Landscape context and microenvironment influences on liana communities within treefall gaps

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Abstract

Questions: How do gap aspect, openness, age and gap density in the surroundings affect diversity and composition of lianas within treefall gaps? Are the variation patterns in liana communities within treefall gaps associated with their climbing mechanisms?

Location: Subtropical montane forests in northwestern Argentina.

Methods: We used ordination analyses (NMDS) and multiple regressions to describe liana communities (species and climbing groups, stems ≥ 1 cm) in 35 gaps located in a 6-ha plot and to assess relationships with aspect, canopy and subcanopy openness, age and density of recent (three to eight years old) and old (> 8 years old) gaps.

Results: Treefall gaps segregated in the ordination diagrams based on their liana species and climbing mechanisms composition: gaps surrounded by a higher density of recent gaps showed higher densities of lianas species using tendrils, spines / hooks and voluble stems. Liana density and richness (independent of stem density) were also positively associated with the density of recent gaps in the surroundings, and negatively associated to gap age. The number of liana species corrected per area was negatively associated to gap aspect and subcanopy openness, and absolute number of liana species was positively associated to gap canopy openness.

Conclusions: This study integrates the analysis of different factors influencing liana communities within treefall gaps, and shows that spatial context of gap density (a variable largely neglected in previous studies) is particularly important on lianas composition and diversity, probably by increasing propagule input and the availability of small trellises for support.

Keywords: Dispersal-structured community; Diversity; Gap dynamics; Montane forest; Yungas.

Nomenclature: Zuloaga & Morrone (1999).

Abbreviation: NMDS = Non-metric multidimensional scaling.

Introduction

Lianas (woody climbers) are life forms that rely on other plants (mostly trees) for mechanical support to increase their light exposure. As they have reduced mechanical demands, they are able to allocate more resources to growth and reproduction (Putz 1983; Hoolbrook & Putz 1996). Many lianas increase their vegetative growth, and flower and fruit in well-lit environments (Putz 2005). In mature forests, these conditions occur at canopy level (Gentry 1991) and within treefall gaps (Brokaw 1985; Schnitzer et al. 2000; Schnitzer & Carson 2001). Treefall gaps provide differential microenvironmental conditions in relation to the undisturbed forest, including higher solar radiation, temperature and evaporation at soil surfaces, and lower air moisture and incidence of pathogens (Brokaw 1985; Veblen 1992). These microenvironmental differences are accentuated in larger gaps (Brokaw 1985) and decrease with time as vegetation regrowths. Additionally, gaps increase the arrival and recruitment of wind-dispersed species and, to a lesser extent, for small seeded animal-dispersed species (Augspurger & Franson 1988; Schupp et al. 1989).

Gaps are frequently colonized by lianas because suppressed liana seedlings are abundant in the forest interior prior to gap formation (Putz & Chai 1987), have vegetative growth and proliferate laterally from gap edges (Peñalosa 1984), regenerate from seed rain and soil seed bank (Schnitzer et al. 2000) and adult liana individuals anchored to trees can survive when they fall (Putz 1984). These characteristics, in combination with the presence of small trellises (supports) within gaps, allow lianas to form heavy tangles that connect the fallen trees with the pre-existing plants placed at gap edges and inside them prior to gap formation (Putz 1984). As a result, gaps contribute to maintain liana abundance and richness (Schnitzer et al. 2000; Schnitzer & Carson 2001).

Liana species can be classified into functional groups according to their climbing mechanisms. Lianas vary in their capacity to climb different sizes of supports, which in turn varies among gaps depending on their canopy and subcanopy regeneration. For example, tendril climbers need small trellises, and scramblers and hook climbers need dense clusters of small diameter supports (Putz

1984; Putz & Chai 1987; Putz & Holbrook 1991; Nabe-Nielsen 2001); and both types of vegetation structures are typical of recent treefall gaps. Lianas having voluble stems may climb thicker supports than do tendril climbers but they still need intermediate size (e.g. < 15 cm diameter) trellises to climb efficiently (Putz 1984; Putz & Chai 1987). On the other hand, lianas that use adventitious roots to climb have no restrictions of support size (Putz & Holbrook 1991; Nabe-Nielsen 2001).

Studies on liana communities within gaps have focussed on the analysis of microenvironmental characteristics, particularly gap size and age, reflected in canopy and subcanopy regeneration. For example, lianas were found to be more abundant in larger gaps (Putz 1984; Babweteera et al. 2000) and, after an initial colonization period of ca. ten years, they tend to decrease with time (Putz 1984; Babweteera et al. 2000). Liana richness tends to show an asymmetric unimodal trend, decreasing at larger and older gaps (Babweteera et al. 2000). Other light related gap characteristics such as aspect and canopy openness also influence the diversity of woody species, including lianas (Poulson & Platt 1989; Babweteera et al. 2000; Carvalho et al. 2000; but see Bolfaur & Bond 1993). In subtropical mountain forests topography strongly conditions the input of solar radiation and hence influences gap microenvironments.

In addition to the microenvironmental characteristics, species composition in a particular site depends on the input of propagules from the surroundings (Shmida & Willson 1985; van der Maarel 1994). Since treefalls are relatively small compared to the undisturbed forest and provide differential microenvironmental conditions during a short period of time, propagule input from the surroundings is expected to strongly influence colonization composition (Dalling et al. 1998, 2002; Hubbell et al. 1999; Grau 2002, 2004; Makana & Thomas 2004). Vegetation composition may also be influenced by the spatial dynamics of gaps, which tend to be spatially aggregated (Hubbell & Foster 1986; Lawton & Putz 1988; Tanaka & Nakashizuka 1997). For example, in the same plot where this study was conducted, Grau (2002) found that the community of pioneer tree species in recent gaps was associated with the gap proximity to previously occurred gaps, as they increase their arrival probabilities to microenvironments favourable for their establishment. This pattern may occur in other life forms such as lianas, and liana diversity within a focal gap may be also favoured by its proximity to previously occurred gaps. Although it is generally acknowledged that the spatial scale and context are key components in understanding ecological phenomena (Auerbach & Shmida 1987; Tilman 1994), previous studies on liana communities within treefall gaps have largely neglected the influence of the spatial context of gap density on their composition and diversity.

Studies within treefall gaps are crucial to understand the structure and dynamics of forest communities as they represent the regeneration phase in the forest cycle in which tree colonization and growth lead to subsequent building and mature phases (Brokaw 1985). However, when gaps are dominated by lianas the gap phase regeneration may be altered (Schnitzer et al. 2000). Thus, studies about liana communities within treefall gaps may contribute to the understanding of forest regeneration dynamics. Most previous studies have focussed on the influences of a small set of characteristics (e.g. age, size) on liana gap dynamics. Instead, we aimed to integrate the analysis of environmental, temporal and spatial characteristics of gaps on liana communities. In particular, we described liana communities addressing two questions: 1. How do gap aspect, openness, age and gap density in the surroundings affect diversity and composition of lianas within treefall gaps? 2. Are the variation patterns in liana communities within treefall gaps associated with their climbing mechanisms?

Methods

Study area

This study was conducted in a six hectare (200 m × 300 m) permanent plot located at 1000 m a.s.l. in the subtropical montane forest of Parque Sierra de San Javier, Tucumán, Argentina (26°76' S, 65°33' W). Annual rainfall is 1300-1500 mm and is distributed in a monsoonal regime with dry winters and rainy summers (Hunzinger 1997). Mean annual temperature is ca. 18 ℃, frost occurs between June and August. The plot includes a wide range of topographic conditions from N-NE facing slopes (warmer, drier and brighter) to S-SW facing slopes (colder, moister and darker). At the scale of study, topography influences tree species distribution and abundance (Brown et al. 1985; Grau et al. 1997).

Forest vegetation is characteristic of the lower montane zone of the Argentine yungas, which is the southernmost extension of neotropical Andean montane forests (Brown et al. 2001). The plot is located in mature forests with ca. 23 species/ha, including deciduous and evergreen species. Canopy height varies between 15 m and 30 m. Composition of canopy trees (> 20 m) is dominated by *Blepharocalyx salicifolius* (*Myrtaceae*), *Cinnamomum porphyrium* (*Lauraceae*) and *Pisonia ambigua* (*Nyctaginaceae*). Subcanopy tree composition (5 - 12 m) is dominated by *Eugenia uniflora* (*Myrtaceae*), *Piper tucumanum* (*Piperaceae*) and *Allophylus edulis* (*Sapindaceae*). The forest experienced a very light selective logging ca. 50 y ago, probably for the species *Cedrela lilloi* (*Meliaceae*) and *Juglans australis* (*Juglandaceae*), of which only two cut stumps were found in the plot. The disturbance regime within this forest plot is dominated by treefall gaps (Grau & Brown 1998; Grau 2002).

Data collection

Grau (2002) dated all treefall gaps (defined as fallen stems > 50 cm diameter) that occurred in the plot from 1945 to 1997 using dendroecological techniques (Grau et al. 2003) and direct observations, and mapped them into an XY coordinate system. Aditionally, in 2002 we registered treefall gaps that occurred during the 1997-2002 period. Among all gaps that occurred between 1945-2002, we considered those in which the fallen tree species was clearly recorded and, among these, we considered those that occurred after 1980 (e.g. not older than 25 years; *n* = 104) to minimize dating errors and to ensure a reliable field mapping and identification. Of these 104 gaps, we selected 35 stratified according to their age, to approximate an even age distribution (Fig. 1A).

In 2005, within each of the 35 gaps we set eight transects radiating at 45° from the centre of the gap to the edge. Transects were set at 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°. Along each transect, we measured all liana stems ≥ 1 cm diameter that crossed the horizontal plane (defined by the longitudinal axis of the transect and a width of 50 cm) of the transect at 1.30 m from the forest floor. In most cases, we identified each stem to species level. Based on field observations and literature (Jankowski et al. 2000; Ayarde 2005) we classified lianas into one of four classes of climbing mechanisms (forked stems, hook / spines, tendrils and voluble stems).

We estimated the area of each gap by measuring the two principal diameters and assuming an elliptic shape (Gap area = π × length × width /4). Gap edge was defined based on the surrounding canopy projection. Old gaps (ca. 20 years) had edges that were easily defined, and although their interior was closed by subcanopy shrubs, small trees and pioneer trees growing into the canopy, this caused no major difficulty when defining the location of the original canopy boundaries (i.e. defined by the surrounding trees already present when the gap was formed). Recorded gaps tended to represent the size distribution in the plot and were distributed across a size range from 11 m² to 130 m² (Fig. 1B), which was similar to the gap size ranges observed in mature forests of Panama (Brokaw 1985; Hubbell et al. 1999; Schnitzer et al. 2000).

For each gap we recorded aspect, canopy and subcanopy openness, age and density of recent and old gaps occurring in the surroundings. Aspect was quantified as an ordinal variable of moisture increase and solar radiation decrease from north (between 10° and 45°) = 1; east (45° to 135°) = 2; south (135° to 225°) = 3 to west (between 225° and 270°) = 4. Gap openness was visually estimated as percentage cover of two vegetation height layers: above 4 m height for canopy level and between the forest floor and 4 m height for subcanopy level. For gaps that occurred prior to 1997, gap age was assigned based on Grau (2002), for gaps that occurred between 1997 and
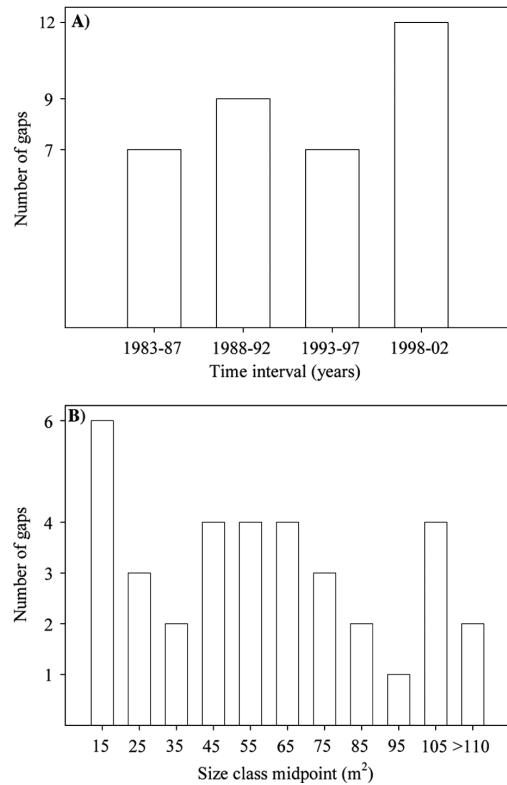

Fig. 1. Number of gaps recorded within the study area plotted against (**A**) five-year intervals from 1983 to 2002 and (**B**) 10-m² size classes.

2002 (e.g. three to eight years old) age was assigned to the mid point interval value (yr 2000 = five years old in 2005). This range of ages includes a variation in the level of vegetation recovery that could potentially introduce noise into the data. However, our personal observations in this forest indicate that pioneer trees are already well established and dominate three year old gaps, and they persist as dominants for several years. Schnitzer & Carson (2001) found no significant differences in liana diversity and density between five and ten year old gaps in Panama forests. Finally, we recorded the density of recent (1997-2002) and old (pre-1997) gaps that occurred in the 20 m × 20 m quadrats including the quadrat of the focal gap and the adjacent quadrats (nine quadrats total in the plot 'interior'). When a focal gap was located in a peripheral quadrat of the plot and we did not register all gaps that occurred in the surroundings, we estimated the gap density in the surroundings as:

$$y = 9x/j \qquad (1)$$

where y = gap density in the surroundings; x = number of counted gaps; j = number of actual quadrats (including the quadrat of the focal gaps and adjacent quadrats).

In total seven focal gaps were located on peripheral quadrats of the plot. If they were removed from the

dataset results tendency did not change.

Data analysis

We described liana species composition and liana climbing mechanism composition within treefall gaps (sampling units) based on liana stem density per species and per climbing mechanism, and evaluated their relationships with the gap characteristics recorded: aspect, canopy and subcanopy openness, age and density of recent and old gaps occurred in the surroundings of a focal gap by using ordination analyses. We evaluated the influence of the gap characteristics on liana density and richness using multiple regression analyses.

To describe the composition of nine liana species and four liana groups of climbing mechanisms within gaps we performed non-metric multidimensional scaling ordinations (NMDS, Kruskal & Wish 1978) based on a Bray-Curtis distance matrix (Legendre & Legendre 1998) between gaps ($n = 33$), calculated from liana stem density (stem/m²). We used liana density to control for gap size. To improve the convergence of the NMDS, before running the ordinations we discarded outliers (those gaps which mean Bray-Curtis distance from every other gap was higher than ± 2 SD) as they can strongly influence multivariate analysis, and we discarded liana species that were only present within one gap (*Hebanthe occidentalis* and *Muehlenbeckia sagitifolia*). In both ordinations, we performed an autopilot procedure (medium mode) to decide which dimension was the best solution (McCune & Grace 2002). We used a two dimensional configuration because the final stress (an index of agreement between the distances in the graph configuration and the distances in the Bray-Curtis matrix) was 20.58 for species and 13.21 for climbing mechanisms (most ecological community data sets have solutions with stress between 10 and 20; McCune & Grace 2002) and was significantly different from chance (Monte Carlo: 30 runs with randomized matrix, $P < 0.05$; McCune & Grace 2002). To determine which liana species or climbing group were influencing gap segregation in the ordination space we calculated their position on each axis by the 'weighted averaging' method (McCune & Grace 2002) in which gap scores are used as weights to find the average position of each species or climbing mechanism along the ordination axes; and their positions accommodate to non-linear unimodal abundance curves along the axes (McCune & Grace 2002). To explore the relationships between gap characteristics and composition of species and climbing groups we used Kendall's correlation coefficients (Sokal & Rohlf 1995) between the scores in the axes of the NMDS and the gap characteristics: aspect, canopy and subcanopy openness, age and density of recent and old gaps in the surroundings.

To determine how liana density and richness within gaps were influenced by aspect, canopy and subcanopy

openness, age and the density of recent and old gaps in the surroundings we performed forward step-wise multiple regressions (Sokal & Rohlf 1995). This type of regression evaluates the independent variables at each step, adding variables in the model based on a particular *F*-value. The output includes the standard values (R^2 adjusted, *F*, *P* and *n*), the *F*-statistic for each variable (if it was ≥ 1 entered the model) and a partial correlation coefficient (*r*) that explains the unique contribution of each independent variable to the prediction of the dependent variable. To evaluate the influence of these variables on liana abundance independently of gap size, we used liana density (stems/m²) as the dependent variable. To evaluate the influence of gap characteristics on liana richness we considered it in three different ways: as absolute (total) richness, per-area richness and per-stem richness. We controlled liana richness for size and stem density because an increase in species richness may result from an increase in the area and stems measured independently of factors that contribute to species coexistence (Denslow 1995). To control liana richness for gap size we adjusted a two-parameter hyperbola (known as Michaelis-Menten
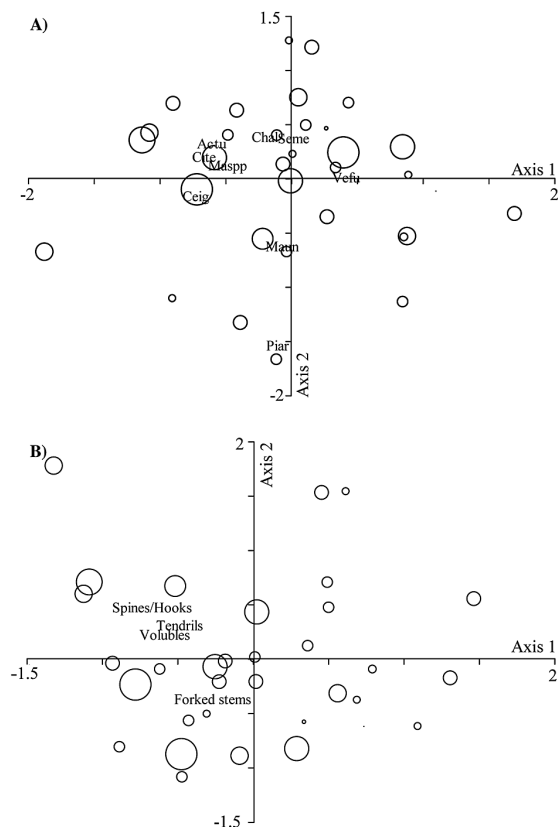

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination diagrams of treefall gaps based on (**A**) liana species, and (**B**) climbing mechanisms composition. Increasing symbol size indicated increasing density of recent gaps in the surroundings. Names of liana species are abbreviated with the first two letters of the genus and species.

Table 1. Liana species registered within treefall gaps, listed by family, climbing mechanism and total abundance (*N*).

