

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

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15 **Running title:** