Liana abundance in a Puerto Rican forest

Katherine Rice[a], Nicholas Brokaw[b,*], Jill Thompson[b]

[a]*Carleton College, 300 North College Street, Northfield, MN 55057, USA*
[b]*Institute for Tropical Ecosystem Studies, University of Puerto Rico, P.O. Box 23341, San Juan, PR 00931-3341, USA*

Abstract

Liana (woody vine) abundance varies among tropical forests and is often high in disturbed forests. In two areas of subtropical wet forest in Puerto Rico, El Verde and Bisley, we recorded the density of liana stems ≥1 cm dbh, and the percent of tree crowns (trees ≥10 cm dbh) that lianas infested. Both study areas have been disturbed by hurricanes several times in the past century; however, sample plots in each area were divided between plots that were less disturbed and those that were more disturbed, by both hurricanes and humans. The mean density and basal area of liana stems at El Verde were significantly higher in the less disturbed plots than in the more disturbed plots. The percent tree crown infested by lianas was higher on certain tree species and on larger trees, both of which characterized the less disturbed forest. Results at Bisley were similar to those at El Verde. Liana density and tree crown infestation in these Puerto Rican forests were low compared with most other tropical forests, contrasting especially with high values in other disturbed forests. Liana abundance varies among forests for complex reasons, including differences in disturbance, biogeography, seasonality, and tree host features.
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Keywords: Disturbance; Hurricane; Land use; Liana; Puerto Rico; Species diversity; Tropical forest

1. Introduction

Lianas are woody climbing plants and a motif of tropical forests (Richards, 1996), where they contribute 10–25% of plant species richness (Gentry and Dodson, 1987; Corlett, 1990; Muthuramkumar and Parthasarathy, 2001; Nabe-Nielsen, 2001; Gentry, 1991). In mature forests lianas proliferate in treefall gaps that provide high light and low vegetation for liana growth and climbing (Putz, 1984b; Schnitzer and Carson, 2001). Lianas are also common in forest disturbed by logging and along edges of forest fragments (Viana and Tabanez, 1996; Laurance et al., 1997). In disturbed areas, lianas can suppress tree regeneration and impede recovery of forest structure (Schnitzer et al., 2000; Tabanez and Viana, 2000; Pérez-Salicrup, 2001).

They also reduce the growth of mature host trees (Putz, 1984a; Clark and Clark, 1990). Laurance et al. (1997) measured the negative effects of lianas on tree regeneration along edges of forest fragments in Amazonia. They showed, given the enormous area of forest edges in Amazonia, that liana infestation contributes to a large additional loss in regional biomass after deforestation. Recent findings also suggest that increased atmospheric CO_2 may be promoting liana growth and altering forest structure and composition in Amazonian forests (Phillips et al., 2002).

Given this large role of lianas in forest diversity and structure, it is important to study the variables influencing liana abundance (Schnitzer and Bongers, 2002). Liana density has been weakly correlated with soil fertility (Putz and Chai, 1987; Gentry, 1991; Schnitzer and Bongers, 2002) and significantly correlated with host species (Campbell and Newbery, 1993; Clark and Clark, 1990; Muthuramkumar and Parthasarathy,

2001). Large trees are more likely to host liana stems at Yasuní, Ecuador, and to support higher liana basal area at La Selva, Costa Rica (Clark and Clark, 1990; Nabe-Nielsen, 2001). In Sabah, East Malaysia, however, there was no relationship between liana infestation and tree diameter, although branch-free bole height was important (Campbell and Newbery, 1993). Large lianas are characteristic of old growth forests (Budowski, 1965, 1970; Clark, 1996), whereas liana density tends to increase in disturbed forest (Dewalt et al., 2000; Putz and Chai, 1987; Lugo and Scatena, 1995; Hegarty and Caballé, 1991; Putz, 1984b; Poncy et al., 1998). Lianas may be more abundant where rainfall is seasonal and light intensity increases below seasonally deciduous tree canopies (Gentry, 1991; S. Schnitzer personal communication). Lastly, storm damage promotes lianas in some forests (Webb, 1958; Allen et al., 1997; Lugo et al., 2000) but not all (Whigham et al., 1999). In this paper, we attempt to explain differences in liana abundance between more- and less-disturbed forests in Puerto Rico, and between Puerto Rican forests and other tropical sites.

