Functional strategies and distribution of climbing plant communities in different vegetation patches in a subtropical dry forest, central Argentina

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Abstract

Aims

In the context of global change, the impacts of forest structure alteration on climbing plants in extra-tropical ecosystems are poorly understood. It also remains little explored, the functional strategies among climbing plant species and its relationship with the local-scale distribution of climbing plant communities. Here, we aimed at three goals: (i) we studied how climbing plant community composition responds to the modification of the original forest structure in a subtropical dry forest; (ii) we characterized climbing plant species according to functional traits related to the acquisition and use of resources; and (iii) we examined whether functional strategies at the community level are also responding to vegetation structure change, a much less addressed topic in the ecology of climbing plants.

Methods

The study was carried out in the Chaco forest of Córdoba Mountains, central Argentina. We selected 18 patches of 'native forests', 'shrublands' and 'Ligustrum lucidum forests'. We counted and identified climbing plant individuals in each patch, including woody and herbaceous species. For each species, we measured 10 functional traits: leaf area, leaf area ratio, leaf dry matter content, leaf tensile strength, specific leaf area, stem density, wood saturated water content, inter-node length, petiole length and plant cover. We compared climbing plant composition, richness and abundance among the three vegetation types. Then, we assessed trends of functional variation of climbing plant species by performing a principal component analysis. Finally, we investigated whether simple mean, weighted mean and Functional Richness index of principal component analysis (PCA) axes differed among the climbing plant communities of the three vegetation types.

Important Findings

Multivariate analysis revealed that climbing plant composition of native forests significantly differed from that of shrublands and L. lucidum forests. Also, L. lucidum forests had the lowest climbing plant species richness. Functional variation of climbers was explained by three PCA axes: axis 1 represented the resource-use strategy, axis 2 was associated with light-foraging strategy, and axis 3 related to plant size. The most abundant species in native forests presented a more acquisitive functional strategy and larger sizes than those of shrublands and L. lucidum forest. Furthermore, the most abundant species in shrublands had shorter internodes and petioles than the most abundant climbers of the other vegetation types. Finally, the climbing plant community in the native forests had the highest Functional Richness index regarding the resource-use and the size strategies. Here, we demonstrated that there are floristic and functional differences among climbing plant communities in patches of three vegetation types in

a subtropical dry forest biome. Particularly, we found climbers spreading along three functional axes which were directly related to climbing plant community distribution among the different patches, highlighting their ecological importance and the need of further research.

INTRODUCTION

Climbing plants represent about 25% of plant biodiversity in tropical and subtropical forests around the world (Gentry 1991). They are key elements in diversity, productivity, structure and dynamics of forest ecosystems (Schnitzer 2005; Schnitzer and Bongers 2002). Climbing plant species richness and abundance respond directly to forest canopy structure and woody species composition (Schnitzer and Bongers 2002). In the context of global environmental change, worldwide forest structure is being drastically transformed (Sala *et al.* 2000) and the composition and abundance of climbers are directly affected by this phenomenon (Laurance *et al.* 2001; Londré & Schnitzer 2006). Although climbing plant species diversity is highest in tropical environments, in extra-tropical regions they can reach high abundance and diversity when herbaceous climbers are taken into account (Durigon *et al.* 2014; Gentry 1991; Gallagher *et al.* 2011). However, the impacts of forest structure alteration on climbing plants in extra-tropical ecosystems are poorly understood (Durigon *et al.* 2014; Gianoli *et al.* 2010; Ladwig and Meiners 2010). The study of climbing plant composition, species richness and ecological strategies in patches with different forest structure, outside tropical rainforests, is relevant because it provides key information for the conservation of the group and improves our understanding of subtropical climbing plant ecology in the context of global change.

It is well known that abundance and species richness of climbers are highest in tropical forests and decrease toward higher latitudes and drier ecosystems (Gentry 1991; Schnitzer 2005; Schnitzer and Bongers 2002). Patterns of climbing plant species richness, at the local scale, have been mostly studied in tropical forests and involved woody climbers (lianas; Durigon *et al.* 2014; Gianoli *et al.* 2010). Abundance and species richness of climbing plants are mostly determined by the woody species composition and the forest structure (e.g. by different physiognomies, along chronosequences; DeWalt *et al.* 2000; Laurance *et al.* 2001; Putz 1984). Specifically, abundance and richness of climbers are higher in forest gaps and edges (Laurance *et al.* 2001; Putz 1984; Schnitzer and Carson 2001), as well as in younger forests than in older ones (DeWalt *et al.* 2000). Nonetheless, this pattern is not conclusive, since an increasing number of studies outside of the tropics have shown that climbing plant species increase their richness and abundance in more conserved patches (Carrasco-Urra and Gianoli 2009; Gianoli *et al.* 2010; Yuan *et al.*2009). These results suggest that patterns of climbing plant species

richness may depend on the ecosystems where they occur. Furthermore, some authors agree in the need for re-evaluating the importance that is given to climbers in regions outside the tropics, especially in the southern hemisphere (Durigon *et al.* 2014; Gianoli *et al* 2010; Ladwig and Meiners 2010). They also suggest that the complete range of climbing plants should be included for a better understanding of this group, since climbing plant communities outside the tropics include a larger proportion of herbaceous species than in the tropics (Durigon *et al.* 2014).

