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Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest

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ABSTRACT

Liana abundance and host tree colonization dynamics during a 10-year period were studied in a subtropical Atlantic Forest in Northeastern Argentina. The impact of liana and woody bamboo cutting on liana abundance and diversity, tree infestation and advanced tree regeneration (individuals >5 cm and <10 cm DBH) was assessed during the same time period. Six permanent 1 ha plots (three control and three cutting plots) were located in the year 2000 in a native forest stand. Three plots were subjected to bamboo and liana cutting (BLC) and other three left as control (C). All lianas regardless of their diameters were cut. Liana abundance and basal area increased more than 50% after ten years in C plots, while the proportion of trees infested with lianas increased from 69% in 2000 to 83% in 2010 in the same plots. In this time period some trees species were able to shed their lianas but increased liana load was observed in other tree species which accounted for the increased proportion of infested trees. In BLC plots the proportion of infested trees was similar (about 60%) in 2000 and 2010, indicating a rapid liana colonization of trees after the treatment. Trees with short branch-free boles were rapidly re-infested compared to taller trees. Liana abundance and basal area were substantially lower in BLC compared to C plots, consistent with the relatively short period of colonization in the cutting plots. Tendriled lianas decreased more than twiners and scramblers. Liana richness and species evenness was not affected by the cutting treatment. Advance tree regeneration was partially affected: tree sapling abundance was similar between C and BLC plots but tree basal area was slightly lower in 2010 in C plots indicating that the treatment enhanced sapling growth. No differences in liana infestation on tree saplings were found between C and BLC plots in 2010. Our results indicate a rapid recovery of lianas after cutting, particularly for individuals smaller than 2.5 cm DBH, and a substantial effect of this silvicultural treatment applied to enhance tree regeneration. Similar to other tropical forests, a relatively large increase in liana abundance and tree infestation, as observed in C plots, is occurring in this semideciduous forest.

1. Introduction

Liana abundance and biomass is increasing worldwide mainly as a result of disturbance in tropical and subtropical forests, and probably enhanced by climate change (Phillips et al., 2002; Schnitzer and Bongers, 2011; Wright et al., 2004). Large gaps resulting from natural or anthropogenic disturbances enhance liana proliferation, which in turn inhibit tree regeneration and stall succession (Putz, 1984; Schnitzer et al., 2000). Lianas decrease the amount of solar radiation available for trees, reduce fecundity, growth and increase tree mortality rates of their hosts (Hegarty and Caballe, 1991; Ingwell et al., 2010; Kainer et al., 2006; Laurance et al., 2001; Nabe-Nielsen et al., 2009; Putz, 1984; Schnitzer and Bongers, 2002). Thus, increasing liana abundance may have profound consequences on carbon, nutrient and water cycling in forests ecosystems (Schnitzer and Bongers, 2011).

Liana growth on canopy trees is a natural phenomenon; however, the term infestation is frequently used to describe liana load. Ingwell et al. (2010) found that the number of trees with severe

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liana infestation (i.e. >75% of their canopy covered by lianas) increased 65% from 1996 to 2007 in a seasonal forest in Panama. Most of the trees in tropical and subtropical forests are colonized by lianas. However, not all the trees are equally infested. Tree species with long branch-free boles and smooth bark are likely to be free of lianas while the opposite is expected for trees with short trunks or rough bark (Campanello et al., 2007b; Campbell and Newbery, 1993). Indeed, according to Ingwell et al. (2010), many trees experienced cycles of heavy crown infestation by lianas followed by periods of relatively light infestation, indicating a rather rapid turnover of lianas in tropical and subtropical forests. The semideciduous Atlantic Forest where this study took place, has a high diversity of liana species (Hora and Soares, 2002; Morellato and Leitão Filho, 1998), and is rich in native woody bamboo species as well, some of which colonize disturbed sites inhibiting regeneration of other plant species (Campanello et al., 2007a; Carvalho et al., 2011; Montti et al., 2011a; Tabarelli and Mantovani, 1999).

Liana infestation has been early identified as a problem in forests managed for timber production. Removal of lianas before harvesting is used to decrease tree damage during logging operations (Alvira et al., 2004; Fox, 1968; Putz, 1991; Vidal et al., 1997) and liana biomass in tree crowns with a concomitant increment on growth rates of canopy trees between harvesting cycles (Putz, 1991). However, not all the species respond to the liana cutting treatment (Campanello et al., 2007b) and liana cutting may have undesirable effects on tree regeneration due to direct damage to tree saplings and seedlings when dead lianas fall to the ground (pers. obs.), on the fauna that uses lianas for food and refuge (Emmons and Gentry, 1983) and in the long term through indirect effects by altering plant–animal interactions such as pollination and seed dispersal (Schnitzer and Bongers, 2002). Lianas tend to use several types of vegetative reproduction including resprouting and thus it is difficult to predict a priori the impact of liana removal treatments.

In this study we assessed if: (1) liana abundance, basal area and tree infestation increased over a 10-year period, (2) liana richness and abundance changed after liana cutting and if this treatment affected differently lianas grouped by climbing mechanism, (3) liana re-infested host trees after 10 years since cutting and (4) if the treatment enhanced advanced tree regeneration in the semideciduous Atlantic Forest in Northern Argentina. To assess these questions, we measured liana abundance, richness and basal area, and quantified tree and sapling infestation in a 10-year-old experiment consisting of three controls (C) and three bamboo and liana cutting (BLC) plots. We expected abundance and basal area of lianas to increase in ten years as reported for other tropical and subtropical forests. Also, an increment of tree infestation due to facilitation (i.e. is easiest for lianas to climb other lianas) and to increased tree size and age was predicted in control plots after 10 years. Re-infestation in BLC plots was expected to be higher in species with short branch-free boles. Finally, an increment in tree sapling basal area was expected due to increased growth rates of saplings in bamboo and liana cutting plots (Campanello, 2004).

