Journal of Tropical Ecology (2017) **33**:241–248. © Cambridge University Press 2017
doi:10.1017/S0266467417000153

Liana density declined and basal area increased over 12 y in a subtropical montane forest in Argentina

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(*Received 29 October 2016; revised 29 May 2017; accepted 1 June 2017; first published online 21 June 2017*)

Abstract: Changes in density and basal area of lianas ≥2 cm diameter were monitored in two 1-ha permanent plots in a subtropical montane mature forest of north-western Argentina. Liana stems were identified and measured at 130 cm from the main rooting point in two censuses conducted in 2003 and 2015. Between censuses, the density of liana stems decreased 13.3%, while basal area increased 11.5%. Density and basal area decreased mainly among lianas of 2–3 cm diameter, but increased in lianas ≥4 cm diameter. *Quechualia fulta* (Asteraceae), *Serjania meridionalis* (Sapindaceae) and *Chamissoa altissima* (Amaranthaceae) suffered large reductions in stem density and basal area. Dissimilar responses of density and basal area of lianas might be a consequence of the suppression of anthropogenic disturbances (e.g. livestock browsing) and the decrease of treefall gap frequency in the studied forest in recent decades. Light-demanding liana species decreased and shade-tolerant species increased possibly in response to the decline in the light availability associated with forest recovery from past disturbance. Lianas increased in basal area to a lesser extent compared with reports from several tropical and subtropical forests where lianas are increasing dramatically.

Key Words: basal area, density, disturbance, lianas, light-demanding species, permanent plot, shade-tolerance, yungas forests

INTRODUCTION

In recent decades, lianas have increased dramatically in abundance and basal area in tropical and subtropical old-growth forests (Campanello *et al.* 2012, Chave *et al.* 2008, Foster *et al.* 2008, Ingwell *et al.* 2010, Laurance *et al.* 2014, Phillips *et al.* 2002, Schnitzer & Bongers 2011, Schnitzer *et al.* 2012, Wright & Calderon 2006, Wright *et al.* 2004, Yorke *et al.* 2013). For example, in a 50-ha plot in Barro Colorado Island (Panama), Schnitzer *et al.* (2012) observed that over a 30-y period lianas ≥1 cm and ≥5 cm diameter increased in density 75% and 140%, respectively. The opposite trend has also been reported in forests of Africa, where lianas are decreasing in density and basal area (Bongers & Ewango 2015, Caballé & Martin 2001, Ewango 2010, Thomas *et al.* 2015).

Lianas compete intensely with trees for both above- and below-ground resources (Chen *et al.* 2008, Schnitzer *et al.* 2005), at least partially because they deploy large leaf areas above their host trees (Schnitzer & Bongers 2011). Liana infestation may affect tree recruitment, growth, fecundity and survival (Campanello *et al.* 2007, Ingwell *et al.* 2010, Putz 1984, Schnitzer *et al.* 2005, Toledo-Aceves & Swaine 2008). Therefore, increases in lianas could alter forest dynamics and reduce the ability of a forest to sequester carbon (i.e. lianas may displace far more biomass than they accumulate) (Ingwell *et al.* 2010, Laurance *et al.* 2014, Schnitzer & Bongers 2011, Schnitzer *et al.* 2014, van der Heijden & Phillips 2009, van der Heijden *et al.* 2015).

Increasing natural and anthropogenic disturbance rates are two of the proposed explanations for liana density increase (Schnitzer 2005, Schnitzer & Bongers 2011). Increasing forest disturbance results in the formation of more edge and gap habitat, where lianas may proliferate (Putz 1984, Schnitzer *et al.* 2000) by using several mechanisms such as seed, advance regeneration (i.e. seedlings and saplings that were present prior to gap formation), lateral growth and long-distance clonal recruitment (Peñalosa 1984, Schnitzer *et al.* 2000). On the other hand, lianas may decrease with decreasing forest disturbances and/or with the ageing of gaps (Malizia & Grau 2008, Putz 1984).

Most lianas species are pioneers or light-demanding due to their high abundance in disturbed and well-illuminated

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areas, such as treefall gaps, young secondary stands and forest edges (DeWalt *et al.* 2000, Londré & Schnitzer 2006, Putz 1984). However, this does not mean that all liana species are shade-intolerant (Gianoli *et al.* 2010), and in fact they appear to show different shade-tolerance levels (Gilbert *et al.* 2006). It has been suggested that with the increase of disturbances, light-demanding liana species might benefit (Roeder *et al.* 2012), while shade-tolerant species may decrease. In addition, a density increase of shade-tolerant species is expected when a decrease in disturbance occurs and the forest understorey becomes darker.

In a mature subtropical montane forest of Sierra de San Javier (Tucuman, Argentina), we monitored lianas ≥2 cm diameter over a 12-y period (2003–2015), to assess how liana density and basal area changed between the two censuses. The hypotheses are: (1) Lianas are common in well-illuminated environments and tend to decrease in density and basal area probably due to the reduction of light availability associated to the forest recovery from past disturbances (DeWalt *et al.* 2000, Ewango 2010). Thus, we expected that lianas became less abundant in respond to the anthropogenic disturbance suppression in the forest since the area was included in a natural reserve in 1973. (2) We expected the greatest decrease in density for light-demanding species due to the decline in light availability.

STUDY SITE

This study was conducted in a subtropical montane mature forest located at ~1000 m asl in Parque Sierra de San Javier (26°45′S, 65°20′W), a 14,000-ha protected area, 10 km west of San Miguel de Tucuman, Argentina. The area represents the southern-most extension of the Andean montane forests, also known as yungas (Cabrera & Willink 1980). The vegetation corresponds to a semideciduous forest, with an average of 23 tree species ha^{-1} ≥10 cm diameter (Grau 2002, Malizia & Grau 2006) and canopy heights of 15–30 m dominated by shade-tolerant species such as *Blepharocalyx salicifolius* (Myrtaceae), *Ocotea porphyria* (Lauraceae) and *Pisonia zapallo* (Nyctaginaceae). The subcanopy (5–12 m) is dominated by *Eugenia uniflora* (Myrtaceae), *Piper tucumanum* (Piperaceae) and *Allophylus edulis* (Sapindaceae), while the shrub *Psychotria carthaginensis* (Rubiaceae) forms a relatively uniform layer in the understorey (Grau 2002, Malizia & Grau 2006, Malizia *et al.* 2013). The forest includes 11 species ha^{-1} of liana ≥2 cm diameter (Malizia *et al.* 2010), and the most abundant species are *Cissus striata* (Vitaceae), *Chamissoa altissima* (Amaranthaceae) and *Celtis iguanaea* (Celtidaceae), which together represent *c.* 60% of the individuals (Malizia & Grau 2006). This mature forest had signs of minor recent human influence. It was selectively logged *c.* 50 y ago (i.e. only two cut stumps were recorded in a 6-ha permanent plot when established in 1992) and subjected to livestock browsing up to 1973 when Parque Sierra de San Javier was created (Grau 2002, Grau & Brown 1998, Malizia *et al.* 2013).

The study area receives ~1300–1600 mm of rainfall annually and has a seasonal monsoonal climate (Bianchi & Yáñez 1992). Mean annual temperature is 18.8°C (Bianchi & Yáñez 1992), but temperatures drop to −5°C about once per decade (Torres Bruchmann 1978).

METHODS

Sampling

In 1992, a 6-ha permanent plot was established in the study area in order to monitor tree demography and gap dynamics over time (Easdale *et al.* 2007, Grau 2002, Malizia *et al.* 2013), and was extended in 2003 to include lianas (Malizia 2007). The 6-ha plot is part of a larger forest monitoring system of the Instituto de Ecología Regional (IER, Universidad Nacional de Tucumán – CONICET) and consists of a 300 × 200 m rectangle, divided in 150 20 × 20 m quadrats (400 m^2) in which all trees ≥10 cm diameter at breast height (dbh) are permanently marked, measured, mapped, identified and re-measured (or recorded as dead) every 5 y (Grau 2002, Malizia *et al.* 2013). In 2003, climbing lianas with stem diameters ≥2 cm were identified, measured at 130 cm from the main rooting point, painted with non-toxic paint, marked with aluminium tags and mapped in a xy coordinate system over the 6-ha plot (Malizia & Grau 2006). A diameter of 2 cm was considered as a threshold since lianas of this size have approximately as much leaf mass as a 10-cm-diameter tree, the common minimum threshold for trees to be considered in a measurement (Gerwing & Farias 2000). When an individual liana had multiple stems, an aluminium tag was attached to the largest diameter stem and nails to the others (Malizia & Grau 2006). Lianas were re-measured during 2015 following the protocol of Gerwing *et al.* (2006), in two 1-ha plots within the 6-ha permanent plot, providing a re-measurement period of 12-y. New liana recruits ≥2 cm dbh were identified, measured in diameter, painted and permanently marked with numbered aluminium tags.

In liana ecology, studies usually define apparent genets, comprised of one or more ramets that are visibly connected (Gerwing *et al.* 2006, Schnitzer *et al.* 2015). In our study, we distinguished apparent genets (hereafter individuals) from liana ramets (hereafter stems) but only through observation of stems connections on or above the soil surface. Stems that were physically attached to another stem were considered part of the same individual, while those not visibly connected were considered separate individuals.

Data analysis

The data collected in the 2015 census were compared with data of the 2003 census to describe changes in liana density and basal area over the 12 y, at plot, species and diameter-size-class levels. These changes were not analysed with statistical tests due to the unreplicated plot design.

To analyse the relationship between liana species density change and their different shade-tolerance levels, we first obtained a continuum axis of shade-tolerant species using a Principal Component Analysis (PCA). This ordination method was chosen to obtain a shade-tolerance gradient of liana species using different proxy variables such as growth and mortality rates (Condit *et al.* 2006), wood density, seed size and the abundance distribution in two contrasting light environments (we sampled young and mature forests in the Sierra de San Javier to represent high and low light conditions, respectively). The reduction of the number of variables into a single synthetic variable (i.e. the first component of the PCA) was considered a useful approach to differentiate shade-tolerant and light-demanding species. However, our approach focused on a gradient of species with different tolerance to shade rather than two distinct groups (i.e. shade-tolerant vs. light-demanding species). The main matrix for this analysis contained liana species in rows and the variables mentioned above in columns. Variables were analysed through PCA correlation matrix and were standardized by the standard deviation before running the analysis due to their different units. First two axes comprised 68.6% of the cumulative variance, but we selected only the first axis that explained 45.5% to interpret the results. Then, we performed a linear regression analysis between species scores on the shade-tolerance axis (PCA1) and changes in their density in the 2003–2015 period (considered as change in percentage between censuses). The variable change in density per species was standardized into a range of 0 to 1 with the 'decostand' function in the 'vegan' package and transformed to logarithm $(X + 1)$ to reduce the variability among species and to fulfil the normality requirement. Shade-tolerance scores were also standardized into a range of positive values from 0 to 1 to remove negative PCA values. All analyses were performed with the statistical program R (R Development Core Team).

RESULTS

In 2015, we surveyed a total of 929 liana stems and 775 liana individuals belonging to 12 species and nine families that range from 2 to 13 cm and have a mean size of 4.3 cm in two 1-ha plots. The most abundant species in 2015 were *Cissus striata* (286 stems and 242 individuals), *Celtis iguanaea* (156 stems and 124 individuals) and *Chamissoa altissima* (119 stems and 94 individuals). The mean density of lianas ≥2 cm diameter in each quadrat (400 m^2) was 19 stems (range = 2–35) and 16 individuals (range = 2–32). Species richness was similar between 2003 and 2015 (11 and 12 species, respectively), but in the 2015 census, one species was not recorded (*Muehlenbeckia sagittifolia* – Polygonaceae) and two were added (*Cissus verticillata* – Vitaceae and *Gonolobus rostratus* – Apocynaceae).

Between 2003 and 2015, the density of lianas stems ≥2 cm diameter decreased from 536 ha^{-1} to 465 ha^{-1} (−13.3%), and the density of liana individuals decreased similarly, from 439 ha^{-1} to 388 ha^{-1} (−11.7%). The density of lianas of 2–3 cm diameter decreased (−54%), but increased in the ≥4 cm diameter classes (+57%; Figure 1). *Quechualia fulta* and *Serjania meridionalis* showed a large reduction in stem density by 65% and 37%, respectively (Table 1). Basal area increased from 0.69 to 0.78 m^2 ha^{-1} (+11.5%) between censuses. There were differences in basal area change among diameter size classes, decreasing for lianas of 2–3 cm (−55%), but increasing for lianas ≥4 cm (+53%; Figure 1). Most species increased in basal area, while only *S. meridionalis* (−29%), *Q. fulta* (−22%), and *C. altissima* (−20%) declined (Table 1).

We obtained a shade-tolerance axis, based on the correlations of wood density, growth, mortality and abundance in young vs. mature forests with axis 1 of the PCA (hereafter referred to as shade-tolerance axis; Figure 2, Table 2). With decreasing scores in shade-tolerance axis, species exhibit higher wood density, lower growth, lower mortality and greater abundance in shaded areas (in mature forests). With increasing scores in axis two, species exhibit larger seeds. Species with higher scores in the shade-tolerance axis (light-demanding) showed the highest decrease in density, while those with lower scores (shade-tolerant) increased ($R^2 = 0.41$, $F = 5.4$, $P = 0.04$; Figure 3).

DISCUSSION

Over a 12-y period, lianas showed dissimilar responses in density and basal area in two 1-ha plots of mature forest at Sierra de San Javier. The decrease occurred mainly in small-sized lianas (2–3 cm diameter), which have high density and a major influence on total density change. Basal area increased annually 0.96 m^2 ha^{-1} in the plots but at lower levels than the reports of other tropical and subtropical forests (e.g. an annual increase of 3.72 m^2 ha^{-1} in Amazonian sites; Phillips *et al.* 2002),

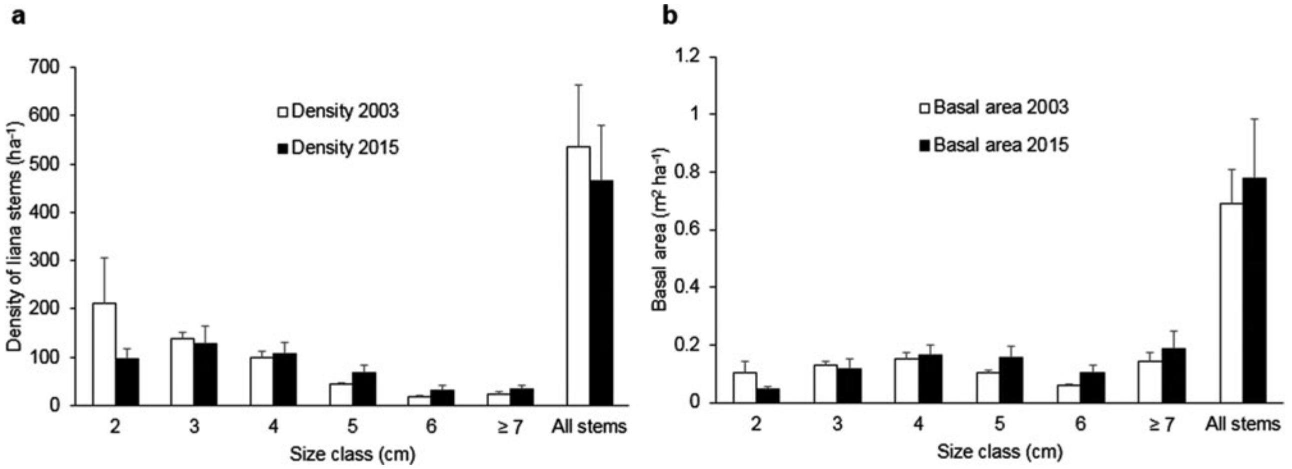

Figure 1. Density (a) and basal area (b) of lianas in 2003 and 2015 by size class recorded at Sierra de San Javier, Tucuman, Argentina. Black and white bars represent liana density per census and error bars represent 1 SD.

and occurred mainly due to the density increase of higher-size lianas (≥4 cm diameter).

The mature forest of the study area exhibited changes in tree structure in the last two decades (Grau *et al.* 2010, Malizia *et al.* 2013). Plots established in this forest had a 54% increase in tree stem density and 6% in tree basal area between 1992 and 2007, which have been mainly attributed to forest recovery of palatable tree species (i.e. nutrient-rich soft-leaved species) after the removal of livestock (Malizia *et al.* 2013). Anthropogenic disturbances (e.g. livestock browsing) decreased when the area was included in a natural reserve in 1973 (Grau *et al.* 2008) and probably influenced liana density decrease within the studied forest, as suggested for lianas in other forests of the world (Bongers & Ewango 2015, Ewango 2010, Pandian & Parthasarathy 2016). For example, lianas are also decreasing in forests that are recovering from past disturbances in Ituri region (Democratic Republic of Congo) (Bongers & Ewango 2015, Ewango 2010). Also, in tropical forests of India, Pandian & Parthasarathy (2016) observed that increases in liana density between 2003–2013 were positively correlated with the increase of different local disturbances. These observations support the notion of Schnitzer & Bongers (2011), which suggest that changes in liana abundance may be a more local than continental phenomenon, with lianas increasing in some areas (Chave *et al.* 2008, Ingwell *et al.* 2010, Laurance *et al.* 2014, Phillips *et al.* 2002, Schnitzer *et al.* 2012) and decreasing or remaining stable in others (Bongers & Ewango 2015, Caballé & Martin 2001, Ewango 2010, Londré & Schnitzer 2006, Thomas *et al.* 2015).

The decrease in the density of gaps within the plots may be another mechanism that explains liana structural and compositional changes. Gaps caused by fallen stems ≥50 cm diameter (monitored every 5 y within the plots using different techniques; Grau 2002) exhibited a maximum density in the 1982–1992 period (i.e. 8–12 gaps ha^{-1}) and a drastic reduction afterwards (i.e. 1–2 gaps ha^{-1} recorded between 2002 and 2012). The factor controlling the change in gap frequency in this forest remains unknown, but might be related to climate (e.g. the rise in the number of gaps was during the 1980s when precipitations increased; H.R. Grau *pers. obs.*). Consequently, light availability decreased within the forest influencing lianas, which usually decline in density when canopy closes (Malizia & Grau 2008, Putz 1984). Light-demanding liana species showed the larger decrease in density while shade-tolerant species increased, probably in response to the shade conditions created when gaps closed. In addition, some of these species, such as *Q. fulta* and *C. altissima* are scramblers (Malizia & Grau 2008), lianas that are common on gaps and low-canopy areas and tend to decrease as the canopy increases its height (Hegarty & Caballé 1991, Putz & Holbrook 1991).

Liana species of this study were distributed along a continuous gradient of shade-tolerance, suggesting that only a few species can be strictly classified as shade-tolerant or shade-intolerant. This notion is supported by Putz (1984), in which from over 65 species from Barro Colorado Island (Panama), only three were classified as gap-phase or early successional and only two as shade-tolerants. Like trees, liana species appear to vary in their tolerance to shade (Gilbert *et al.* 2006) and this pattern is related to the trade-off between high survival and rapid growth (Cai *et al.* 2007, Ewango 2010, Gerwing 2004, Gilbert *et al.* 2006), which reflects the resource allocation to survival-enhancing traits (Kitajima 1994). In addition to this trade-off, we noted that liana species with high survival and low diameter growth possessed higher wood density, which was not previously reported for lianas to our knowledge.

Table 1. Changes in density (stems ha^{-1}) and basal area (m^2 ha^{-1}) between 2003 and 2015 for liana species of two 1-ha plots of Sierra de San Javier, Tucuman, Argentina

Species	Family	Density 2003 (stems ha^{-1})	Density 2015 (stems ha^{-1})	Density change (%)	Basal area 2003 (m^2 ha^{-1})	Basal area 2015 (m^2 ha^{-1})	Basal area change (%)
Acacia tucumanensis Griseb.	Fabaceae	39 ± 4	44.5 ± 4.5	14	0.06 ± 0.02	0.09 ± 0.00	43
Chamissoa altissima (Jacq.) Kunth	Amaranthaceae	77.5 ± 5.5	61.5 ± 4.5	– 21	0.10 ± 0.01	0.08 ± 0.00	– 20
Celtis iguanaea (Jacq.) Sarg.	Celtidaceae	84 ± 12	79 ± 2	– 6	0.16 ± 0.01	0.16 ± 0.00	13
Cissus striata Ruiz & Pav.	Vitaceae	153.5 ± 70.5	144 ± 71	– 6	0.16 ± 0.06	0.22 ± 0.10	34
Dolichandra unguis-cati (L.) L.G. Lohmann	Bignoniaceae	24 ± 9	27 ± 12	13	0.03 ± 0.02	0.04 ± 0.02	20
Hebanthe occidentalis (R.E. Fr.) Borsch & Pedersen	Amaranthaceae	21 ± 3	20.5 ± 2.5	– 2	0.04 ± 0.00	0.05 ± 0.01	11
Heteropterys dumetorum (Griseb.) Nied.	Malpighiaceae	22 ± 10	26.5 ± 8.5	20	0.03 ± 0.01	0.04 ± 0.00	38
Pisoniella arborescens (Lag. & Rodr.) Standl.	Nyctaginaceae	6.5 ± 4.5	9.5 ± 7.5	46	0.01 ± 0.01	0.02 ± 0.01	38
Quechualia fulta (Griseb.) H. Rob.	Asteraceae	67 ± 29	23.5 ± 0.5	– 65	0.06 ± 0.02	0.05 ± 0.01	– 22
Serjania meridionalis Cambess.	Sapindaceae	39.5 ± 4.5	25 ± 4	– 37	0.04 ± 0.00	0.03 ± 0.01	– 29
Muehlenbeckia sagittifolia (Ortega) Meisn.	Polygonaceae	2	0	–	–	–	–
Gonolobus rostratus (Vahl) Roem. & Schult.	Apocynaceae	0	1	–	–	–	–
Cissus verticillata (L.) Nicolson & C.E. Jarvis	Vitaceae	0	1	–	–	–	–

Table 2. Correlations between variables and PCA axes.

Variables	Axis 1	Axis 2
Wood density	– 0.74	0.38
Seed size	– 0.23	0.84
Mortality	0.83	0.01
Growth	0.65	0.51
Abundance	0.75	0.19

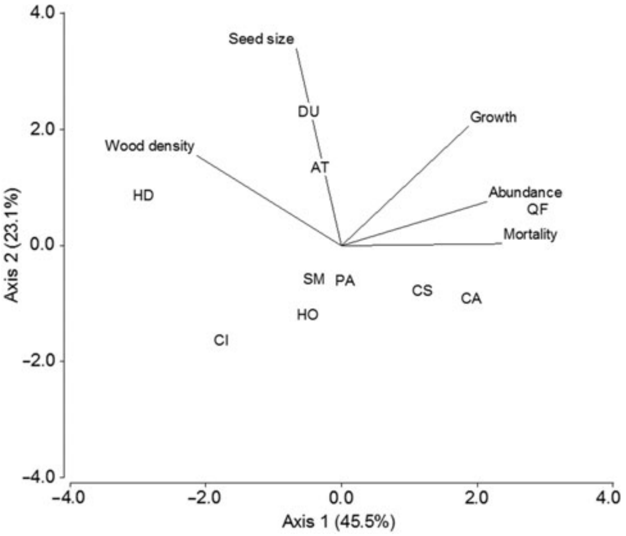

Figure 2. Ordination diagram (PCA) used to identify a shade-tolerance axis among liana species, defined by demographic and functional variables (Appendix 1). Variables are represented by vectors and species by labels: AT (*Acacia tucumanensis*), CA (*Chamissoa altissima*), CI (*Celtis iguanaea*), CS (*Cissus striata*), DU (*Dolichandra unguis-cati*), HO (*Hebanthe occidentalis*), HD (*Heteropterys dumetorum*), PA (*Pisoniella arborescens*), QF (*Quechualia fulta*), and SM (*Serjania meridionalis*).

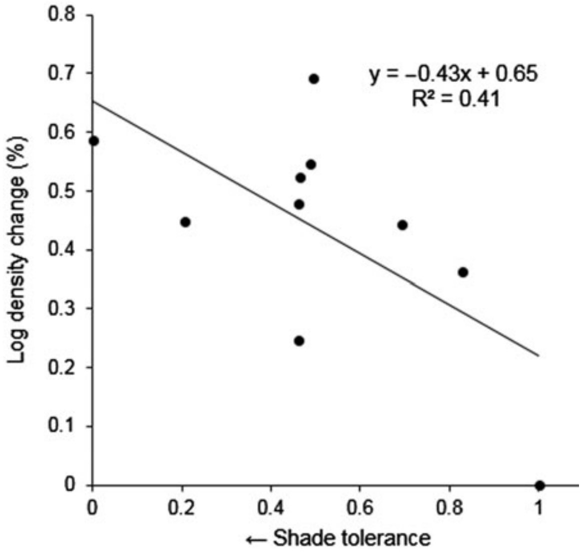

Figure 3. Linear regression between the shade-tolerance axis and change in species density over a 12-y period (2003–2015) at Sierra de San Javier, Tucuman, Argentina. The shade tolerance increases towards lower scores in x-axis. Change in species density was logarithmically transformed. Each species is represented by a black circle.

Shade tolerance is an important trait that has been scarcely taken into account for lianas, despite its relevance to species response to forest succession and disturbances (i.e. processes that change light environment in forests). It has been suggested that adaptation to light exploitation of liana species explains their abundance across a disturbance-mediated light gradient (Gianoli *et al.* 2010, Mori *et al.* 2016). Consequently, we may predict that light-demanding species will benefit from increasing disturbance, while shade-tolerant species will benefit in forests recovering from past disturbance. This prediction can be supported by the higher decrease in density and basal area of light-demanding species found in this study (e.g. *Q. fulta*, *S. meridionalis* and *C. altissima*) and in DR Congo (e.g. *Manniophytom fulvum*), probably in response to a reduction in forest disturbance (Ewango 2010). Additionally in a temperate forest, the shade-tolerant liana *Euonymus fortunei* could increase its abundance under the current lack of large and intensive disturbances (Mori *et al.* 2016). However, more studies are necessary to improve our knowledge of the strategies of liana species that are changing in density in different forests of the world.

CONCLUSION

The density and basal area of lianas showed dissimilar changes over a 12-y period in a mature forest of Sierra de San Javier. Even though density decreased, basal area increased but at lower levels than reported in other tropical and subtropical forests where lianas are becoming more dominant. Light-demanding liana species decreased while shade-tolerant species increased in density. We suggest that these changes are controlled by the reduction in both natural (treefall gap frequency) and anthropogenic disturbances (livestock browsing) in recent decades, which may influence liana density due to their close relation with forest disturbance dynamics. We recommend that density change of species with different shade-tolerance should be assessed in long-term monitoring of lianas, due to its relevance in front of the current increase of disturbances and forest recovery processes in several regions.

ACKNOWLEDGEMENTS

We thank José Tisone and Ivan Jerez for field assistance; Instituto de Ecología Regional (IER) for allowing us to work in their forest monitoring system; Francis E. Putz at the Department of Biology of the University of Florida for providing me with an office and facilities for data analysis; Sofía Nanni for the help with the English version of this manuscript. This research was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and by Cooperación Internacional UF-CONICET (526/15).

LITERATURE CITED

BIANCHI, A. R. & YÁÑEZ, C. 1992. *Las Precipitaciones del Noroeste Argentino*. INTA, Salta. 383 pp.

BONGERS, F. & EWANGO, C. E. N. 2015. Dynamics of lianas in DR Congo. Pp. 23–35 in Schnitzer, S. A., Bongers, F., Burnham, R. J. & Putz, F. E. (eds). *Ecology of lianas*. Wiley Blackwell, Oxford.

CABALLÉ, G. & MARTIN, A. 2001. Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecology* 152:167–173.

CABRERA, A. L. & WILLINK, A. 1980. *Biogeografía de América Latina*. Monografía No. 13. OEA, Washington, DC. 121 pp.

CAI, Z. Q., POORTER, L., CAO, K. F. & BONGERS, F. 2007. Seedling growth strategies in *Bauhinia* species: comparing lianas and trees. *Annals of Botany* 100:831–838.

CAMPANELLO, P. I., GARIBALDI, J. F., GATTI, M. G. & GOLDSTEIN, G. 2007. Lianas in a subtropical Atlantic Forest: host preference and tree growth. *Forest Ecology and Management* 242:250–259.

CAMPANELLO, P. I., VILLAGRA, M., GARIBALDI, J. F., RITTER, L. J., ARAUJO, J. J. & GOLDSTEIN, G. 2012. Liana abundance, tree crown infestation, and tree regeneration ten years after liana cutting in a subtropical forest. *Forest Ecology and Management* 284:213–221.

CHAVE, J., OLIVIER, J., BONGERS, F., CHÂTELET, P., FORGET, P. M., VAN DER MEER, P., NORDEN, N., RIÉRA, B. & CHARLES-DOMINIQUE, P. 2008. Aboveground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology* 24:355–366.

CHEN, Y. J., BONGERS, F., CAO, K. F. & CAI, Z. Q. 2008. Above- and below-ground competition in high and low irradiance: tree seedling responses to a competing liana *Byttneria grandifolia*. *Journal of Tropical Ecology* 24:517–524.

CONDIT, R., ASHTON, P., BUNYAVEJCHEWIN, S., DATTARAJA, H. S., DAVIES, S., ESUFALI, S., EWANGO, C., FOSTER, R., GUNATILLEKE, I. A., GUNATILLEKE, C. V., HALL, P., HARMS, K. E., HART, T., HERNANDEZ, C., HUBBELL, S., ITOH, A., KIRATIPRAYOON, S., LAFRANKIE, J., DE LAO, S. L., MAKANA, J. R., NOOR, M. N., KASSIM, A. R., RUSSO, S., SUKUMAR, R., SAMPER, C., SURESH, H. S., TAN, S., THOMAS, S., VALENCIA, R., VALLEJO, M., VILLA, G. & ZILLIO, T. 2006. The importance of demographic niches to tree diversity. *Science* 313:98–101.

DEWALT, S. J., SCHNITZER, S. A. & DENSLOW, J. S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* 16:1–19.

EASDALE, T. A., HEALEY, J. R., GRAU, H. R. & MALIZIA, A. 2007. Tree life histories in a mountain subtropical forest: forest species differ independently by shade-tolerance, turnover rate and substrate preference. *Journal of Ecology* 95:1234–1249.

EWANGO, C. E. N. 2010. *The liana assemblage of a Congolian rainforest: diversity, structure and dynamics*. Ph.D. thesis, Wageningen University, the Netherlands.

FOSTER, J. R., TOWNSEND, P. A. & ZGANJAR, C. E. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sensing of Environment* 112:2104–2117.

GERWING, J. J. 2004. Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *Forest Ecology and Management* 190:57–72.

GERWING, J. J. & FARIAS, D. L. 2000. Integrating liana abundance and forest stature into an estimate of aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* 16:327–336.

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.

GIANOLI, E., SALDAÑA, A., JIMÉNEZ-CASTILLO, M. & VALLADARES, F. 2010. Distribution and abundance of vines along the light gradient in a southern temperate rain forest. *Journal of Vegetation Science* 21:66–73.

GILBERT, B., WRIGHT, S. J., MULLER-LANDAU, H. C., KITAJIMA, K. & HERNANDEZ, A. 2006. Life history trade-offs in tropical trees and lianas. *Ecology* 87:1281–1288.

GRAU, H. R. 2002. Scale-dependent relationships between treefalls and species richness in a neotropical montane forest. *Ecology* 83:2591–2601.

GRAU, H. R. & BROWN, A. D. 1998. Structure, composition, and inferred dynamics of a subtropical montane forest of northwestern Argentina. Pp. 715–726 in Dallmaier, F. & Comiskey, J. A. (eds). *Forest biodiversity in North, Central and South America, and the Caribbean. Research and monitoring*. MAB Series, Parthenon, Carnforth.

GRAU, H. R., HERNÁNDEZ, M. E., GUTIERREZ, J., GASPARRI, N. I., CASAVECCHIA, M. C., FLORES, E. E. & PAOLINI, L. 2008. A peri-urban Neotropical forest transition and its consequences for environmental services. *Ecology and Society* 13:35.

GRAU, H. R., PAOLINI, L., MALIZIA, A. & CARILLA, J. 2010. Distribución, estructura y dinámica de los bosques de la sierra de San Javier (Tucumán, Argentina). Pp. 33–50 in Grau, H. R. (ed.). *Ecología de una interfase natural-urbana. La sierra de San Javier y el Gran San Miguel de Tucumán*. EDUNT, San Miguel de Tucumán, Argentina.

HEGARTY, E. E. & CABALLÉ, G. 1991. Distribution and abundance of vines in forest communities. Pp. 313–335 in Putz, F. E. & Mooney, H. A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.

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. *Journal of Ecology* 98:879–887.

KITAJIMA, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.

LAURANCE, W. F., ANDRADE, A. S., MAGRACH, A., CAMARGO, J. L. C., VALSKO, J. J., CAMPBELL, M., FEARNSIDE, P. M., EDWARDS, W., LOVEJOY, T. M. & LAURANCE, S. G. 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forest. *Ecology* 95:1604–1611.

LONDRÉ, R. A. & SCHNITZER, S. F. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. *Ecology* 87:2973–2978.

MALIZIA, A. 2007. *Interacciones entre lianas y árboles en una selva montana madura de las yungas argentinas*. Ph.D. thesis, Universidad Nacional de Tucumán, Argentina.

MALIZIA, A. & GRAU, H. R. 2006. Liana-host tree associations in a subtropical montane forest of north western Argentina. *Journal of Tropical Ecology* 22:331–339.

MALIZIA, A. & GRAU, H. R. 2008. Landscape context and microenvironments influences on liana communities within treefall gaps. *Journal of Vegetation Science* 19:597–604.

MALIZIA, A., GRAU, H. R. & LICHSTEIN, J. W. 2010. Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. *Journal of Vegetation Science* 21:551–560.

MALIZIA, A., EASDALE, T. A. & GRAU, H. R. 2013. Rapid structural and compositional change in an old-growth subtropical forest: using plant traits to identify probable drivers. *PLoS ONE* 8:e73546.

MORI, H., KAMIJO, T. & MASAKI, T. 2016. Liana distribution and community structure in an old-growth temperate forest: the relative importance of past disturbances, host trees, and microsite characteristics. *Plant Ecology* 217:1171–1182.

PANDIAN, E. & PARTHASARATHY, N. 2016. Decadal (2003–2013) changes in liana diversity, abundance and aboveground biomass in four inland tropical dry evergreen forest sites of peninsular India. *Journal of Forestry Research* 27:133–146.

PEÑALOSA, J. 1984. Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica* 16:1–9.

PHILLIPS, O. L., VÁSQUEZ MARTÍNEZ, R., ARROYO, L., BAKER, T. R., KILLEN, T., LEWIS, S. L., MALHI, Y., MONTEAGUDO MENDOZA, A., NEILL, D., NÚÑEZ VARGAS, P., ALEXIADES, M., CERÓN, C., DI FIORE, A., ERWIN, T., JARDIM, A., PALACIOS, W., SALDIAS, M. & VINCETI, B. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774.

PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.

PUTZ, F. E. & HOLBROOK, N. M. 1991. Biomechanical studies of vines. Pp. 73–97 in Putz, F. E. & Mooney, H. A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.

ROEDER, M., HÖLSCHER, D. & KOSSMANN-FERRAZ, I. D. 2012. Traits and growth of liana regeneration in primary and secondary forests of central Amazonia. *Applied Vegetation Science* 15:108–118.

SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262–276.

SCHNITZER, S. A. & BONGERS, F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.

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. *Journal of Ecology* 88:655–666.

SCHNITZER, S. A., KUZEE, M. & BONGERS, F. 2005. Disentangling above and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93:1115–1125.

SCHNITZER, S. A., MANGAN, S. A., DALLING, J. W., BALDECK, C. A., HUBBELL, S. P., LEDO, A., MULLER-LANDAU, H., TOBIN, M. F., AGUILAR, S., BRASSFIELD, D., HERNANDEZ, A., LAO, S., PEREZ, R., VALDEZ, O. & YORKE, S. R. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7:e52114.

SCHNITZER, S. A., VAN DER HEIJDEN, G., MASCARO, J. & CARSON, W. P. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology* 95:3008–3017.

SCHNITZER, S. A., MANGAN, S. A. & HUBBELL, S. P. 2015. The lianas of Barro Colorado Island, Panama. Pp. 76–90 in Schnitzer, S. A., Bongers, F., Burnham, R. J. & Putz, F. E. (eds). *Ecology of lianas*. Wiley Blackwell, Oxford.

THOMAS, D., BURNHAM, R. J., CHUYONG, G., KENFACK, D. & SAINGE, M. N. 2015. Liana abundance and diversity in Cameroon's Korup National Park. Pp. 11–22 in Schnitzer, S. A., Bongers, F., Burnham, R. J. & Putz, F. E. (eds). *Ecology of lianas*. Wiley Blackwell, Oxford.

TOLEDO-ACEVES, T. & SWAINE, M. D. 2008. Effect of lianas on tree regeneration in gaps and forest understory in a tropical forest in Ghana. *Journal of Vegetation Science* 19:717–728.

TORRES BRUCHMANN, E. 1978. Las clasificaciones climáticas de Koppen y Thornthwaite. *Serie Didáctica Facultad de Agronomía y Zootecnia UNT* 48:1–27.

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., POWERS, J. S. & SCHNITZER, S. A. 2015. Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences USA* 112:13267–13271.

WRIGHT, S. J. & CALDERON, O. 2006. Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters* 9:35–44.

WRIGHT, S. J., CALDERON, O., HERNANDEZ, A. & PATON, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–489.

YORKE, S. R., SCHNITZER, S. A., MASCARO, J., LETCHER, S. G. & CARSON, W. P. 2013. Increasing liana abundance and basal area in a tropical forest: the contribution of long-distance clonal colonization. *Biotropica* 45:317–324.

Appendix 1. Growth, mortality, recruitment, wood density, seed size and abundance of the 10 most common liana species of two 1-ha plots of Sierra de San Javier, Tucuman, Argentina. *N* is the number of stems used to calculate mean growth rate per species. The range of growth per species between 2003 and 2015 is indicated in parentheses. Abundance has two classes: 1 (species more abundant in mature forests) and 2 (species abundant in both young and mature forest). No species was more abundant in young forests.

Species	*N*	Mean growth (mm y^{-1})	Annual mortality (% y^{-1})	Annual recruitment (% y^{-1})	Wood density (g cm^{-3})	Seed size (length in mm)	Abundance
Acacia tucumanensis	51	1.10 (0-3.58)	3.81	4.81	0.58	5	2
Chamissoa altissima	50	0.91 (0-2.78)	8.93	7.13	0.28	2	2
Celtis iguaneae	119	0.59 (0-3.19)	2.57	2.10	0.42	1.1	1
Cissus striata	170	0.98 (0-5.36)	4.84	4.30	0.33	0.4	2
Dolichandra unguis-cati	32	0.71 (0-4.06)	3.38	4.36	0.39	2	2
Hebanthe occidentalis	30	0.66 (0-3.28)	2.33	2.33	0.38	1	2
Heteropterys dumetorum	38	0.65 (0-3.09)	1.22	2.77	0.65	8	1
Pisoniella arborescens	13	0.94 (0-3.35)	0.62	3.59	0.35	3	2
Serjania meridionalis	36	0.63 (0-3.02)	6.53	2.67	0.45	4.3	2
Quechualia fulta	37	1.38 (0-5.16)	11.67	2.15	0.32	3.3	2