2. Methods

2.1. Study areas

This study was carried out in subtropical wet forest (Ewel and Whitmore, 1973) in the Luquillo Experimental Forest (LEF), Luquillo Mountains ($18°$N, $65°$W), Puerto Rico. There were two study areas, about 5 km apart: El Verde Research Area (managed by the University of Puerto Rico) and the Bisley Experimental Watersheds (US Department of Agriculture, International Institute of Tropical Forestry). Both study areas receive about 3500 mm of rain per year, with usually no month receiving less than 200 mm (Scatena, 1989; Waide and Reagan, 1996). El Verde is at about 350 m and Bisley at 300 m elevation. These areas represent the vegetation and environment of the "tabonuco forest", so named for a dominant tree *Dacryodes excelsa* Vahl (Odum, 1970).

The study area at El Verde was the 16-ha Luquillo Forest Dynamics Plot (LFDP). The LFDP is part of the Center for Tropical Forest Science (Smithsonian Institution) network of forest research plots, and is also a component of the Luquillo Long-Term Ecological

Research Program (US National Science Foundation). In the LFDP, all self-supporting woody plants ≥ 1 cm diameter at 130 cm above ground (dbh) have been tagged, identified, and measured for dbh (Thompson et al., 2002).

We worked in two areas of the LFDP representing different land use histories and amount of damage sustained during recent hurricanes. Until the early 1930s, the northern area of the LFDP had been variously clearcut for timber or used for agriculture such as coffee plantations (Thompson et al., 2002). The southern area of the LFDP had apparently never been cleared, but there was some selective logging and thinning in the 1930s and 1940s (Odum, 1970). As a result the more disturbed area had more stems per ha (4572) and less basal area (810.6 m^2 ha^{-1}), than the less disturbed area (4325 stems ha^{-1}, 826 m^2 ha^{-1} basal area; Thompson et al., 2002).

Severe hurricanes strike the Luquillo Mountains about every 60 years, but intervals vary (Weaver, 1986). The forest at El Verde suffered significant hurricane damage in 1928, 1932, 1989, and 1998 (Crow, 1980; Zimmerman et al., 1994; J. Thompson, personal observation). Damage from the two recent hurricanes, Hurricane Hugo in 1989 and Georges in 1998 was more severe in the northern part of the LFDP than the southern. Stem damage, assessed as percent basal area for tree stems that were snapped off or tipped up, was 20.1% in the northern area and 12.8% in the southern area of the LFDP during Hurricane Hugo, and 18.0 and 11.6% in the north and south, respectively, during Hurricane Georges (J. Thompson, unpublished data).

Thus the northern (hereafter "more disturbed") area of the LFDP has suffered both more human and more hurricane disturbance than the southern (hereafter "less disturbed") area. (These areas represent "cover class 3" and "cover class 4" as described in Thompson et al., 2002.) To compare the amount of lianas in these areas having different disturbance histories, we randomly selected 10 20 m × 20 m plots in each of the more and less disturbed areas of the LFDP.

The Bisley study was carried out to corroborate the main results from El Verde and was not intended to exactly replicate the study at El Verde (described above). Parts of the Bisley study area were intensively used until about the 1950s for charcoal manufacture, mining, farming, timber cutting and tree plantation (Scatena, 1989; García-Montiel and Scatena, 1994).

As at El Verde, the Bisley forest area was damaged by Hurricane Hugo in 1989 and Hurricane Georges in 1998 (Basnet et al., 1992; N. Brokaw, pers. observ.). At Bisley we selected a stratified random sample of five 10 m × 50 m belt transects in which to assess lianas. These transects all fell in highly disturbed forest, judging from structure and tree species composition (N. Brokaw, pers. observ.). Therefore we added three 10 m × 50 m transects purposefully sited in available patches of less disturbed forest, evidenced by large stems of mature forest tree species.