2. Methods

2.1. Study area

The research was conducted in a native subtropical semideciduous forest in northern Argentina (258580S, 548130W). The forest was subjected to selective logging of commercial trees in the 1960s and again in 2000. Mean annual rainfall at the study site is about 2000 mm, evenly distributed throughout the year, and the average annual temperature is 21 °C with mean monthly amplitude of 10 °C (Cabrera, 1976). Frost seldom occurs during winter. The number of days with freezing temperatures ranges from 2 to 9, depending on river proximity and altitude of the site (Ligier, 1999). Temperatures can reach -5 °C but values lower than -1.5 °C were observed only 11 times in a 30 year period (Servicio Meteorológico Nacional, Argentina, 2005). The soils are derived from basaltic rocks containing high concentration of Fe, Al and Si, correspond to the 6a complex type according to local descriptions (Ligier et al., 1990) and include Alfisols, Mollisols and Inceptisols (Soil Survey Staff, 1992). Soils in the study area have a relatively high exchangeable nitrogen of about 11 and 10 mg g^{-1} of NH_4^+ and $NO)_3^-$, respectively, and low concentrations of available *P* (less than 2 mg g^{-1} of *P* determined with anion resin beads) (Campanello, 2004). Some of the dominant canopy trees are: *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), *Nectandra megapotamica* (Spreng.) Mez (Lauraceae), *Bastardiopsis densiflora* (Hook. & Arn.) Hassler (Malvaceae), *Cedrela fissilis* Vell. (Meliaceae), *Cordia americana* L. (Boraginaceae) and *Lonchocarpus leucanthus* Burkart (Fabaceae). Lianas are abundant particularly in forest gaps and disturbed sites. The most abundant liana species belong to the Bignoniaceae and Fabaceae families, and species in the genera *Adenocalymna*, *Fridericia* and *Acacia* are common. The understory has abundant bamboo grasses (*Chusquea ramosissima* Lindman and *Merostachys clausenii* var. *clausenii* Munro). The species *C. ramossissima* can be an aggressive colonizer after human disturbance. The culms of this rhizomatous species can be either erect or scandent and have a length of 4–15 m (Montti et al., 2011b). In logged forests, *C. ramosissima* is very abundant and forms a dense stratum 2–3 m in height (Campanello et al., 2007a), which represents an aerial biomass of 4000–5500 kg ha^{-1} (unpublished results) that significantly reduces solar radiation reaching the ground and inhibits canopy tree regeneration (Campanello et al., 2009).

2.2. Experimental design

We conducted this study in six permanent 1 ha plots that are part of an experiment established in May 2000. These plots were located in a forest with similar canopy dominance and understory vegetation. A 20 m buffer zone was established around each plot. Three of these plots had a treatment consisting of bamboo and liana cutting (BLC) and the other three were their control (C). Plots were arranged in a randomized complete block design. Blocking was based on soil type, topographic position, understory vegetation (i.e. *C. ramosissima* abundance) and stand basal area. In each plot, all the trees greater than 10 cm in diameter at 1.30 m above ground (DBH) were identified, marked, mapped, and their DBH measured with a diameter tape. Stand basal area in C and BLC plots was 19.5 ± 2.5 and 20.4 ± 0.9 m^2 ha^{-1} with 280 ± 28 and 329 ± 22 tree individuals ha^{-1}, respectively. In September 2000, selective harvesting of 2–6 large individuals ha^{-1} was performed according to local laws. The resulting average basal area was 17.1 ± 1.8 m^2 ha^{-1} with 256 ± 19 tree individuals ha^{-1} in C plots, and 18.5 ± 0.2 m^2 ha^{-1} with 304 ± 14 tree individuals ha^{-1} in BLC plots.

In November 2000, all lianas regardless of their diameter were cut with a machete at 20 cm above the ground in the BLC treatment. Gaps were completed cleared from bamboos and lianas. The same treatment was applied inside the inner 10 m of the buffer zone. The cut lianas and bamboos were allowed to decompose *in situ*. A year later the treatment was repeated and liana resprouting recut. The dominant semelparous bamboo species *C. ramosissima* started to flower in both control and cutting plots in the year 2002. The non-synchronous (i.e. non-gregarious) flowering pattern of this species and the fast-growing bamboo seedlings enhanced a rapid recover of bamboo abundance after flowering in C plots (Montti et al., 2011b). Bamboo did not recover in BLC plots because sexual reproduction was prevented by the cutting treatment.

2.3. Liana abundance, richness and climbing mechanisms

Three 20 × 20 m subplots per plot were established within the three 1 ha C and BLC plots (total area surveyed per plot was 0.24 ha). In C plots the subplots were randomly selected among the six subplots surveyed in the year 2001 (Campanello et al., 2007b). All lianas larger than 1 cm diameter were identified, stem diameter measured at 1.3 m from the rooting point following Gerwing et al. (2006) and Schnitzer et al. (2008). Climbing mechanisms of liana species were classified into one of the following categories: (a) tendril climbers, (b) main stem or branch twiners, and (c) scramblers. Also, all trees larger than 10 cm DBH present in the 20 × 20 m subplots were registered and their stem diameter measured.

2.4. Liana infestation

In each 1 ha plot, 2 subplots 20 × 100 m were established in 2010 and all trees larger than 10 cm DBH were identified, stem diameter and main stem height (from the ground to the first conspicuous branch) were measured. Data on liana infestation for the year 2000 was available for all the trees larger than 10 cm DBH in C and BLC plots. In 2010 we quantified liana infestation in BLC and C plots in the 20 × 100 m subplots. Each tree was classified into one of the following categories: (1) trees with crowns free of lianas, (2) trees slightly infested by lianas (<50% of the crown affected), and (3) trees severely infested (>50% of the crown affected). Inside 20 × 100 m subplots we measured all trees between 10 and 20 cm DBH that were not sampled in 2000 for having less than 10 cm DBH. This information allowed us to determine if there was an effect of tree age and size on liana infestation.

2.5. Advanced tree regeneration and bamboo abundance in the understory

All the tree saplings (individuals with DBH larger than five and lower than 10 cm) in the 20 × 20 m subplots were identified and measured in the six C and BLC plots. The same three categories of liana infestation used for trees were employed to study liana infestation in tree saplings inside 20 × 20 m subplots. Also, we counted all the bamboo culms rooted inside the subplots as an estimation of changes in bamboo abundance in C and BLC plots.

2.6. Data analysis

To assess whether liana abundance and basal area of individuals >2.5 cm increased over 10 years in C plots we used a t test for paired samples. Differences in liana basal area and abundance of lianas between C and BLC plots were assessed by a two way ANOVA (RCBD) with two treatments and three replicates each. The analysis was done for all the individuals and lianas with stem diameters between 1 and 2.5 cm, and larger than 2.5 cm. Another ANOVA was performed to test differences in liana abundance and basal area according to their climbing mechanism (climbing mechanism was included as a treatment in the analysis). Rarefaction curves for liana richness estimation in C and BLC plots were performed with the software EstimateS 8 (Colwell, 2006). The species were ranked from high to low basal area and the logarithms of their relative basal area were plot against ranking scores for a graphic description of liana species abundance distribution and evenness, and to assess if there were differences in liana communities in C and BLC plots.

To examine liana resprouting and changes in tree infestation the following analysis was performed. First, we tested whether liana infestation increased in C plots over 10 years. We analyzed each infestation category separately performing a *t* test for paired samples (percentage data were root-square transformed). The same analysis was used to test the existence of differences between each category of liana infestation among trees with DBH between 10 and 20 cm in 2000 and 2010. Second, the McNemar non-parametric test was used to test differences between paired (2000–2010) proportions of liana infestation scores in C and BLC plots. The analysis indicated whether individuals that had lianas in the year 2000 also had in 2010 and vice versa after liana removing compared to control. This test was done for all the trees and for each of six abundant species in the 20 × 100 m subplots (*B. riedelianum*, *B. densiflora*, *Chrysophyllum gonocarpum* (Mart. & Eichler) Engl., *Holocalyx balansae* Micheli, *Machaerium stipitatum* (DC.) Vogel, and *N. megapotamica*). These species have relatively small leaves and do not have phylomorphic branches that could represent an advantage for liana shedding. Third, the degree to which lianas were associated with trunk height of trees in BLC was assessed by means of a logistic regression using the presence/absence of lianas reaching the trees crowns. The resulting 'odds ratios' indicate how much more likely it is that lianas are present over tree crowns when the branch-free bole height of the tree is increased by a unit of height (Hosmer and Lemeshow, 1989). The percentage of trees and sapling in each of the three categories in liana infestation in C and BLC plots was analyzed by a two way ANOVA (RCBD) with two treatments and three replicates each. Data were root-squared transformed to fulfill ANOVA requirements. The effect of bamboo and liana cutting on the abundance and basal area of tree saplings was also analyzed by a two way ANOVA with blocks and treatments as the main factors. A *p*-value of 0.05 was used as the alpha level. However, due to the low number of replicates, in a few cases values between 0.05 and 0.1 were considered significant and are indicated in the text.

3. Results

3.1. Liana abundance, richness and climbing mechanisms

A total of 51 liana species were sampled in both C (control) and BLC (bamboo and liana cutting) plots (see Table S1 in Supplementary content). The most abundant species were *Chamissoa altisima*, *Acacia velutina*, *Adenocalymna marginatum*, *Adenocalymna paulistarum*, *Fridericia mutabilis*, *Condylocarpon isthmicum*, *Dalbergia frutescens*, *Pereskia aculeata*, and *Seguieria aculeata*. This latter species was excluded from subsequent analysis because most adult individuals were free-standing (may become attached to a host tree at a latter stage) and they were not equally cut in all the plots in 2000. This scrambler species behave more as a tree than as a liana in the study area because very infrequently can be observed climbing trees.

Liana abundance and basal area of individuals with diameters larger than 2.5 cm increased by 68% and 50%, respectively, over ten years in C plots (Fig. 1). In 2010, ten years after liana cutting, liana abundance of individuals <2.5 cm was similar in C and BLC plots ($p = 0.25$; Table 1). When considering all the lianas and lianas > 2.5 cm, a tendency to decreased liana abundance was observed in BLC compared to C plots (but the *p*-values were only 0.10 and 0.06, respectively). Basal area of lianas was significantly lower in BLC compared to C plots when considering all the individuals and lianas > 2.5 cm ($p < 0.05$; Table 1), indicating a reduction of basal area in the plots where lianas were cut in the years 2000 and 2001. Larger lianas represented the 28% of all lianas in C plots compared with only a 19% in BLC plots.

Tendriled lianas were the most abundant group followed by scramblers and twiners both in C and BLC plots (Fig. 2a, Supplementary information). The higher value of basal area in C plots was due to a significantly higher basal area of lianas with tendrils

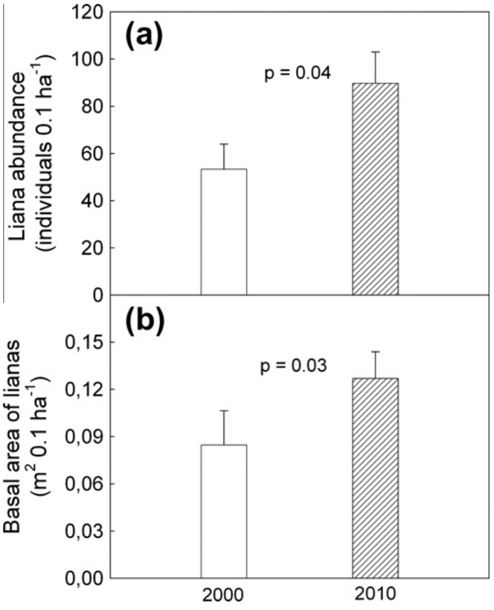

Fig. 1. Liana abundance (a) and basal area (b) of individuals with diameters >2.5 cm in control plots in the years 2000 (solid bar) and 2010 (hatched bar). Bars are means + SE (t values for paired samples are -3.83 and -3.28, respectively).

Table 1
Abundance (N; individuals 0.1 ha^{-1}) and basal area (BA, m^2 0.1 ha^{-1}) of lianas in C (control) and BLC (bamboo and liana cutting) plots in the year 2010 (ten years after the treatment) for all the individuals and lianas with stem diameters between 1 and 2.5 cm, and larger than 2.5 cm. Values are mean ± SE. The F and P-values of the treatments are indicated.

	C	BLC	$F_{1,2}$	P-value
All				
N	317.8 ± 29.7	226.1 ± 51.8	8.19	0.10
BA	0.172 ± 0.021	0.085 ± 0.016	23.6	0.04
<2.5 cm				
N	227.7 ± 21.5	183.1 ± 43.4	2.54	0.25
BA	0.049 ± 0.004	0.037 ± 0.009	4.75	0.18
>2.5 cm				
N	89.7 ± 13.3	43.1 ± 8.7	15.9	0.06
BA	0.127 ± 0.017	0.048 ± 0.009	24.4	0.04

compared to the same group in BLC plots and also to lianas with other climbing mechanisms (Fig. 2b). In BLC plots, the basal area of twiners was significantly lower to the basal area of scramblers and tendriled lianas (e.g. the abundance and basal area of the twiner *C. isthmicum* were three and five times lower in BLC compared to C plots, see Supplementary information). Liana richness was not affected by BLC treatment as showed by rarefaction curves (Fig. 3). The number of species as a function of individuals was preferred over area sampled to discard liana density effects on species richness. Lianas did not show substantial differences in the distribution of their relative specific abundances and species evenness as indicated by the similar slopes of rank–abundance curves of C and BLC plots (Fig. 4).

3.2. Liana infestation in control plots

The percentage of trees without lianas in their crown decreased while trees severely infested increased from 2000 to 2010 (Fig. 5). Trees with DBH between 10 and 20 cm in 2000 and in 2010 had similar scores of liana infestation indicating an effect of tree size and age on liana infestation of trees measured in 2000 and 2010 ($F_{1,2} = 0.2$, $p = 0.70\%$ for tree free of lianas; $F_{1,2} = 0.002$, $p = 0.96\%$ for trees slightly infested; $F_{1,2} = 0.14$, $p = 0.74\%$ for trees severely infested; data not shown).

Most of the trees (64.3%) in C plots remained infested after 10 years (Table 2). Only 12.2% of the trees free of lianas in 2000 were not infested in 2010 and the 18.8% of trees free of lianas in 2000 were infested in 2010. A small percentage (4.8) of trees appeared to have shed lianas from their crowns (Table 2). In three of the six tree species analyzed all the individuals that were free of lianas in 2000 were infested in 2010. In the case of *H. balansae*, all the trees were infested by lianas in 2000 in C plots, and a 7.7% of the individuals lost their lianas by 2010. All the trees of *M. stipitatum* were infested by lianas in 2010 in C plots. This last species, as well as, *B. densiflora* and *N. megapotamica* were not capable of shedding lianas from their crowns (all the trees infested in 2000 had lianas in 2010 in C plots).

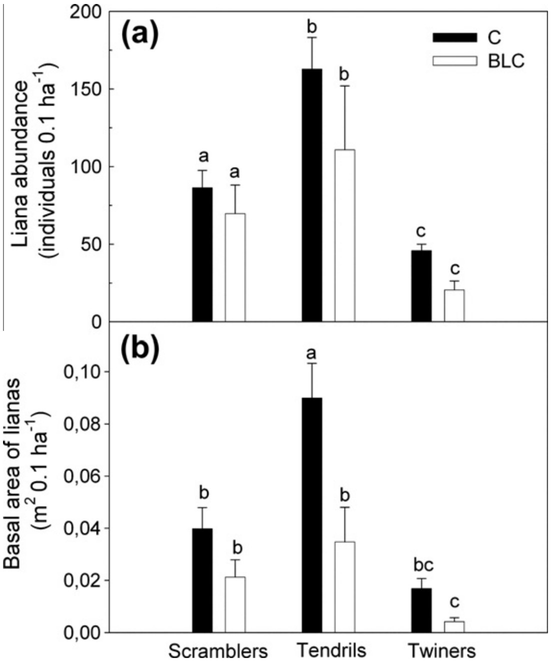

Fig. 2. Liana abundance (a) and basal area (b) in control (C) and bamboo and liana cutting (BLC) plots in the year 2010 grouped by climbing mechanisms. For abundance, treatment*mechanism P-value = 0.54 with $F_{2,10} = 0.64$, mechanism p-value = 0.0003 with $F_{2,10} = 26.36$, and treatment P-value = 0.04 with $F_{1,10} = 5.54$. For basal area, treatment*mechanism P-value = 0.01 with $F_{2,10} = 6.99$, mechanism p-value < 0.001 with $F_{2,10} = 35.95$, and treatment P-value = 0.002 with $F_{1,10} = 32.73$.

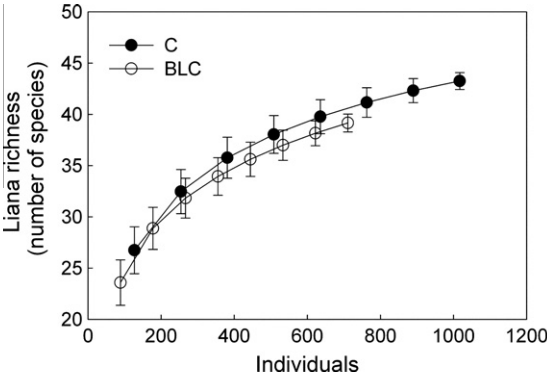

Fig. 3. Coleman rarefaction curves for liana species as a function of the number of individuals measured in control (C) and bamboo and liana cutting (BLC) plots in the year 2010. Symbols are means ± SE. Curves represent the expected species richness for different number of individuals.

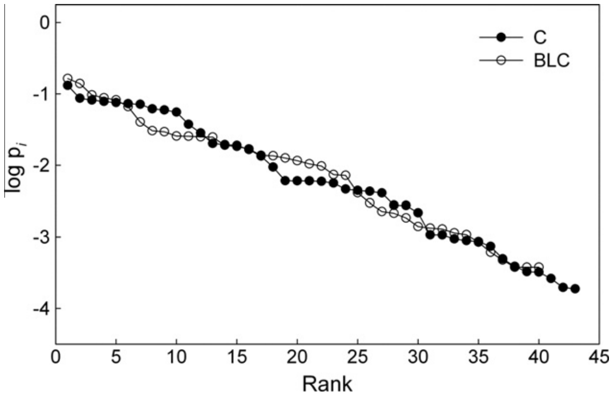

Fig. 4. Rank–abundance plots comparing liana communities in control (C) and bamboo and liana cutting (BLC) plots 10 years after treatment. The *Y*-axis represents the logarithm of the basal area of each species ranked in *X*-axis from higher to lower basal area.

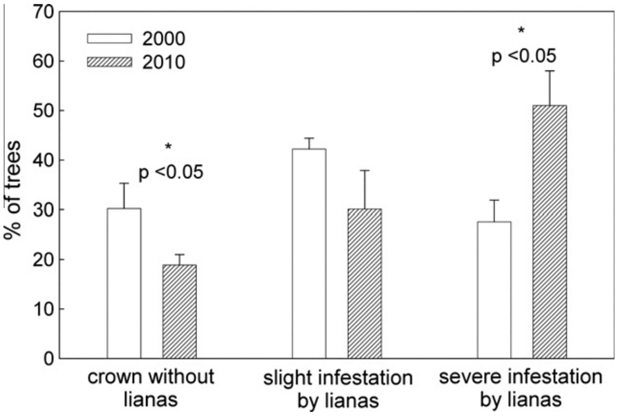

Fig. 5. Changes in tree crown infestation by lianas for a total of 740 trees in control plots between the years 2000 (solid bar) and 2010 (hatched bar) (*t* values for paired samples are −3.43 for trees without lianas and 3.14 for trees severely infested).

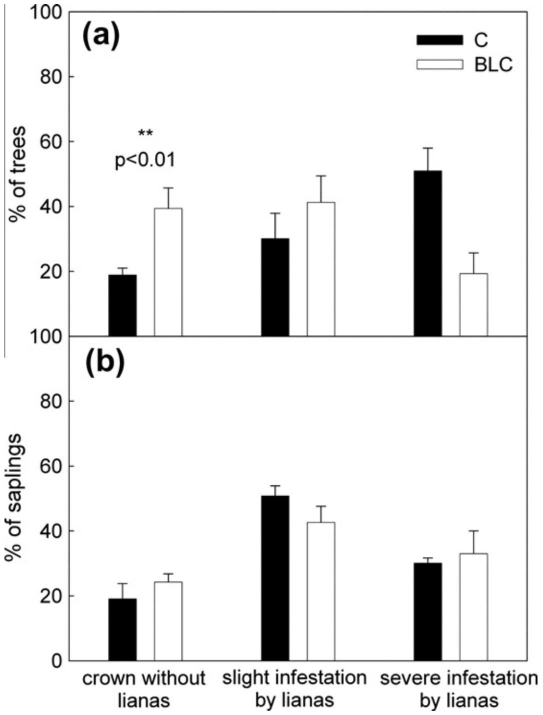

Fig. 6. Liana infestation in adult trees (a) and saplings (b) in control (C) and bamboo and liana cutting (BLC) plots in the year 2010. Values are means + SE. A total number of 335 and 407 trees and 460 and 461 saplings were measured in C and BLC plots, respectively. $^{**}P$-value for the treatment was <0.005 with $F_{1,8}$ = 15.

3.3. Liana re-infestation in BLC plots

In BLC plots the probability of having lianas in 2010, if they had not in 2000, was similar to the probability of not having lianas in 2010 for trees infested in 2000 (16.1% and 16.7%, respectively) (Table 2). The 42.9% of the trees in BLC plots that had lianas in their crowns in 2000 was re-infested by 2010. The proportion of trees with lianas in their crown was around 60% in both 2000 and 2010. Approximately 24% of trees remained without lianas in BLC plots 10 years after treatment was first applied (Table 2). A relatively high percentage of trees was liana free in BLC compared to C plots in 2010 (Fig. 6a). In the case of *B. riedelianum*, the species with the largest branch-free bole and smooth bark, only 3.8% of trees were re-infested. For *C. gonocarpum* and *M. stipitatum*, both species with short trunks, the proportion of re-infested trees, on the other hand, was high (71.9% and 68.4%, respectively).

The logistic regression analysis between presence/absence of lianas reaching tree crowns showed that trunk height of trees was important for predicting liana re-infestation (Table 3). As trunk height increases, the likelihood of liana presence decreases. The analysis demonstrated a good predictive ability (63% correct predictions), but not a well-defined threshold for the presence

Table 2
McNemar symmetry χ-square and *P*-values from contingency analysis of changes in liana infestation from 2000 to 2010 in C (control) and BLC (bamboo and liana cutting) plots (d.f. = 1 for all comparisons). The abundance of individuals in each combination is the percentage of the total abundance (*N*) in each case. For the species the average height (±SE) of the trunk in meters is indicated.

	2000	With		Without		McNemar symmetry test		
	2010	With	Without	With	Without	X^2	*P*	*N*
All trees	C	64.3	4.8	18.8	12.1	21.39	<0.001	272
	BLC	42.9	16.7	16.1	24.3	0.009	0.92	329
B. riedelianum	C	25.9	8.33	33.3	33.3	0.8	0.371	12
(8.6 ± 0.4 m)	BLC	3.8	23.1	19.2	53.8	0.00	1	26
B. densiflora	C	42.8	0.0	38.1	19.0	6.12	0.01	21
(7.5 ± 0.4 m)	BLC	50.0	20.0	20.0	10.0	0.25	0.62	10
C. gonocarpum	C	82.8	6.9	10.3	0.0	0.00	1	29
(5.0 ± 0.2 m)	BLC	71.9	15.6	9.4	3.1	0.125	0.72	32
H. balansae	C	92.3	7.7	0.0	0.0	0.00	1	13
(6.6 ± 0.4 m)	BLC	47.1	29.4	5.9	17.6	1.5	0.27	17
M. stipitatum	C	85.7	0.0	14.3	0.0	0.50	0.45	14
(5.3 ± 0.3 m)	BLC	68.4	15.8	15.8	0.0	0.17	0.68	19
N. megapotamica	C	46.6	0.0	46.7	6.7	5.14	0.02	15
(5.6 ± 0.2 m)	BLC	31.0	17.2	41.4	10.4	2.12	0.14	29

Table 3
Logistic regression between liana infestation and height of the branch-free bole of adult trees. Total number of trees in the analysis is 323 (134 trees without lianas, 189 trees with lianas).

	Parameter	EE	Odds ratio	Confidence intervals (95%)	Waldχ^2	*P*-value
Constant	1.50	0.30	4.49	2.47–8.15	24.33	<0.0001
Height	−0.17	0.04	0.84	0.77–0.91	17.08	<0.0001

The model is log $(\pi/(1-\pi) = \alpha + \beta\chi$; where π is the probability of liana presence from the tree crown given χ, χ is the branch-free bole height, α is the constant, and β is the parameter estimate. Odds ratio is the probability lianas present:the probability lianas absent.

Table 4
Results of ANOVA for sapling abundance (individuals 0.1 ha^{-1}) and basal area (m^2 0.1 ha^{-1}) in C (control) and BLC (bamboo and liana cutting) plots. Values are means ± SE. The *F* and *P*-values of the treatments (C and BLC) are indicated.

	C	BLC	$F_{1,2}$	*P*-value
Abundance	117.8 ± 30.0	125.3 ± 25.4	0.98	0.426
Basal area	0.238 ± 0.058	0.297 ± 0.052	12.75	0.070

and absence of lianas. For branch-free bole height < 8.5 m, the probability to find lianas on tree crowns increase over 50%.

3.4. Advanced tree regeneration

There were 1.1 ± 0.2 stems of *C. ramosissima* per square meter in C plots while a total of 38 culms were counted in BLC plots indicating that control of bamboo abundance was achieved. Tree sapling abundance was similar in C and BLC plots and basal area was higher in BLC plots at a *p*-value of 0.07 (Table 4). A total of 66 tree species were found. In both BLC and C plots the most abundant species were subcanopy trees (*Actinostemon concolor*, *Sorocea ilicifolia*, *Chrysophylum gonocarpum*, *Pilocarpus pennatifolius*, *Trichilia elegans*, *Trichilia catigua*, *Solanum inaequale*), but also three canopy trees species were abundant among saplings (*N. megapotamica*, *B. densiflora* and *L. leucanthus*). No differences in the percentage of saplings in each of the three categories of liana infestation were found between C and BLC plots (Fig. 6b).

4. Discussion

4.1. Liana abundance and infestation are increasing over time

According to our results in C plots, basal area and abundance of lianas are increasing in Northern Argentina as observed in other forests around the world (Schnitzer and Bongers, 2011). An increment of more than 50% in 10 years was observed in our study for lianas larger than 2.5 cm, which is consistent with increasing values reported by Phillips et al. (2002) in the Amazon forests for large lianas (i.e. more than 10 cm in diameter). Putative mechanisms explaining increasing liana abundance and biomass includes higher rates of natural and anthropogenic disturbances, increased evapotranspiration with climate change and the ability of lianas to growth during adverse drought conditions and elevated atmospheric CO_2, which gives them a relative advantage over trees (Schnitzer, 2005; Schnitzer and Bongers, 2011). The subtropical forest of Northern Argentina is considered a seasonally dry tropical forest mainly because of the tree species composition according to Pennington et al. (2000, 2009) and Prado and Gibbs (1993). Short dry spells (i.e. 20–30 days without rainfall) occur frequently but precipitation is relatively high and evenly distributed throughout the year. Even though there is not a dry season such as in seasonal dry tropical forests, seasonality is driven by the low temperatures occurring in the short winter season. In this forest, about 25–50% of the tree species are deciduous or semi-deciduous (Leite and Klein, 1990), while most lianas tend to retain leaves longer in the mild cold season (pers. obs). Thus, it is plausible that lianas are being favored by the low leaf area index during winter as proposed for seasonal dry tropical forests (Andrade et al., 2005; Cai et al., 2009; Schnitzer, 2005; Swaine and Grace, 2007), and particularly in logged forests (DeWalt et al., 2000; Schnitzer et al., 2000; Laurance et al., 2001).

Disturbance, in general, enhances liana abundance in tropical forests (Schnitzer and Bongers, 2002). In Misiones province, forests with relatively high basal area (e.g. 30 m^2 ha^{-1}) subjected to low logging intensity in the past have a relatively low liana infestation (i.e. more than 50% of the trees does not have any lianas and only 2% of the trees has lianas covering most of their crown). In contrast, heavily logged forests (e.g. basal area of 19 m^{-2} ha^{-1}) have few trees without lianas and more than 28% of the trees has lianas covering most of their crown (Campanello et al., 2009). Lianas grow rapidly and climb suitable host trees covering most of the upper canopy when incoming solar radiation is high. Lianas reaching tree crowns also act as climbing supports, facilitating other lianas access to the upper canopy (Campanello et al., 2007b; Nabe-Nielsen, 2001; Putz, 1984). Furthermore, lianas may colonize new gaps delaying the gap-phase regeneration process and the recovery of a tall mature forest (Schnitzer et al., 2000). They have also a detrimental direct effect on trees, decreasing growth and increasing mortality rates (Grauel and Putz, 2004; van der Heijden and Phillips, 2009; Ingwell et al., 2010; Schnitzer and Carson, 2010), ultimately enhancing gap formation (Schnitzer and Bongers, 2011). This positive feedback loop between disturbance and liana abundance may contribute to explain the increasing liana basal area and tree infestation in the forest of Northeastern Argentina (Campanello et al., 2009).

In this study, liana infestation on tree crowns increased during a 10 year period. Liana infestation in the trees measured in the year 2000 in C plots increased from 69% to 83% in 2010, which is one of the highest percentage infestation value reported for neotropical forests (van der Heijden et al., 2008; Ingwell et al., 2010) and similar to values reported in a Bolivian forest (Alvira et al., 2004). Small trees (i.e. 10–20 cm DBH) in 2000 and 2010 had similar liana loads, which indicates that liana infestation in trees larger than 20 cm DBH was enhanced as a result of facilitation, increased tree size and aging. The age of the host tree should play an important role in liana abundance because older trees provide more opportunities and time for liana colonization. Thus, trees of slow growing species such as *H. balansae* are normally severely infested (Campanello et al., 2007b). Liana shedding was observed for some individuals while others became infested in C plots, but three of the focal species studied were not able to shed lianas or were rapidly re-colonized. Although liana infestation is a dynamic process, liana shedding was more infrequent in this study than results reported recently by Ingwell et al. (2010) in Panama (i.e. less than 5% in Misiones forests versus 11% in Barro Colorado Island).

4.2. Effect of treatment on liana species, tree infestation and forest dynamics

The severity of the treatment applied in 2000 and 2001 (i.e. all the liana stems were cut twice in BLC plots) did not largely affect liana species composition after 10 years. As indicated by rarefaction and rank–abundance plots, liana species were similarly abundant in both C and BLC plots. On the other hand, a tendency for a reduced liana load was observed consistent with a decrease of abundance and basal area of all the lianas in BLC plots. Basal area and abundance of individuals >2.5 cm in diameter were significantly lower in BLC plots compared to C plots, which suggest that a longer period of time is necessary for a complete recovery of the larger lianas.

Lianas grouped by climbing mechanisms responded differently. The most affected group in BLC plots were tendriled lianas, which is also the most abundant group in the semideciduous Atlantic Forest studied (Campanello et al., 2007b) and in forest remnants in Southern Brazil (Santos et al., 2009). In both cases most of the species belong to the Bignoniaceae. On the other hand, twining lianas were the least abundant group in Northern Argentina, while in other forests where the most abundant species belong to the Fabaceae, Apocynaceae, Rutaceae, Asclepiadaceae and Malpighiaceae among other families, twiners constitute the most abundant group of lianas (e.g. Nabe-Nielsen, 2001; Padaki and Parthasarathy, 2000; Senbeta et al., 2005).

Overall, these results indicate a rapid partial recovery of liana biomass in BLC plots. Lianas have ecophysiological traits that make them a distinctive functional group with invasive potential in disturbed forest. They allocate relatively little biomass to structural support and a higher proportion to leaves than other woody plants (Schnitzer and Bongers, 2002). Moreover, they have greater photosynthetic rates compared to trees (Cai et al., 2009; Zhu and Cao, 2009). Besides, the vascular systems of lianas have a broad array of tissues that prevent stem breakage or help heal damaged stems (Isnard and Silk, 2009; Putz and Holbrook, 1991). After disturbance, recruitment can derived from vegetative reproduction such as sprouting of damaged individuals. Experimental gaps created by cutting have shown a strong sprout response. For example, 46% of cut lianas resprouted in an Amazonian forest (Gerwing and Vidal, 2002) and 41% in a lowland forest of Bolivia (Alvira et al., 2004). All of these traits combined should contribute to a rapid liana recovery. In a Bolivian forest, Perez-Salicrup et al. (2001) found that, liana cutting reduced tree infestation for at least two years, but the treatment was very expensive to be applied for liana control. However, in another Bolivian tropical forest, the effects of removing lianas persisted for four years (Peña-Claros et al., 2008) and the authors considered that the treatment was cost effective to improve tree regeneration.

Schnitzer and Carson (2010) in a seasonal tropical forest in Panama showed that competition between lianas and trees constrains tree recruitment, survival and diversity in gaps. In their study, lianas were particularly harmful to shade-tolerant species. In the subtropical forest of Misiones, as found in other forests (e.g. Addo-Fordjour et al., 2009) the abundance of lianas is directly related to the abundance of trees (Campanello et al., 2007b). In this semideciduous forest, bamboos are successful competitors in gaps suppressing both trees (Campanello et al., 2007a; Montti et al., 2011a) and possibly lianas (pers. obs.). In similar stands of the Atlantic Forest in Brazil, lianas were comparatively less abundant in bamboo-dominated areas than in forests without bamboos (Carvalho et al., 2011). For this reason, liana abundance and basal area may have been enhanced by the simultaneous bamboo and liana cutting.

Liana re-infestation in BLC plots was also a rather rapid process. The percentage of trees without lianas in BLC plots was 40% compared to 20% in C plots but another 40% in the BLC plots showed slight infestation and 20% was severely infested. At least a 10% of the slightly infested trees in 2010 will probably become severely infested within a short period of time. Furthermore, saplings were equally and highly infested in both C and BLC plots, which is indicating a relative low efficacy of the treatment to prevent liana infestation after ten years. Species-specific characteristics of the tree trunk (i.e. length and type of bark) were found to affect liana colonization of potential tree hosts (Campanello et al., 2007b). Accordingly, in this study we observed that the length of the branch-free bole affected the re-colonization scores of host trees in BLC plots (i.e. trees with short trunks, besides being unable of shedding lianas, were quickly re-colonized).