Other aspect that has been poorly explored in the literature is the functional variability among climbing plant species. The functional trait approach attempts to identify general strategies by which organisms acquire, use and restore resources under the physical and biological conditions imposed by their environment and independently of their taxonomic identity (Díaz *et al.* 2004). Climbing plant species have been traditionally considered a homogeneous ecological group of fast growing and light demanding structural parasites. They invest relatively few resources in structural support, leading to high resource allocation to reproduction, canopy development, and stem and root elongation (Ewers *et al.* 1991; Schnitzer and Bongers 2002). However, if climbers can occupy a variety of forest patches at the local scale, differences in functional strategies can be expected among species. Moreover, we would expect these functional differences to affect not only the presence of climbing plant species in a particular vegetation patch but also their abundances (Cingolani *et al.* 2007). In other words, species presence and abundance could be differentially affected by environmental filters and modulated by the functional attributes of the species (Cingolani *et al.* 2007; Cornwell and Ackerly 2009). To our knowledge, only two studies have evaluated the relationship between environmental conditions and some functional traits in climbers at the local scale. Gianoli *et al.* (2012) found in a temperate forest that leaf size and specific leaf area variation across a light gradient did not explain dominance of climbing plants. Kusumoto *et al.* (2013) found in a subtropical forest that the leaf economic spectrum is associated with different topographic position and not with forest structure. Both studies highlight the importance of studying changes in functional traits of climbing plant species living under different environmental conditions.

The 'Gran Chaco' forest, one of the most extensive dry forests in the world (Archibold 1995), is suffering a significant fragmentation and degradation process (Vallejos *et al.* 2015), as most worldwide forest. Particularly in the Chaco forest of central Argentinean mountains (hereafter Chaco Serrano),

human disturbances are, nowadays, the main mechanisms underlying forests dynamics (Gavier-Pizarro *et al.* 2012; Gavier-Pizarro and Bucher 2004; Hoyos *et al.* 2010; Zak and Cabido 2002). Cattle grazing, intentional or accidental fires, urbanization and invasion significantly affect forest structure, leading to a mosaic of degraded vegetation patches with different physiognomies and plant species composition (Zak and Cabido 2002; Zeballos *et al.* 2014). Moreover, previous studies have shown that light availability, soil moisture, soil nutrients and vertical structure conditions are different among these vegetation patches (D'Agostino *et al.* 2012; Hoyos *et al.* 2010; Zeballos *et al.* 2014; Kowaljow *et al.*, unpublished work; Whitworth-Hulse, unpublished work). This environmental variability may promote a particular floristic and functional composition of the climbing community in each type of patch. Accordingly, the subtropical dry forest of Chaco Serrano represents an ideal system to study how composition of climbing plant communities responds to alterations of the original forest structure. In addition, we can inquire if functional strategies are also responding to these changes, a much less addressed topic in climbing plant ecology. Therefore, the aims of the study were: (i) to describe patterns of climbing plant community composition, abundance and richness in patches of different vegetation types (secondary native forest, shrublands and exotic *Ligustrum lucidum* forest) of a dry forest in Central Argentina; (ii) to characterize climbing plant species according to their functional traits, mainly those related to the acquisition and use of resources; and (iii) to analyse whether functional strategies of the climbing plant communities vary among different vegetation patches.

MATERIALS AND METHODS

The study was conducted in the Reserva Hídrica Natural Parque La Quebrada (31°09′00″S, 64°20′44″W), located on the eastern slope of the Córdoba mountains, Central Argentina. Climate is subtropical, with highly seasonal precipitations occurring during the warm season (October–April), and water deficit occurring in the dry season (Capitanelli 1979; De Fina 1992). Mean annual temperature and mean annual precipitations are 15.6°C and 750 mm, respectively (De Fina 1992). Vegetation of the area corresponds to the Chaco Serrano district (Cabrera 1976), a xerophytic semi-deciduous forest. Some representative species of the area are the native trees *Lithraea molleoides* (Vell.) Engl., *Zanthoxylum coco* Gillies ex Hook. f. & Arn. and *Celtis ehrenbergiana* (Klotzsch) Liebm., the native shrub *Vachellia caven* (Molina) Seigler & Ebinger and the tussock grass *Jarava pseudoichu* (Caro) F. Rojas. As mentioned earlier, owing to human land use and biological invasions, the original forest has become a mosaic of three main vegetation cover types corresponding to different degrees of structure modification (Gavier-Pizarro and Bucher 2004, Hoyos *et al.* 2010, Zak and Cabido 2002). Secondary native forests (hereafter 'native forests') are the most preserved vegetation type in the study area (Gavier-Pizarro and Bucher 2004; Gavier-Pizarro *et al.*