2.2. Field methods

We defined lianas as woody vines rooted in the ground, thus excluding herbaceous vines, epiphytes, and hemiepiphytes. At both El Verde and Bisley we determined liana stem density by counting the number of all liana stems ≥1 cm dbh, that is, all liana stems passing through a plane 130 cm above ground within the plot, whether rooted in the plot or not. We measured dbh of all stems to calculate liana basal area. We also determined the approximate number of liana individuals, by counting as one individual liana all stems clearly connected to each other. At El Verde lianas were identified following Acevedo-Rodríguez (1985); lianas were not identified at Bisley. At El Verde we also counted and measured the stems (≥1 cm dbh) of

Philodendron angustatum Schott (Araceae), because it was a common herbaceous climber. However, *P. angustatum* usually becomes a ''secondary epiphyte'' when it loses root contact with the ground. We analyzed liana and *P. angustatum* data separately.

We determined categories of tree crown infestation by lianas for individual trees (including palms) ≥10 cm dbh. At El Verde we estimated percentage of crown infestation by lianas on a five point scale (0, 1–25, 26–50, 51–75, 76–100% [cf. Clark and Clark, 1990]). If a tree crown had no visible lianas but liana stems touched the tree stem this was also noted. The diameter of each host tree ≥10 cm dbh was recorded at the time of assessment. Tree species identities at El Verde were obtained from the LFDP census data. At Bisley we recorded only presence or absence of lianas in individual tree crowns; host species was not recorded. The liana assessment at El Verde was made in June and July 2001. The assessment at Bisley was made between October 2001 and September 2002.

3. Results

3.1. Liana species, stems, and basal area

We counted a total of 419 liana stems in the twenty 20 m × 20 m plots within the LFDP at El Verde.

Table 1
Density of liana stems and individuals (see text), liana basal area, density of the herbaceous climber *P. angustatum*, and crown infestation (trees ≥10 cm dbh) in forest plots at El Verde, Puerto Rico

	Liana stems 0.1 ha^{-1}	Liana individuals 0.1 ha^{-1}	Liana basal area cm^2 0.1 ha^{-1}	*P. angustatum* stems 0.1 ha^{-1}	Crown infestation incl. *P. acuminata* (not incl. *P. acuminata*)
All plots	52.4 (6.98)	39.9 (5.83)	289.4 (69.56)	55.1 (13.50)	16.8 (26.3)
	2.5–125	2.5–102.5	11.1–759	0.0–198	
Less disturbed	67.5 (9.08)[*]	53.8 (6.17)[*]	423.6 (70.48)[**]	64.3 (16.92) ns[a]	23.4[***]
	25–125	25–102.5	58.3–759	2.5–163	(33.5)[***]
More disturbed	37.3 (8.48)	26.0 (7.94)	155.0 (37.38)	46.0 (21.56)	10.2 (16.7)
	2.5–70	2.5–57.5	11.1–354	0.0–198	

Data are from twenty 20 m × 20 m subplots, 10 in more disturbed and 10 in less disturbed plots in the Luquillo Forest Dynamics Plot. Data are: mean (standard error) range. Values are significantly different between more and less disturbed plots, except for density of *P. angustatum*. Student's *t*-test was used for stems, individuals, and basal area; a test for the equality of two percentages was used for percent crown infestation (Sokal and Rohlf, 1969). Crown infestation data are given for all trees, including the palm *P. acuminata*, and, in parentheses, without *P. acuminata*.

[a] ns: not significant; for comparisons between less and more disturbed.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

We identified 84% of these stems, totaling six species in six genera. The remaining stems disappeared into the canopy, presenting no identifiable features, and may have included additional species. Of the identified lianas *Marcgravia* spp. (Macgraviaceae) were the most abundant (comprising almost 50% of liana stems counted). These *Marcgravia* spp. maintained stems rooted in the ground. Other important species (in descending order of abundance) were *Rourea surinamensis* Miq. (Connaraceae), *Schlegelia brachyantha* Griseb. (Scrophulariaceae), *Paullinia pinnata* L. (Sapindaceae), *Dioscorea altissima* Lam. (Dioscoreaceae), and *Hippocratea volubilis* L. (Hippocrateaceae).

For all plots in the LFDP at El Verde, there was a mean of 52.4 (S.E. = 6.98) liana stems 0.1 ha^{-1} (Table 1). There were more liana stems in the less disturbed plots than in the more disturbed plots ($t = 2.44$, $P < 0.05$). Liana individuals showed the same pattern, with a mean of 39.9 (S.E. = 5.83) individuals 0.1 ha^{-1} among all plots and significantly more ($t = 2.76$, $P < 0.05$) in the less disturbed than in

the more disturbed plots (Table 1). At Bisley there were 22.3 (S.E. = 8.64) liana stems 0.1 ha^{-1} for all plots combined, and differences between more and less disturbed forest were consistent with differences at El Verde but were not statistically significant. Mean basal area of lianas for all plots at El Verde was 289.4 cm^2 0.1 ha^{-1} (S.E. = 69.56, Table 1). Basal area of lianas was higher in the less disturbed plots ($t = 3.37$, $P < 0.01$, Table 1). At El Verde *P. angustatum* stems were as abundant as liana stems (mean 55.1 stems 0.1 ha^{-1}, S.E. = 13.50; Table 1) and were recorded in all 10 of the less disturbed plots, as opposed to only five of the more disturbed plots, but they were not statistically more abundant in the former.

3.2. Tree crown infestation by lianas

Of the 739 trees ≥10 cm dbh assessed at El Verde, 16.8% had lianas in their crowns and 20.56% had lianas touching their stems but not infesting their
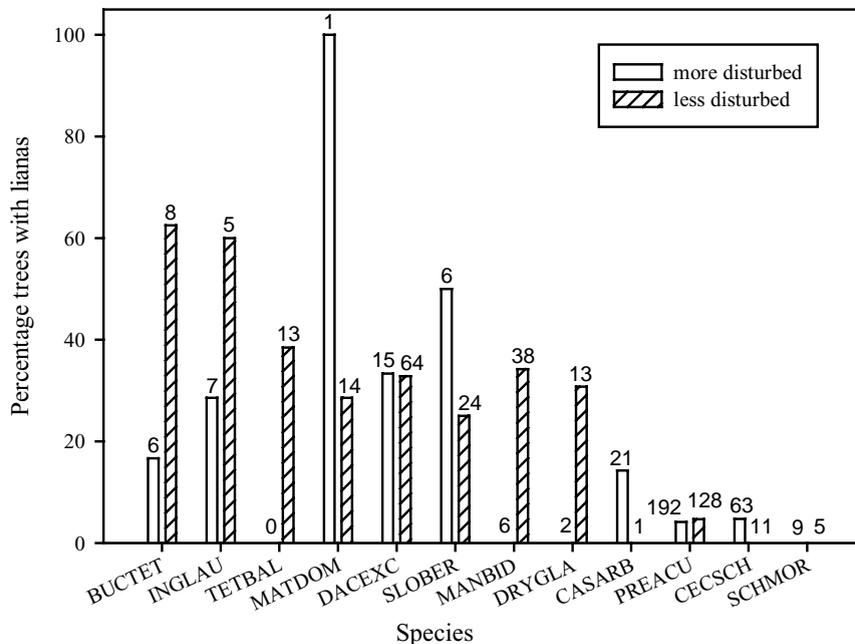

Fig. 1. Percent of individuals of various tree species with liana (any crown infestation class) in more and less disturbed forest (see text) at El Verde, Puerto Rico. Data are shown for tree species with ≥12 individuals ≥10 cm dbh in the study plots ($\chi^2 = 93.3$, $P < 0.0001$). Number of individuals is shown at the top of each bar. BUCTET: *Buchenavia tetraphylla*; CASARB: *Casearia arborea* (Rich.) Urb.; CECSCH: *Cecropia schreberiana*; DACEXC: *Dacryodes excelsa*; DRYGLA: *Drypetes glauca* Vahl; INGLAU: *Inga laurina*; MANBID: *Manilkara bidentata* (A. DC.) A. Chev.; MATDOM: *Matayba domingensis*; PREACU: *Prestoea acuminata*; SCHMOR: *Schefflera morototoni*; SLOBER: *Sloanea berteriana* Choisy; TETBAL: *Tetragastris balsamifera* (botanical authors given here when not in text).
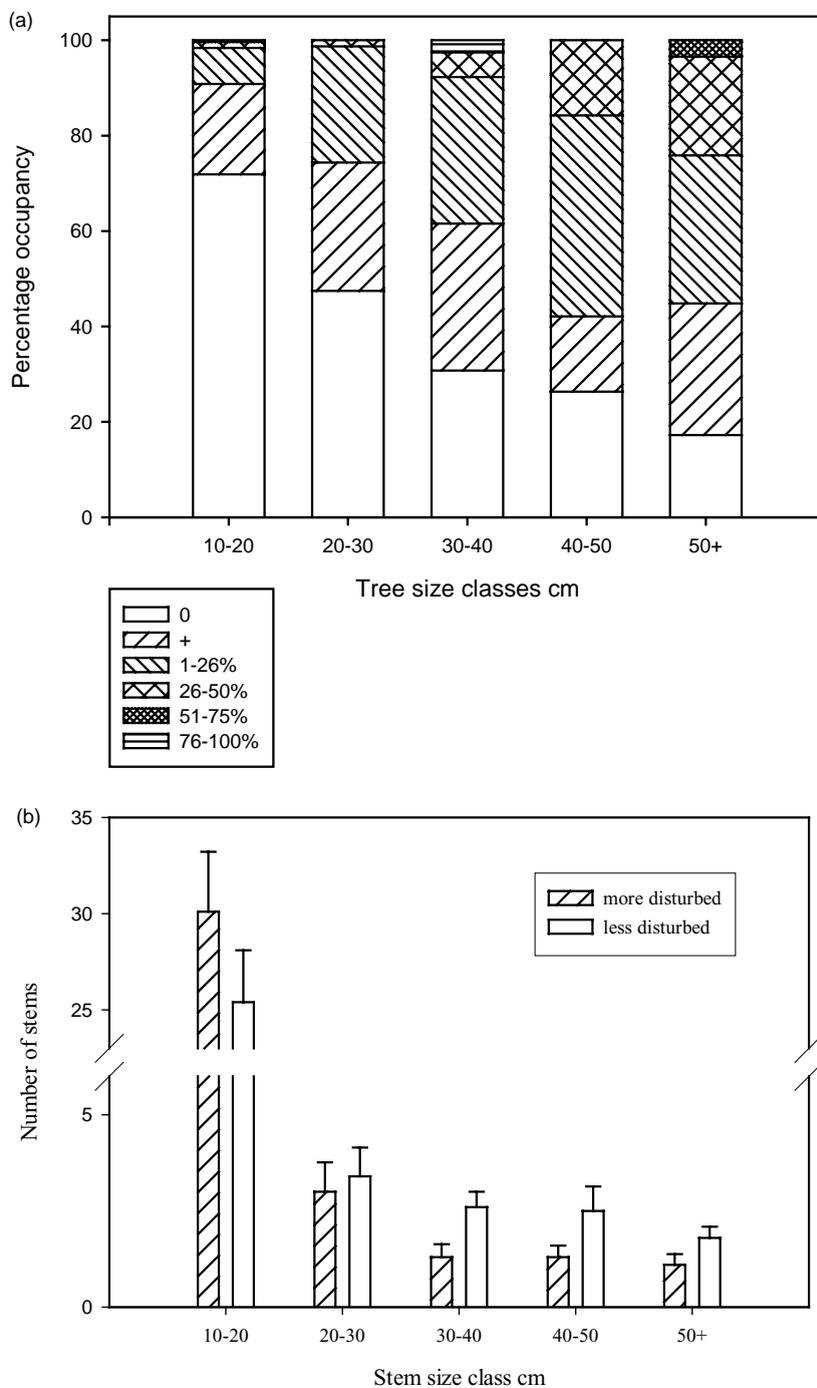
Fig. 2. (a) Percentage crown occupancy (liana infestation, see text) for different tree diameter classes at El Verde, Puerto Rico ($\chi^2 = 86.6$, $P < 0.0001$). (b) Mean number and standard error of trees of different diameter classes per plot (20×20 m) in the less disturbed and more disturbed plots at El Verde.

crowns. At Bisley 4.9% of trees ≥10 cm dbh had lianas in their crowns. Differences between less and more disturbed plots were consistent with differences in liana density (Table 1).

At El Verde, tree species with ≥12 stems in the study plots varied significantly in the proportion having lianas in their crowns ($\chi^2 = 93.3$, $P < 0.0001$, Fig. 1). *Buchenavia tetraphylla* (Aubl.), *Inga laurina* (Sw.) Willd., *Tetragastris balsamifera* (Sw.) Kuntze, and *Matayba domingensis* (DC) Radlk. each had more than 33% of their individuals with lianas; whereas *Prestoea acuminata* (Willd.) H.E. Moore, *Cecropia schreberiana* Miq., and *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin had the lowest proportions of individuals with lianas. Tree species with more crown infestation by lianas were more abundant in the less disturbed plots of the LFDP, whereas lightly infested species, especially *P. acuminata*, were more abundant in the more disturbed plots (Fig. 1). Crown infestation overall is strongly related to the abundance of *P. acuminata* (Table 1).

Larger trees tended to have higher percent crown infestation by lianas (Fig. 2a). Among trees in three diameter classes (10–30, 30–50, 50–70 cm dbh, excluding the palm *P. acuminata*, whose diameter varies little), larger diameters were more infested ($\chi^2 = 86.6$, $P < 0.0001$). In the LFDP, tree diameter, and thus liana infestation, was larger in the less disturbed plots (Fig. 2b; $t = 3.87$, $P < 0.001$).

4. Discussion

This study in the Luquillo Experimental Forest (LEF), Puerto Rico, recorded more stems, individuals, and basal area of lianas in less disturbed than in more disturbed forest plots. Over all the plots, but especially characterizing the less disturbed plots, large trees and certain tree species were relatively more infested with lianas. The more disturbed plots, with fewer lianas, were located in areas heavily used by humans (in some places cleared) 70–100 years before our study (Thompson et al., 2002), and relatively more damaged by hurricanes. Similarly, Budowski (1965, 1970) and Clark (1996) noted lower abundances of large lianas in younger forest in Costa Rica, and Dewalt et al. (2000) documented this effect in Panama. As in young forests elsewhere, our more disturbed plots contained many pioneer trees, such as *C. schreberiana* and *S. morototoni*, that had low liana crown infestation, perhaps because their fast growth, smooth bark, and rapid turnover of branches and leaves discourage liana infestation (cf. Putz, 1984a; Clark and Clark, 1990). Palms are also typically liana-free, and the palm *P. acuminata* was abundant throughout the study areas, but especially in the more disturbed plots (Thompson et al., 2002).

Whether more or less disturbed, there were fewer liana species (cf. Gentry, 1991) and fewer stems, or less crown infestation by lianas, in these plots than in most other tropical forests with extant data (Table 2). Our record of six species identified in 0.8 ha at El Verde probably missed some species, yet taxonomic surveys for all of El Verde Research Area (*c*. 40 ha) include only 48 species of ''vines and lianas'' (i.e., including both herbaceous and woody vines; Lawrence, 1996). By contrast, there were 51 liana species in one ha in Bolivia (Pérez-Salicrup et al., 2001) and 138 species in 0.4 ha in Ecuador (Nabe-Nielsen, 2001). The different methods and definitions used among studies may explain some differences in apparent liana abundance, but resolving those differences would probably not change the overall result of fewer liana species and individuals, and less crown infestation, in these Puerto Rican forests.

Several causes may combine to reduce the diversity and abundance of lianas in the LEF. Liana species richness is generally lower on islands (Gentry, 1991), such as Puerto Rico, perhaps because a disproportionate number of liana species are wind-dispersed and may be less successful at long-distance dispersal from mainland areas, compared to animal-dispersed plants (Gentry, 1991). At El Verde, for example, *Macfadyena ungis-cati* (L.) A. Gentry is the only wind-dispersed liana in the Bignoniaceae, compared with about 24 such species on Barro Colorado Island, Panama (Croat, 1978). Liana density may also be low because the relatively aseasonal rainfall of the Luquillo Mountains permits an evergreen canopy. This precludes the seasonally high light under a semi-deciduous canopy that may promote liana establishment and growth in the understory (S. Schnitzer, personal communication). Yet the high levels of disturbance by humans and hurricanes in the LEF would seem to provide the ideal high light and low vegetation for successful liana growth and