Limited regeneration of trees, particularly of light demanding species, has been observed in tropical and subtropical forests (Campanello et al., 2007a; Dickinson and Whigham, 1999; Fredericksen and Mostacedo, 2000; Mostacedo and Fredericksen, 1999). Potential causes for impeded regeneration include the absence of seed trees, the lack of appropriate environmental conditions for seed germination and seedling establishment, and the proliferation of invasive plants that compete with tree sapling and seedling for light and nutrients (Mostacedo and Fredericksen, 1999). Bamboos and lianas are ubiquitous competitors in gaps, prevent tree regeneration and slow down gap-phase regeneration processes in many neotropical forests (Griscom and Ashton, 2003; Oliveira-Filho et al., 1994; Schnitzer et al., 2000, 2005; Tabanez and Viana, 2000; Tabarelli and Mantovani, 2000), including subtropical forests in Northern Argentina (Campanello et al., 2007a). The monocarpic bamboo *C. ramosissima* started to flower in different areas of Northeastern Argentina in 2001 (Montti et al., 2011b). Our BLC treatment drastically reduced bamboo cover mainly because, coincidentally, flowering and die-back of the most abundant species *C. ramosissima* occurred after cutting and hence was not able to reproduce in BLC plots (pers. obs.). A reduction of liana basal area and abundance was observed in BLC plots after a 10-year period, particularly for larger lianas. However, the treatment may not be as effective in reducing liana load and infestation in the long term as tree saplings were similarly infested in C and BLC plots. In agreement with our previous results, the BLC treatment did not increase tree sapling abundance but enhanced tree sapling growth (Campanello, 2004; Campanello et al., 2007a). The slight increment of tree sapling basal area in 2010 is denoting that there was an effect of the silvicultural treatment applied to enhance tree regeneration. If the effect is expected to be long lasting, liana cutting should be done more frequently. However, increasing the frequency of the treatment will substantially increase the cost of the management practices and may have undesirable effects on plant-animal interactions and biodiversity in the long term.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.07.043.

References

Addo-Fordjour, P., Obeng, S., Addo, M.G., Akyeampong, S., 2009. Effects of human disturbances and plant invasion on liana community structure and relationship with trees in the Tinte Bepo forest reserve. Ghana For. Ecol. Manage. 258, 728–734.

Alvira, D., Putz, F.E., Fredericksen, T.S., 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. For. Ecol. Manage. 190, 73–86.

Andrade, J.L., Meinzer, F.C., Goldstein, G., Schnitzer, S.A., 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. Trees Struct. Funct. 19, 282–289.

Cabrera, A.L., 1976. Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería, Tomo II, Fascículo 1, Acme, Buenos Aires, Argentina, pp. 85.

Cai, Z.-Q., Schnitzer, S.A., Bongers, F., 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. Oecologia 161, 25–33.

Campanello, P., 2004. Diversidad, crecimiento y fisiología de árboles en la selva misionera: efectos de los cambios en la estructura y funcionamiento del ecosistema producidos por la invasión de lianas y bambúseas. PhD thesis, Universidad de Buenos Aires, Argentina.

Campanello, P.I., Gatti, M.G., Ares, A., Montti, L., Goldstein, G., 2007a. Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. For. Ecol. Manage. 252, 108–117.

Campanello, P.I., Garibaldi, J.F., Gatti, M.G., Goldstein, G., 2007b. Lianas in a subtropical Atlantic Forest: host preference and tree growth. For. Ecol. Manage. 242, 250–259.

Campanello, P.I., Montti, L., Goldstein, G., Mac Donagh, P., 2009. Reduced impact logging and post-harvesting forest management in the Atlantic Forest: alternative approaches to enhance canopy tree growth and regeneration and to reduce the impact of invasive species. In: Grossberg, S.P. (Ed.), Forest Management. Nova Science, New York, pp. 39–59.

Campbell, E.J.F., Newbery, D.M.C., 1993. Ecological relationship between lianas of trees in lowland rain-forest in Sabah. E. Malaysia J. Trop. Ecol. 9, 469–490.

Carvalho, P.G., Mellis, J.V., Ascenção, B.M., Cestari, F.M., Alves, L.F., Grombone-Guaratini, M.T., 2011. Abundância e biomassa de lianas em um fragmento de floresta Atlântica. Hoehnea 38, 307–314.

Colwell, R.K., 2006. EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Useŕs guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>.

DeWalt, S.J., Schnitzer, S.A., Denslow, J.S., 2000. Density and diversity of lianas along a seasonal tropical forest chronosequence in central Panama. J. Trop. Ecol. 16, 1–19.

Dickinson, M.B., Whigham, D.F., 1999. Low rates of natural regeneration of mahogany in felling gaps after selective logging in Quintana Roo, Mexico. Int. For. Rev. 1, 35–39.

Emmons, L.H., Gentry, A.H., 1983. Tropical forest structure and the distribution of gliding and prehensile tailed vertebrates. Am. Nat. 121, 513–524.

Fox, J.E.D., 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. Malay. For. 31, 326–347.

Fredericksen, T.S., Mostacedo, B., 2000. Regeneration of timber species following selection logging in a Bolivian dry tropical forest. For. Ecol. Manage. 131, 47–55.

Gerwing, J.J., Vidal, E., 2002. Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonia forest. Conserv. Biol. 16, 544–548.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E., Thomas, D.W., 2006. A standard protocol for liana censuses. Biotropica 38, 256–261.

Grauel, W.T., Putz, F.E., 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien. Panama For. Ecol. Manage. 190, 99–108.

Griscom, B.W., Ashton, P.M.S., 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. For. Ecol. Manage. 175, 445–454.

Hegarty, E.E., Caballe, G., 1991. Distribution and abundance of vines in forest communities. In: Putz, F.E., Mooney, H.A. (Eds.), The Biology of Vines. Cambridge University Press, Cambridge, pp. 313–335.

Hora, R.C., Soares, J.J., 2002. Estrutura fitossociológica da comunidade de lianas em uma floresta estacional semidecidual na Fazenda Canchim, São Carlos. S.P. Rev. Bras. Bot. 25, 323–329.

Hosmer, D., Lemeshow, S., 1989. Applied Logistic Regression. John Wiley, Sons, New York.

Ingwell, L.L., Wright, S.J., Becklund, K.K., Hubbell, S.P., Schnitzer, S.A., 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island. Panama J. Ecol. 98, 879–887.

Isnard, S., Silk, W.K., 2009. Moving with climbing plants from Charles Darwin's time into the 21st century. Am. J. Bot. 96, 1205–1221.

Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D.A.P., Capanu, M., 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. J. Trop. Ecol. 22, 147–154.

Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E., 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82, 105–116.

Leite, P.F., Klein, R.M., 1990. Regiao Sul. Rio de Janeiro. In: Geografia do Brasil. Instituto Brasileiro de Geografia e Estatística – IBGE, Brasil, pp. 113–150.

Ligier, H.D., 1999. Caracterización Geomorfológica y Edáfica de la Provincia de Misiones. Fundación Vida Silvestre Argentina, Buenos Aires, Argentina.