2012). They have been defined as low woodland types with a maximum vegetation height between 8 and 10 m (for more details, see Giorgis *et al.* 2017). These native forests correspond to areas with low grazing intensity, which have not been burnt for >60 years (Carbone *et al.* 2016, Giorgis *et al.* 2013). Shrublands (and scrubby grasslands) suffered a significant loss of tree cover and canopy height. They present significantly higher quantity and quality of light than native secondary forest (D'Agostino *et al.* 2012). Moreover, it is known that patches that have frequently being exposed to fire (every 2 to 10 years), which is common for shrublands (Argañaraz *et al.* 2015), have lower total nutrient stock (consequence of soil loss, Kowaljow *et al.*, unpublished work) and water content (Carbone and Aguilar 2016) in comparison with unburned patches. For the last 30 to 40 years, there has been a rapid increase in the cover of the exotic tree *L. lucidum* (W.T. Aiton), occupying nowadays up to 20% of the total forest area (Hoyos *et al.* 2010; Gavier-Pizarro *et al*. 2012). *Ligustrum lucidum* dominated patches (hereafter '*L. lucidum* forests') present a simpler vertical structure, and a meaningful reduction of light availability (because of the dense canopy) and soil water content, in comparison with native forest (Hoyos *et al.* 2010; Zamora Nasca *et al.* 2014; Whitworth-Hulse, unpublished work).

Climbing plant species surveys

To characterize composition, abundance and species richness of climbing plants, we selected 18 patches (between 770 and 890 m a.s.l.): seven corresponding to 'native forests', seven to 'shrublands' and four to '*L. lucidum* forests' (see detailed information of each patch in online supplementary Table S1). Patches were separated for at least 100 m from the nearest patch. Given the degree of degradation of the study area, patches were heterogeneous in size, although all of them were at least 100 × 100 m. Thus, to homogenize sampling units, in each patch we established three 3 × 15 m plots parallel to the slope where we sampled climbing plants. During summer season 2009–2010, we counted and taxonomically identified sexually mature climbing individuals with their roots inside the plots. We defined 'climber' as any climbing plant that has its roots in the soil, regardless of its climbing mechanism, and included both woody and herbaceous ones. Sexual maturity was determined by the presence of flowers or fruits, or evidence that these processes had occurred (e.g. traces of flowers, fruits or seeds). We could apply this criterion because in the study area the growing, flowering and fruiting season of all species occurs between September and April (e.g. Giorgis *et al.* 2015; Torres and Galetto 2011), which coincides with the humid and warm part of the year (Capitanelli 1979, De Fina 1992). We consider genets as one individual plant. When it was unclear whether stems were connected or not, we treated them as distinct individuals (according to DeWalt *et al.* 2000 and Yuan *et al.* 2009).

Measurements of functional traits

For each climbing plant species recorded in the surveys, we studied 10 vegetative functional traits (Pérez-Harguindeguy

et al. 2013; see online supplementary Table S2). We measured traits related to resource-use strategy (mainly nutrients and carbon) and associated to growth rate: leaf area (LA), leaf area ratio (LAR), leaf dry matter content (LDMC), leaf tensile strength (LTS), specific leaf area (SLA), stem density (SD) and wood saturated water content (Wsat; Westoby *et al.* 2002; Wright *et al.* 2004). We also measured inter-node length (IL) and petiole length (PL) due to their relationship with plant light-foraging strategies (Takenaka 1994; Gianoli 2001). Finally, we measured plant size, which is related to species competitive ability (Pérez-Harguindeguy *et al.* 2013; Westoby *et al.* 2002). All traits were measured on six healthy (without any damage due to herbivory or diseases), sexually mature individuals of each climbing species that were in well-lit environments (Pérez-Harguindeguy *et al.* 2013). Individuals were selected at any vegetation patch provided they fulfil the standard criterions for trait determination. For each plant, we took one or two stem segments ca. 70 cm long, with all leaves expanded and sun-exposed. Techniques for trait measurements were made following protocols of Ackerly (2004), Pickup *et al.* (2005) and Pérez-Harguindeguy *et al.* (2013). To determine plant size, we measured mean cover of individuals as absolute area occupied by the plant, since we assume that climbers can spread horizontally (and not vertically) independently of support size. Therefore, we took one measurement in the direction of the longest extension of the crown and another one perpendicular to that measurement, and then calculated the cover area of the individual. In this way, we determined one mean value of each trait for each climbing plant species under standard conditions.

Data analysis

To analyse climbing plant species composition, we performed a non-metric multidimensional scaling analysis (NMDS), based on species abundance per patch data. Distance matrix was constructed using Hellinger normalizing and Euclidean distances (Oksanen 2015, http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf). To analyse if differences in climbing plant composition among the three types of patches were statistically significant, we performed a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). 'A posteriori' pairwise comparisons were made with the same permutational analysis but taking into account two vegetation types each time, as suggested by Anderson (2001). To assess differences in climbing plant species richness and climbing individuals abundance among the three types of patches, we performed generalized linear models assuming Poisson and Quasi-poisson distribution of the response variables, respectively.

To analyse main trends of functional variation of climbing plant species, we performed a principal component analysis (PCA) based on mean values per species of 10 traits measured in 23 species. We used correlation matrix of the traits as input, which is equivalent to standardize traits values and made them comparable (i.e. avoiding distortion caused by different magnitudes of the traits; Johnson and Wichern 2002). Also, cover, leaf tensile strength and petiole length values were log-transformed and LA was root square transformed before performing ordination analysis in order to subtract the influence of extreme trait values.

We explored the possibility of association between functional strategies of the climbing plant community and their spatial distribution among patches of Chaco Serrano, by considering functional traits of the complete set of climbing plant species present in each patch (Cingolani *et al.* 2007). We calculated the simple and weighted mean value of each PCA axis for the climbing plant community of each patch. Simple mean can be interpreted as the result of a filter that determines which species are present and which are not (species occurrence). Weighted mean based on species abundance (i.e. each species is assigned a 'weight' according to its relative abundance in each patch) can be interpreted as the result of the previously described filter plus a second level filter that determines which species may become more abundant (Cingolani *et al.* 2007; Keddy 1992). In order to measure variability of functional strategies of the climbing plant communities, we calculated the Functional Richness index proposed by Mason *et al.* (2005) for each one of the PCA axes. This index shows the proportion of the total functional variability (i.e. considering all the patches together) that is present in each patch community. It is calculated as:

$$\mathrm{FR}_{ci} = \frac{\mathrm{Max}_{ci} - \mathrm{Min}_{ci}}{\mathrm{Max}_{c} - \mathrm{Min}_{c}} \quad \begin{array}{l} c = 1,2,3 \\ i = 1,\ldots,17 \end{array}$$

where FR_{ci} is the Functional Richness index of PCA axis 'c' in the climbing plant community of patch 'i', $\mathrm{Max}_{ci} - \mathrm{Min}_{ci}$ is the difference between maximum and minimum species score on the PCA axis 'c' of the climbers in the community of patch 'i', and $\mathrm{Max}_{c} - \mathrm{Min}_{c}$ is the difference between maximum and minimum species score on PCA axis 'c' considering the climbing plant communities of the complete set of sampled patches. FR_{ci} values range from 0, when there is no variability in functional strategies among climbers of a community (i.e. minimum and maximum species scores of PCA axis in a patch have the same value) to 1, when a community includes all the functional variability (i.e. minimum and maximum species scores in the patch match with the minimum and maximum of all the communities together). Finally, statistically significant differences in the simple and the weighted mean were evaluated by performing general linear models with patch type as a factor and adding a variance function to cope with heteroscedasticity, when it was necessary. We tested differences in Functional Richness index among patches using a Kruskal–Wallis test.

For statistical analysis, we considered only three *L. lucidum* forests because one of them hosted only one climbing individual, causing important distortions in data analysis. The climbing species *Passiflora mooreana* Hook. f. was also excluded because it occurred in only one patch. Statistical analyses

were performed using Infostat (version 2013, Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina); NMDS ordination and PERMANOVAs were done using the R statistical software, package 'vegan: Community Ecology Package' (version 2.3–1, https://CRAN.R-project.org/package=vegan).

RESULTS

Composition and diversity patterns of climbing plants

A total of 1409 climbing adult individuals, representing 24 climbing plant species, of 19 genera and 12 families were recorded (see online supplementary Table S3). The families with the highest number of species were Fabaceae (5) and Apocynaceae (4), and those with the highest number of individuals were Fabaceae (51.0%), Apocynaceae (13.3%) and Bignoniaceae (12.3%). The most abundant species were the herbaceous climbers *Rhynchosia edulis* Griseb. and *Cologania broussonetti* (Balb.) DC., representing 25.8% and 17.5% of all individuals recorded, respectively. Two climbing plant species were exotic in the area: *Asparagus setaceus* (Kunth) Jessop (which is native to Africa) and *Vigna caracalla* (L.) Verdc. (which is native to subtropical South America but not to the study area). Only one of the recorded species, *Dolychandra cynanchoides* Cham., was a woody climber (i.e. liana growth form), whereas the other climbers were herbaceous or present little lignified stems. Out of the 24 climbing plant species recorded, eight were present in the three types of patches. One species, *P. mooreana*, was exclusive to shrublands, and two were exclusive to the native forest (*Cardiospermum halicacabum* L. and the alien *V. caracalla*). *Ligustrum lucidum* forests did not have any exclusive climbing plant species (Fig. 1). Shrublands and native forests shared most of their climbing plant species (Fig. 1). Along NMDS axis 1, climbing plant communities present in the native forest patches were segregated from those found in the shrublands and *L. lucidum* forests, which were more similar (at the negative extreme of the axis; Fig. 1). Results of PERMANOVA confirmed this trend (complete model pseudo-F = 37.09; P = 0.001): climbing species composition of the native forests significantly differed from that of the shrublands (P = 0.04) and *L. lucidum* forests (P = 0.02). Composition of shrublands and *L. lucidum* forests did not differ significantly (P = 0.33). Finally, there was a significant effect of patch type on species richness (P = 0.0059). *Ligustrum lucidum* forest presented the lowest mean species richness (5.25 ± 1.15 standard error [SE]), while native forest (11.00 ± 1.25 SE) and shrublands (8.86 ± 1.12 SE) did not differ between them. The three types of patches did not differ in climbing individuals abundance (P = 0.0983); however, there was a tendency of *L. lucidum* forest to have fewer mean climber abundance (43.25 ± 14.98 SE) than shrublands (99.71 ± 17.19 SE) and native forest (76.86 ± 15.10 SE).

Functional characterization of climbing plant species

The first three PCA axes accounted for 81.2 % of total variation in climbing plant functional traits. PC1 showed that the main trend of functional variation was among species with large and soft leaves, high SLA and low stem density, and species with the opposite attributes (Fig. 2). PC2 separated climbing plant species with long internodes and petioles and large leaves with low SLA from climbing plant species with the opposite attributes (Fig. 2). Finally, PC3 was related to the plant size axis, separating species whose individuals have larger mean cover from those species with smaller individuals (Fig. 2).
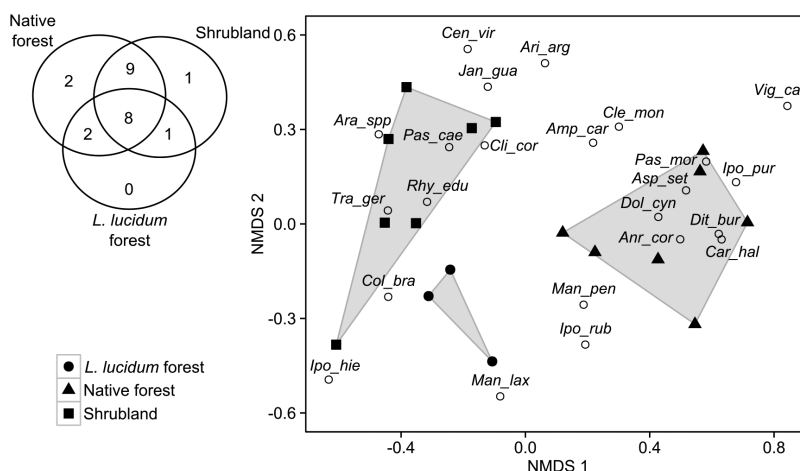

Figure 1: Venn diagram showing the distribution of climbing species richness among native forest, shrubland and *Ligustrum lucidum* forest (left), and non-metric multidimensional scaling ordination (NMDS, right) based on 17 sites × 23 climbing species abundance matrix of Chaco Serrano ecosystem in Cordoba, Argentina (two-dimensional solution, stress = 0.0983). Grey figures connect surveys of climbing plants corresponding to the same type of patch. Scientific names are abbreviated using the first three letters of the genus and species (see full name in online supplementary Table S3).

Relationship between climber community functional strategies and distribution

Regarding simple means, significant differences were only found in PC3 (P = 0.0102). The climbing plant community of native forests presented species with larger size individuals (i.e. larger PC3 simple mean) than communities of shrublands and *L. lucidum* forests, which did not differ between them ([Fig. 3](#)). Concerning weighted means, there were significant differences among patches in PC2 and PC3 and marginally significant differences in PC1. PC1-weighted mean was marginally (P = 0.0581) higher in the climbing plant community of native forests than in those of shrublands and *L. lucidum*
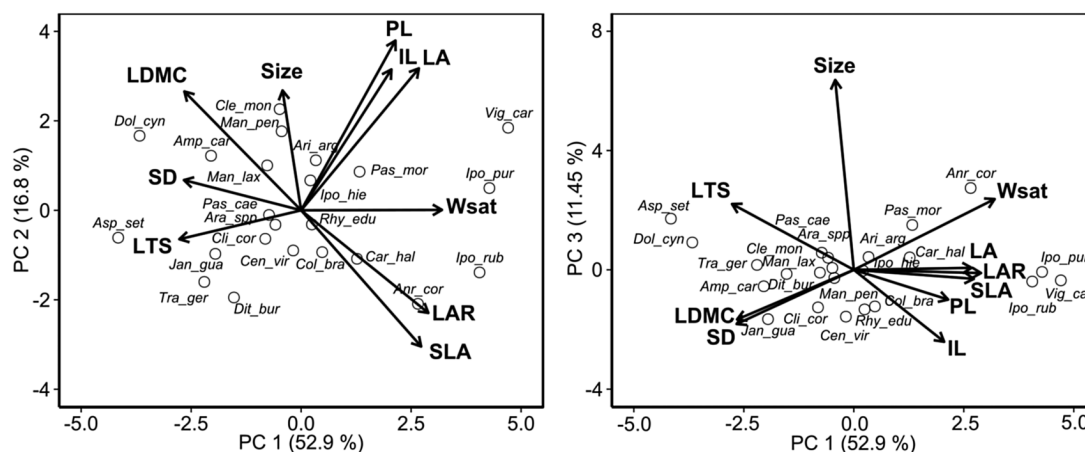

Figure 2: biplot of PCA based on a correlation matrix of 10 functional traits measured in 23 climbing species. Left: PC1 vs PC2. Right: PC1 vs PC3. Scientific names are abbreviated using the first three letters of the genus and species (see full names in online supplementary Table S3).
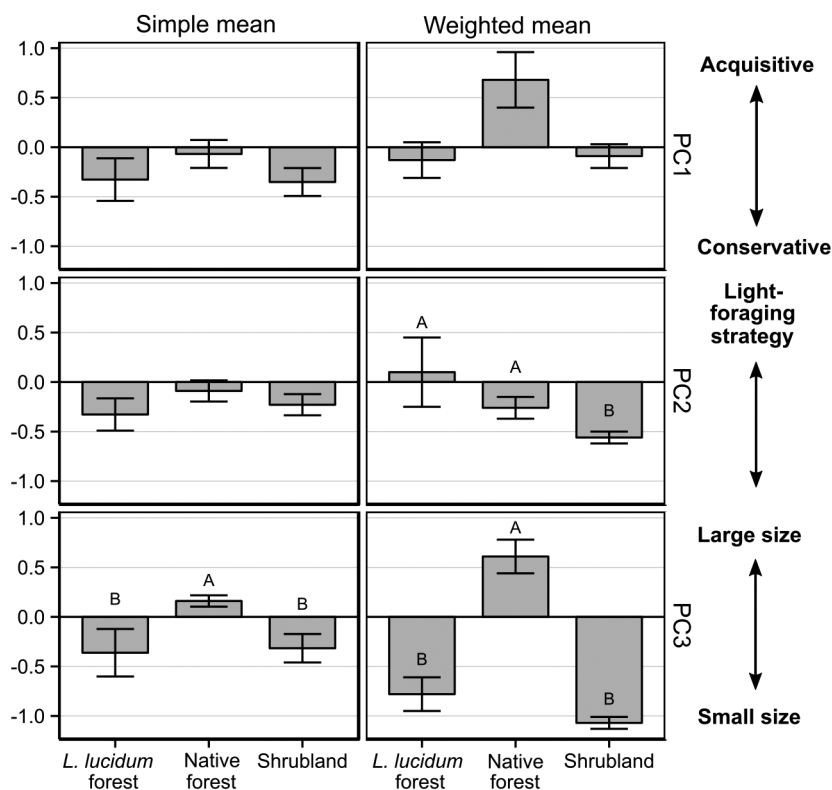

Figure 3: simple (left) and weighted (right) means and standard errors of PCA axes species scores of the three Chaco Serrano vegetation types. Different letters above bars indicate significant differences between means (LSD-Fisher test, P < 0.05). On the right of the graph, the functional strategies related to each PCA axis are described to help with interpretation of the means.

forests (Fig. 3). Climbing plant communities of shrublands had significantly lower weighted mean values of PC2 than native forests and *L. lucidum* forest. The latter vegetation types did not differ between them, although there was a tendency for the climbing community of *L. lucidum* forests to have larger mean values. PC3-weighted mean was significantly higher in climbing plant communities of native forests than in those of shrublands and *L. lucidum* forests (Fig. 3). These results for weighted means indicated that the most abundant climbing species in the native forest presented more acquisitive functional strategy and larger size than those of shrublands and *L. lucidum* forests. In addition, the most abundant species of shrublands had shorter internodes and petioles and higher SLA than those occurring in the native and invaded forests patches (Fig. 3). Finally, functional richness of PC1 was significantly higher in climbing plant communities of native forest than in those of shrublands and *L. lucidum* forests, whereas functional richness of PC2 did not differ among patches (Table 1). Functional richness of PC3 was marginally higher in native forest and shrublands than in *L. lucidum* forests (Table 1). Therefore, the community of the native forests was more heterogeneous in terms of resource acquisition strategy and the communities of both the native forests and the shrublands were marginally more heterogeneous regarding the size strategy than that of the *L. lucidum* forests.

DISCUSSION

Our study provides important information about the ecology of climbing plant species in a subtropical dry forest biome. We also included herbaceous species, which are an important component of climbing plant diversity outside the tropics (Durigon *et al.* 2014). We found an important effect of the vegetation structure and composition on climbing plant community composition, richness and functional characteristics. The observed patterns contradict some commonly reported results for tropical forests, highlighting the importance of addressing the study of climbers in other environments. This research is, to our knowledge, one of the few studies that address climbing plant ecology from a functional strategy approach (*sensu* Díaz *et al.* 2004; Reich *et al.* 2003). We found climbers spreading along the main functional axes described in the literature for plants (i.e. the resource-use and the size specialization axes; Westoby *et al.* 2002; Wright *et al.* 2004).

Finally, we were also able to relate these functional strategies, at the community level, to climbing plant species spatial distribution among patches.