Liana species	Family	Climbing mechanism	*N*
Chamissoa altissima	*Amaranthaceae*	Forked stems	131
Vernonia fulta	*Asteraceae*	Forked stems	101
Cissus tweediana	*Vitaceae*	Tendrils & adventitious roots	76
Celtis iguanaea	*Celtidaceae*	Hooks / spines	35
Malpigeaceae spp.	*Malpighiaceae*	Voluble stems	29
Macfadyena unguis-cati	*Bignoniaceae*	Hook tendrils & adventitious roots	20
Acacia tucumanensis	*Fabaceae*	Hooks / spines	19
Serjania meridionalis	*Sapindaceae*	Tendrils	17
Pisoniella arborescens	*Nyctaginaceae*	Forked stems	11
Hebanthe occidentalis	*Amaranthaceae*	Forked stems	3
Muehlenbeckia sagittifolia	*Polygonaceae*	Voluble stems	1
Total			**443**

equation) between gap size and number of liana species in order to generate a curve of the number of expected species per area, and used the deviates from this curve as liana per-area richness. To control liana richness for stem density we performed an accumulation curve of liana species every ten liana stems, to which we adjusted a two parameter hyperbola to generate a curve of the number of expected liana species per number of stems, and used the deviates from this curve as liana per-stem richness. In each regression model we checked for the normality of residuals and discarded outliers (data which residuals were higher than ± 2 SD) or which Mahalanobis distance (distance of a data to the centroid of all data in a space defined by all independent variables) was ≥ twice the distance immediately below. As a result, each regression model presents a different '*n*'.

We performed multivariate analyses with PC-ORD 4.01 (McCune & Mefford 1999), univariate analyses with STATISTICA 6.1 (Anon. 2003), species accumulation curve and curve fitting with ECOSIM 7.58 (Gotelli & Entsminger 2003) and SIGMAPLOT 8.02 (Anon. 2002), respectively.

Results

We recorded 11 liana species belonging to ten families within the 35 gaps. The most abundant species, with 69% of the stems, were *Chamissoa altissima*, *Vernonia fulta* and *Cissus tweediana* (Table 1). The most common climbing mechanism was scrambling with forked-stems or hooks /spines, and to a lesser extent voluble stems and the use of tendrils. Two of the three liana species having tendrils also had adventitious roots (Table 1).

Gaps tended to disperse along two NMDS dimensions based on their liana species composition. *Acacia tucumanensis*, *Celtis iguanaea*, *Cissus tweediana* and *Malpigeaceae* spp. were positioned towards the negative side of axis 1 while *Vernonia fulta* was placed towards the positive side of this axis. *Macfadyena unguis-cati* and *Pisoniella arborescens* were positioned towards the negative side of axis 2 (Fig. 2A). Kendall's correlation analyses identified that the density of recent gaps in the surroundings was negatively (but weakly and not visibly obvious in the diagram) associated with the first axis ($r = -0.25$, $P = 0.04$; Fig. 2A), while aspect was positively and marginally non-significantly associated with the second axis ($r = 0.22$, $P = 0.08$).

Table 2. Results of forward step-wise multiple regression analyses performed between gap characteristics and liana density (R^2 adj = 0.23; $F_{(2,29)} = 6.24$; $P < 0.01$; $n = 32$), liana per stem richness (R^2 adj = 0.17; $F_{(4,29)} = 2.67$; $P = 0.05$; $n = 34$), liana richness per unit area (R^2 adj = 0.24; $F_{(2,28)} = 5.74$; $P < 0.01$; $n = 31$) and absolute liana richness (R^2 adj = 0.13; $F_{(2,30)} = 3.34$; $P < 0.05$, $n = 33$). Models included independent variables with $F \geq 1$. *F*-values, partial correlation coefficient (*r*) and *P*-level for each variable are reported. Bold numbers indicated significant and marginally non-significant values.

