Rourea glabra</i>	3	0.3	3.9	0.00
Connaraceae	<i>Rourea suerrensii</i>	8	0.7	10.3	7.32
Convolvulaceae	<i>Dicranostyles ampla</i>	22	1.9	28.3	5.32
Convolvulaceae	<i>Maripa nicaraguensis</i>	8	0.7	10.3	7.32
Cucurbitaceae	<i>Psiguria warscewiczii</i>	8	0.7	10.3	7.32
Dichapetalaceae	<i>Dichapetalum stipulatum</i>	7	0.6	9.0	4.18
Dilleniaceae	<i>Davilla</i> sp.	35	3.0	45.0	8.36
Dilleniaceae	<i>D. nitida</i>	92	7.9	118.3	10.50
Dilleniaceae	<i>Doliocarpus coriaceus</i>	36	3.1	46.3	9.76
Dilleniaceae	<i>D. dentatus</i>	70	6.0	90.0	8.78
Euphorbiaceae	<i>Adelia triloba</i>	2	0.2	2.6	0.00
Euphorbiaceae	<i>Omphalea diandra</i>	2	0.2	2.6	0.00
Euphorbiaceae	<i>Plukenetia stipellata</i>	1	0.1	1.3	29.27
Fabaceae	<i>Bauhinia guianensis</i>	9	0.8	11.6	0.00
Fabaceae	<i>Machaerium floribundum</i>	1	0.1	1.3	0.00
Fabaceae	<i>Machaerium seemannii</i>	2	0.2	2.6	14.63
Gnetaceae	<i>Gnetum-leyboldii</i>	2	0.2	2.6	14.63
Loganiaceae	<i>Strychnos</i> sp.	1	0.1	1.3	0.00
Malpighiaceae	<i>Hiraea smilacina</i>	3	0.3	3.9	19.51
Malpighiaceae	<i>Hiraea</i> sp.	1	0.1	1.3	29.27
Malpighiaceae	<i>Stigmaphyllon lindenianum</i>	1	0.1	1.3	29.27
Olacaceae	<i>Heisteria scandens</i>	49	4.2	63.0	5.97
Phytolaccaceae	<i>Trichostigma polyandrum</i>	2	0.2	2.6	14.63
Piperaceae	<i>Piper multiplinervium</i>	6	0.5	7.7	0.00
Piperaceae	<i>Sarcorhachis naranjoana</i>	7	0.6	9.0	4.18
Polygalaceae	<i>M. aculeata</i>	198	17.1	254.6	3.40
Polygonaceae	<i>Coccoloba</i> sp.	7	0.6	9.0	8.36

Polypodiaceae	<i>Salpichlaena volubilis</i>	14	1.2	18.0	25.09
Rubiaceae	<i>Randia altiscandens</i>	4	0.3	5.1	0.00
Sapindaceae	<i>Paullinia baileyi</i>	1	0.1	1.3	0.00
Sapindaceae	<i>Paullinia granatensis</i>	70	6.0	90.0	7.94
Sapindaceae	<i>Paullinia fibrigera</i>	1	0.1	1.3	0.00
Sapindaceae	<i>Paullinia fuscescens</i>	24	2.1	30.9	8.54
Sapindaceae	<i>Paullinia pinnata</i>	20	1.7	25.7	7.32
Sapindaceae	<i>Paullinia robusta</i>	1	0.1	1.3	0.00
Sapindaceae	<i>Paullinia serjaniaefolia</i>	1	0.1	1.3	0.00
Scrophulariaceae	<i>Schlegelia</i> sp.	3	0.3	3.9	19.51
Scrophulariaceae	<i>Schlegelia sulfurea</i>	5	0.4	6.4	0.00
Smilacaceae	<i>S. domingensis</i>	38	3.3	48.9	7.70
Smilacaceae	<i>Smilax mollis</i>	2	0.2	2.6	29.27
Smilacaceae	<i>Smilax</i> sp.	20	1.7	25.7	14.63
Solanaceae	<i>Solanum siparunoides</i>	1	0.1	1.3	0.00
Verbenaceae	<i>Aegiphila cephalophora</i>	5	0.4	6.4	0.00
Unidentified	Unidentified	136	11.7	174.9	24.53
Totals		1161	100.0	1493.1	9.66

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