Composition and diversity patterns of climbing plant species

Climbing plant species composition differed among native forests and shrublands and invaded *L. lucidum* forests patches. These results suggest that changes in forest original structure are associated with changes in climbing plant species composition, as previously reported (e.g. DeWalt *et al.* 2000; Yuan *et al.* 2009). Since most species are shared among patches (see Venn diagrams in Fig. 1), differences among climbing plant communities are mainly determined by species abundances. Therefore, at the patch scale, environmental conditions seem to affect the species dominance (i.e. second level filter; Cingolani *et al.* 2007) but not the presence-absence of each species (i.e. first level filter).

We also detected higher climbing plant species richness in the native forests and shrublands than in *L. lucidum* forests. It has already been reported that *L. lucidum* invasion leads to the loss of native plant species richness and abundance (Lichstein *et al.* 2004; Hoyos *et al.* 2010), specially, climbing plant species (Ceballos *et al.* 2015; Lichstein *et al.* 2004). The effect of *L. lucidum* invasion on climbing plant community has been attributed to the simplification of vertical structure, the predominance of smooth bark and few low branches (Lichstein *et al.* 2004), as well as the low light levels of highly invaded patches (Ceballos *et al.* 2015; Hoyos *et al.* 2010). In addition, the climbing plant community in the *L. lucidum* forests presented low abundance of individuals, although not statistically significant, and did not show a characteristic composition.

Climbing plant species richness and abundance did not differ between native forests and shrublands. This result disagrees with other studies, mainly of tropical rainforest, which reported an increase in climbing species richness and abundance at plots where tree canopy has been lost (i.e. early successional stages, forest gaps) and that attributed it to an increase in light availability (e.g. DeWalt *et al.* 2000; Laurance *et al.* 2001). However, several studies have found that climbers proliferate equally well in patches with different levels of original canopy opening, and even became more abundant and diverse in more conserved plots. Some of these results have been reported for temperate and subtropical forests (e.g.

Table 1: median values of functional richness index of the Chaco Serrano vegetation types and H value and P value of the Kruskal–Wallis test

| PCA axis | Functional richness index | | | *H* value | *P* value |
	Native forest	Shrubland	*Ligustrum lucidum* forest		
PC 1	0.9519b	0.7138a	0.7058a	8.0215	0.0173
PC 2	0.8862	0.8631	0.7737	3.3277	0.1620
PC 3	1.0000	0.9258	0.3391	4.6321	0.0799

Different letters indicate significant differences ($P < 0.05$).

Carrasco-Urra and Gianoli 2009; Gianoli *et al.* 2010; Ladwig and Meiners 2010; Yuan *et al.* 2009). Consequently, a possible explanation of such pattern is that the effect of disturbance on the climbing plant community may depend on ecosystem type. For example, light is the major limiting resource in rainforest ecosystems (Chazdon 1988), hence, a disturbance that produces a canopy opening reduces stress on climbers. As mentioned before, canopy open in shrublands increase radiation (D'Agostino *et al.* 2012) and, consequently, soil evaporation may be increased (Magliano *et al.* 2016). Then, opposite to tropical forests, in the Chaco Serrano xerophytic forest where water is one of the major limiting resources (Zeballos *et al.* 2014), forest structure degradation, may reduce water availability in the soil profile, increasing stressing conditions for vines and likely preventing greater proliferation.

Functional characterization of climbing plant species

We were able to describe three functional axes for climbers. To our knowledge, this is the first study that explicitly assesses intra-group functional variation in climbing plants, including non-woody and non-tropical climbers. Along PC1, we observed a shift from acquisitive climbing plant species with large specific LA, and low wood density and leaf tensile strength to climbers having the opposite attributes. PC1 is related to the resource-use strategy axis, which has been consistently found in diverse plant groups across regions and is amply accepted in the literature (Díaz *et al.* 2004; Reich *et al.* 2014; Wright *et al.* 2004). This represents a trade-off between species with acquisitive use, retention and release of resources, mainly nutrients (N, P) and carbon, to species that have the opposite conservative resources-use syndrome. PC2 separated climbing plant species with long internodes and petioles and large leaves from climbing species with the opposite attributes. One possible interpretation of trait variation described by PC2 is in relation to light-foraging strategies. Attributes at the positive extreme of PC2 match with descriptions of species that grow successfully in the understory (Reich *et al.* 2003; Valladeres and Niinemets 2008). Long internodes, petioles and large LA would maximize light interception in shady environments by minimizing self-shading and maximizing light interception (Gianoli 2001; Falster and Westoby 2003). Since we found differences among vegetation types in relation to this axis, we assumed that the associated trait syndromes have an ecological importance that deserves further exploration. PC3 is related to the size functional axis (Pérez-Harguindeguy *et al.* 2013; Westoby *et al.* 2002). Large plants are considered better competitors and more resistant to some stress than small ones (Grime 1977; Pérez-Harguindeguy *et al.* 2013; Westoby *et al.* 2002). Therefore, among climbers, a larger size would provide them with some benefits, such as greater leaf exposure to light, better access to available support structures, and better resistance to physical stress and likely to some biological stress (i.e. diseases, parasites and insect attack) than smaller climbers.