Gap characteristics	Liana density	Liana per stem richness	Liana richness per unit area	Absolute liana richness
Age	$F = 7.06$ ***r* = –0.34; *P* = 0.06**	$F = 3.01$ ***r* = –0.38; *P* = 0.03**	-	-
Aspect	-	$F = 1.88$ $r = 0.30$; $P = 0.1$	$F = 4.42$ ***r* = –0.37; *P* = 0.04**	$F = 2.71$ $r = -0.29$; $P = 0.1$
Canopy openness	-	-	-	$F = 3.77$ ***r* = 0.33; *P* = 0.06**
Density of recent gaps in the surroundings	$F = 3.70$ ***r* = 0.49; *P* = 0.005**	$F = 3.38$ ***r* = 0.38; *P* = 0.03**	-	-
Subcanopy openness	-	$F = 1.76$ $r = 0.21$; $P = 0.2$	$F = 6.31$ ***r* = –0.49; *P* = 0.006**	-

Gaps also tended to disperse along the two NMDS dimensions based on their composition of liana climbing mechanisms. All mechanisms (spines / hooks, tendrils, voluble stems and forked stems) were positioned towards the negative side of axis 1 (Fig. 2B). Among the gap characteristics recorded, the density of recent gaps in the surroundings was negatively associated with the first axis ($r = -0.33$, $P = 0.04$, Fig. 2B). None of the gap characteristics were asociated with axis 2 ($P < 0.1$).

Liana stem density was correlated positively with the density of recent gaps in the surroundings and negatively (but non-significant; $P = 0.06$) with gap age (Table 2). Also, liana per-stem richness was positively associated with the density of recent gaps in the surroundings and negatively correlated with gap age (Table 2). Liana per-area richness was negatively associated with subcanopy openness and aspect (Table 2), and total liana species richness was positively associated with canopy openess (but non-significant; $P = 0.06$; Table 2). The density of old gaps in the surroundings showed no correlations with lianas density and richness.

Discussion

The most influential characteristic controlling liana communities in treefall gaps of NW Argentina subtropical forests was the spatial context of gap density. Specifically, the density of three to eight-year old gaps occurring in the surroundings of a focal gap was the variable with the highest level of association with the composition of climbing groups and to a lesser extent with liana species composition, liana density and liana per-stem richness.

The influence of surrounding gaps in the ordinations was due to the fact that liana species having spines / hooks such as *Celtis iguanaea* and *Acacia tucumanensis*, liana species using tendrils such as *Cissus tweediana* and voluble stems lianas such as *Malpigeaceae* spp. showed higher densities in gaps surrounded by recent gaps in a 20 m buffer area. Gaps occurring close to each other in both space and time may imply an enhanced availability of liana propagules and also may involve a higher density of small trellises (for example, of gap-dependent tree species). Lianas with tendrils require small-sized trellises to climb while scrambling lianas aided by spines or hooks depend not only on small vegetation supports but also on their dense arrangements (Putz 1984; Putz & Chai 1987; Putz & Holbrook 1991; Nabe-Nielsen 2001). Lianas having voluble stems may use thicker trellises than do tendril-climbers but still climb on rather small supports (Putz 1984; Putz & Chai 1987). Consequently, lianas display a strong spatial structure at small scales (≤ 40 m of radial distance) within this same plot (Malizia & Grau 2006) which may result, at least in part, from these gap dynamics. Also, the density of recent gaps in the surroundings was positively correlated with liana density and liana per-stem richness. Recent gaps would increase the probabilities of more species reaching

and proliferating in other recent gaps occurring close to each other in both space and time.

These spatial dynamics may imply an important influence of dispersal limitation in controlling community composition, hence favouring a 'neutral' dynamics of the community (Hubbell 2001), in which favourable and isolated microenvironments (e.g. treefall gaps not surrounded by recent previous treefalls) would not be colonized by the most competitive species (including lianas) due to the lack of timely dispersal into the site. Thus, recruitment would default to less competitive species which are better able to disperse (Tilman 1994; Hurtt & Pacala 1995). By not providing opportunities for niche separation, these dynamics would reduce the effects of treefall gaps in maintaining species coexistence (Hubbell et al. 1999).