Ligier, H.D., Matteio, H.R., Polo, H.L., Rosso, J.R., 1990. Provincia de Misiones. In: Atlas de suelos de la República Argentina, Tomo II. Centro de Investigaciones de Recursos Naturales, INTA, Secretaria de Agricultura, Ganadería y Pesca. Buenos Aires, Argentina, pp. 111–154.

Montti, L., Campanello, P.I., Gatti, M.G., Blundo, C., Austin, A.T., Sala, O.E., Goldstein, G., 2011a. Understory bamboo flowering provides a very narrow light window of opportunity for canopy tree recruitment in a neotropical forest of Misiones Argentina. For. Ecol. Manage. 262, 1360–1369.

Montti, L., Campanello, P.I., Goldstein, G., 2011b. Flowering, died-back and recovery of semelparous woody bamboo in the Atlantic Forest. Acta Oecol. 37, 361–368.

Morellato, L.P.C., Leitão Filho, H.F., 1998. Levantamento florístico da comunidade de trepadeiras de uma floresta semidecidua no sudeste do Brasil. Bol. Mus. Nac. 103, 1–15.

Mostacedo, B., Fredericksen, T., 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. For. Ecol. Manage. 124, 263–273.

Nabe-Nielsen, J., 2001. Diversity and distribution of lianas in a neotropical rainforest, Yasuni National Park, Ecuador. J. Trop. Ecol. 17, 1–19.

Nabe-Nielsen, J., Kollmann, J., Peña-Claros, M., 2009. Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical. For. Ecol. Manage. 257, 987–993.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L., Carvalho, D.A., 1994. Effect of flooding regime and understorey bamboos in the physiognomy and tree species composition of a tropical semideciduous forest in Southeastern Brazil. Vegetatio 113, 99–124.

Padaki, A., Parthasarathy, N., 2000. Abundance and distribution of lianas in tropical lowland evergreen forest of Agumbe, Central Western Ghats, India. Trop. Ecol. 41, 143–154.

Peña-Claros, M., Peters, E.M., Justiniano, M.J., Bongers, F., Blate, G.M., Fredericksen, T.S., Putz, F.E., 2008. Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest. For. Ecol. Manage. 255, 1283–1293.

Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and quaternary vegetation changes. J. Biogeogr. 27, 261–273.

Pennington, R.T., Lavin, M., Oliveira-Fhilo, A., 2009. Woody plant diversity, evolution, and ecology in the Tropics: perspectives from seasonally dry Tropical Forests. Ann. Rev. Ecol. Evol. Syst. 40, 437–457.

Perez-Salicrup, D.R., Claros, A., Guzman, R., Licona, J.C., Ledezma, F., Pinard, M.A., Putz, F.E., 2001. Cost and efficiency of cutting lianas in a Lowland Liana forest of Bolivia. Biotropica 33, 324–329.

Phillips, O.L., Vasquez, M.R., Arroyo, L., Baker, T., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neillq, D., Núñez Vargas, P., Alexiades, M., Cerón, C., Di Fiore, A., Erwinkk, T., Jardim, A., Palacios, W., Saldías, M., Vinceti, B., 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418, 770–774.

Prado, D.E., Gibbs, P.E., 1993. Patterns of species distributions in the dry seasonal forests of South America. Ann. Miss. Bot. Gard. 80, 902–927.

Putz, F.E., 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 68, 1713–1724.

Putz, F.E., 1991. Silvicultural effects of lianas. In: Putz, F.E., Mooney, H.A. (Eds.), The Biology of Vines. Cambridge University Press, pp. 493–501.

Putz, F.E., Holbrook, N.M., 1991. Biomechanical studies of vines. In: Putz, F.E., Mooney, H.A. (Eds.), The Biology of Vines. Cambridge University Press, Cambridge, pp. 53–72.

Santos, K., Kinoshita, L.S., Rezende, A.A., 2009. Species composition of climbers in seasonal semideciduous forest fragments of Southeastern Brazil. Biota Neotrop. 9, 175–188.

Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. Am. Nat. 166, 262–276.

Schnitzer, S.A., Bongers, F., 2002. The ecology of lianas and their role in forests. Trends Ecol. Evol. 17, 223–230.

Schnitzer, S.A., Bongers, F., 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecol. Lett. 14, 397–406.

Schnitzer, S.A., Carson, W.P., 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecol. Lett. 13, 849–857.

Schnitzer, S.A., Dalling, J.W., Carson, W.P., 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88, 655–666.

Schnitzer, S.A., Kuzee, M., Bongers, F., 2005. Disentangling above and belowground competition between lianas and trees in a tropical forest. J. Ecol. 93, 1115–1125.

Schnitzer, S.A., Rutishauser, S., Aguilar, S., 2008. Supplemental protocol for censusing lianas. For. Ecol. Manage. 255, 1044–1049.

Senbeta, F., Schmitt, C., Denich, M., Demissew, S., Velk, P.L.G., Preisinger, H., Woldemariam, T., Teketay, D., 2005. The diversity and distribution of lianas in the Afromontane rain forests of Ethiopia. Divers. Distrib. 11, 443–452.

Servicio Meteorológico Nacional, Argentina, 2005. <http://smn.gov.ar>.

Soil survey staff, 1992. Keys to Soil Taxonomy, fifth ed. SMSS Technical Monograph no. 19, Pocahontas Press Inc., Blacksburg, VA, USA.

Swaine, M.D., Grace, J., 2007. Lianas may be favoured by low rainfall: evidence from Ghana. Plant Ecol. 192, 271–276.

Tabanez, A.A., Viana, V.M., 2000. Patch structure whithin Brazilian Atlantic Forest fragments and implications for conservation. Biotropica 32, 925–933.

Tabarelli, M., Mantovani, W., 1999. Clareiras naturais e a riqueza de especies pioneiras em uma Floresta Atlantica montana. Rev. Brasil. Biol. 59, 484–489.

Tabarelli, M., Mantovani, W., 2000. Gap-phase regeneration in a tropical montane forest: the effects of gap structure and bamboo species. J. Plant Ecol. 148, 149–155.

van der Heijden, G.M.F., Phillips, O.L., 2009. Liana infestation impacts tree growth in a lowland tropical moist forest. Biogeosciences 6, 2217–2226.

van der Heijden, G.M.F., Healey, J.R., Phillips, O.L., 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. J. Veg. Sci. 19, 747–756.

Vidal, E., Johns, J., Gerwing, J., Barreto, P., Uhl, C., 1997. Vine management for reduced impact logging in eastern Amazonia. For. Ecol. Manage. 98, 105–114.

Wright, S.J., Calderón, O., Hernández, A., Paton, S., 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85, 484–489.

Zhu, S.-D., Cao, K.-F., 2009. Hydraulic properties and photosynthetic rates in co-occuring lianas and trees in a seasonal tropical rainforest in southwestern China. Plant Ecol. 204, 295–304.