Relationship between community functional strategies and distribution patterns

Forest structure showed an effect on functional strategies and functional richness of climbing plant communities. The main differences in functional strategies were related to dominant species (represented by weighted means) and, to a lesser extent, to the variety of functional strategies presented in the patches (represented by Functional Richness index). With respect to resource-use strategies (described by PC1), climbing plant communities of native forest patches presented the highest functional diversity (i.e. higher Functional Richness index) with a tendency of dominant species to be more acquisitive than in the other patches. Lebrija-Trejos *et al.* (2010), Lohbeck *et al.* (2013) and Bhaskar *et al.* (2014) proposed two processes acting consecutively in the assembly of plant communities along succession in a tropical dry forest. At early successional stages, when the forest is less structured and environmental conditions are more restrictive (limited water supply, high solar irradiance and high evaporative demand; Lebrija-Trejos *et al.* 2010), there is a strong effect of abiotic environmental filters that leads to a convergence towards few 'successful' functional strategies (i.e. low functional richness). At advanced successional stages, when forests are more structured, the abiotic conditions become less stressful but the increase of stand biomass results in greater biological competition for resource access. This situation promotes a divergence of functional strategies as a way to avoid competitive exclusion, which translates into greater functional richness. Similar processes may explain patterns of resource-use strategy in our study system. Patches of native forests provide benign abiotic conditions and resources for climbers (i.e. intermediate light availability, high support availability, higher humidity; D'Agostino *et al.* 2012; Hoyos *et al.* 2010; Withworth-Hulse, unpublished work). However, high stand biomass would imply strong competition. Then, on the one hand, the climbing community of native forest patches is expected to exhibit greater functional richness in order to avoid competitive exclusion. On the other hand, it is still expected that the more abundant species have acquisitive functional strategy, which allows them to capture resources more rapidly and to grow faster, conferring an advantage in a benign environment (Díaz *et al.* 2004). On the contrary, *L. lucidum* forests and shrublands offer harsher environmental conditions for climbers (very low or high irradiance, lower support availability and lower soil humidity; D'Agostino *et al.* 2012; Hoyos *et al.* 2010; Withworth-Hulse, unpublished work), which would explain the occurrence of climbing plant communities with lower functional richness and the convergence towards a more conservative strategy that ensures survival under stress conditions (Díaz *et al.* 2004).

The dominant climbing plant species of both native and *L. lucidum* forests had longer internodes and petioles, larger leaves and lower SLA than dominant climbers in shrublands (significant differences of PC2 weighted means). Although

not significant, there is also a tendency of the climbing community of *L. lucidum* forest to have a greater weighted mean than the climbing communities of native forests ([Fig. 3](#)). This pattern can be understood considering that *L. lucidum* forests are environments where light can be a limiting resource in the understory ([Hoyos *et al.* 2010](#); Withworth-Hulse, unpublished work) and shrublands, on the contrary, are subject to high irradiance ([D'Agostino *et al.* 2012](#)). Thus, having a strategy to search for light in the understory would mean an advantage for dominant species, mainly at *L. lucidum* forests, but also at native forests. The functional attributes found in the dominant climbing plant species of the studied patches support the interpretation of PC2 related to light capture strategies.

Climbing species in native forests patches were, on average, bigger than species of shrublands and *L. lucidum* forests. A greater plant cover ensures access to light and support, and therefore climbing species that occupy a large area are better competitors than climbers occupying smaller areas. For instance, [DeWalt *et al.* (2000)](#) and [Yuan *et al.* (2009)](#) found that liana size increases with forest age and structure. In the case of *L. lucidum* forests, despite their high tree cover, the simplification of vertical structure and the fast growth of *L. lucidum* ([Hoyos *et al.* 2010](#); [Lichstein *et al.* 2004](#)) would limit the proliferation of larger climbing plant species capable of reach the top of the canopy.

Here, we showed floristic and functional differences among climbing plants communities in patches of three vegetation types of the subtropical dry forest biome. In general, the more conserved secondary native forest patches were floristically and functionally different from the more degraded shrublands and *L. lucidum* forest patches. Particularly, we observed that invaded forests involve a serious impoverishment of the climbing plant community. Regarding functional variation, we found climbing plant species spreading along three functional axes associated with the resource-use strategy, the size strategy and also a 'new' spectra of variation, which we related to light-foraging. Moreover, we found that the three functional axes were directly related to climbing plant community distribution among the different patches, highlighting their ecological importance. We were able to observe climbers as a diverse ecological group, adapted to different environmental conditions, even at the small patch scale. We emphasize the need of further exploring functional strategies of climbers, especially regarding the light-foraging axis in order to assess its importance. It is also necessary to continue the study of climbing plant ecology in non-tropical ecosystems, as a way to detect the influence of different biotic and abiotic factors in this group of plants.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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