However, studies have found that treefall gaps do increase lianas diversity (Schnitzer et al. 2000; Schnitzer & Carson 2001). The aggregated spatial dynamics of treefall gaps of this forest (Grau 2002) which is consistent with patterns found in other mature forests (Hubbell & Foster 1986; Lawton & Putz 1988; Tanaka & Nakashizuka 1997) is probably reducing the importance of dispersal limitation, by increasing the chances of a treefall gap being located close to a source of propagules (e.g. a recent treefall gap), similar to observations for pioneer tree species in this forest (Grau 2002). Although previous studies have largely ignored the influence of the spatial context of gap density, this characteristic of the landscape seems to play a central role in structuring liana communities.

In addition, microenvironmental characteristics were also associated to liana community composition in treefall gaps. Gap aspect tended to be associated to species such as *Macfadyena unguis-cati* and *Pisoniella arborescens*, and were also correlated with liana richness per unit area. Aspect is probably associated to a topographically controlled microenvironment gradient from N-E facing gaps which receive more solar radiation and have lower moisture (where lianas showed higher richness per unit area) than S-W facing gaps with moister and darker conditions. Lianas benefit from well-lit conditions (Gentry 1991; Putz 2005) and seem to perform better in light exposed gaps, although they might not be more light demanding than other life forms such as trees (Gilbert et al. 2006). In addition, in this study, lianas seemed to prefer (or at least tolerate) the relatively drier and warmer conditions within NE facing gaps. The comparatively harsh conditions may be similar to those found in seasonally dry tropical forests where lianas compete well and are very abundant (Schnitzer 2005). The attributes that enable lianas to proliferate in dry forests may also allow them to take advantage, at a local scale, of the high light availability following disturbance (Schnitzer 2005). Few studies (e.g. Bolfaur & Bond 1993) have considered the influence of gap orientation on liana communities as the majority of them have been carried out in lowland tropical forests where aspect does not have a strong effect controlling

solar radiation input. Nevertheless, aspect is a dominant feature in subtropical montane forest landscapes, and apparently influences gap microenvironments and liana communities.

Canopy gap openness tended to associate positively with absolute liana richness, probably due to an increase in light availability within gaps, as lianas tend to perform better under suitable light conditions (Gentry 1991; Putz 2005). These results differ from the study of Babweteera et al. (2000) which found highest liana diversity when canopy openness varies between 30% and 40%. Subcanopy openness was negatively associated with liana richness per unit area. Closed subcanopies showed high abundance of the shrub *Psychotria carteginensis* (*Rubiaceae*), which may imply availability of small trellises to climb. Many liana species growing within the plot are scramblers, which depend on the density of small supports or use tendrils and twining stems which climb small to intermediate-sized trellises (Putz 1984; Putz & Chai 1987; Nabe-Nielsen 2001). Nabe-Nielsen (2001) also found that liana diversity and density was higher in forest areas with more tree saplings and small trees, respectively. Alternatively, shrubs may discourage lianas by providing shade and reducing air saturation deficit but, in this study, this seems to play a less important role compared to the availability of supports.

In agreement with previous studies (Putz 1984; Babweteera et al. 2000) gap age also had some association with liana density and liana per stem richness. Recent gaps have greater availability of resources (e.g. light and soil nutrients) that would favour the recruitment and growth of different plant groups (Brokaw 1985; Veblen 1992). Many liana species in the plot are wind-dispersed or have small to intermediate-sized seeds dispersed by animals, the arrival and survival of which would be favoured in recent gaps (Augspurger & Franson 1988; Schupp et al. 1989).

In summary, this study integrated the analysis of different characteristics influencing liana communities within treefall gaps. As in previous studies, abiotic microenvironmental characteristics controlled by canopy and subcanopy regeneration such as aspect, canopy openness and age had some influence on liana communities. However, this study showed that gap density in the surroundings of each focal gap, a characteristic not considered in previous studies, has a stronger influence on the regeneration dynamics of lianas than local microenvironmental characteristics.

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