Table 2
Comparison of liana densities and % trees with lianas in tropical forests

Location	Forest type	Study area (ha)	Liana size	Lianas 0.1 ha^{-1}	Tree size	% trees with lianas	Reference
Puerto Rico: El Verde	Subtropical wet, "less disturbed"	0.4	≥1.0 cm dbh	67.5 stems 53.8 inds.	≥10 cm dbh	23.4 (33.5)	This study
Puerto Rico: El Verde	Subtropical wet, "more disturbed"	0.4	≥1.0 cm dbh	37.3 stems 26.0 inds.	≥10 cm dbh	10.2 (16.7)	This study
Puerto Rico: Bisley	Subtropical wet, "less disturbed"	0.15	≥1.0 cm dbh	40.0 stems	≥10 cm dbh	4.7	This study
Puerto Rico: Bisley	Subtropical wet, "more disturbed"	0.25	≥1.0 cm dbh	11.6 stems	≥10 cm dbh	5.1	This study
Costa Rica	Primary tropical wet	150.0	–	–	≥10 cm dbh (946 spp.)		Clark and Clark (1990)
Panama	Tropical moist	–	–	–	–	49	Putz (1982) in Putz (1983)
Venezuela	Evergreen tropical rain	0.2	–	–	≥10 cm dbh	42.1	Putz (1983)
Ecuador	Old-growth tropical moist	0.4	≥1.0 cm dbh	94.5	>40 cm dbh	52	Nabe-Nielsen (2001)
Bolivia	Lowland semi-deciduous	2.2	≥2.0 cm dbh	247.1	≥10 cm dbh	86.3	Pérez-Salicrup et al. (2001)
India	Tropical evergreen	30.0	≥1.0 cm dbh	37.3	≥30 cm gbh	28	Muthuramkumar and Parthasarathy (2001)
East Malaysia	Virgin dipterocarp	8.0	≥2.0 cm gbh	88.2	≥30 cm gbh	57	Campbell and Newbery (1993)
Sarawak, Malaysia	Primary dipterocarp	1.0	>1.0 cm dbh	55 (valley) 29 (ridge)	>10 cm dbh	52.3 (valley) 33.9 (ridge)	Putz and Chai (1987)

For "% trees with lianas" variable criteria may have been used among studies to define a tree with lianas; see the individual studies for clarification. For Puerto Rico sites "% trees with lianas" refers to trees with lianas in their crowns, and values including and (in parentheses) not including the palm *P. acuminata* as a host tree are given (see Table 1). For Puerto Rico sites "more disturbed", "less disturbed", "inds." (individuals), and "stems" are defined in Methods. "gbh": girth at breast height.

climbing (cf. Webb, 1958; Laurance et al., 1997; Phillips et al., 2002).

However, natural disturbances such as hurricanes may exacerbate the negative effects of human disturbance on lianas documented above. At El Verde, Hurricane Hugo damaged the secondary tree species in the more disturbed forest more than the old growth species in less disturbed forest (Zimmerman et al., 1994). Thus, human and natural disturbance together may maintain a rapid cycle of comparatively small, secondary tree species that is inimical to liana development. In the old growth forest areas of the LFDP Hurricane Hugo did less damage, but presumably it stripped lianas from trees, as it stripped off branches that can support lianas (Brokaw and Grear, 1991). Likewise, in South Carolina, USA, Hurricane Hugo killed many lianas in an old growth floodplain forest, and Allen et al. (1997) suggested that if this mortality was not offset by increased recruitment, liana density would decline. In apparent contrast to our results, Chinea (1999) recorded heavy growth of vines in an area of the LEF soon after Hurricane Hugo, but his observations included many herbaceous climbers, and, in any case, their abundance quickly declined.

The causes of liana abundance are varied. They may include biogeography and seasonality, and certainly include disturbance. Disturbance influences host tree size and species, which affect liana density and tree crown infestation. Disturbance is usually thought to increase liana abundance, but events such as hurricanes may reduce them, by stripping lianas and branch supports from trees. We suggest that frequent hurricanes can explain the low abundance of lianas in this study. But we cannot yet explain why lianas thrive in some disturbed forests but not others.

Acknowledgements

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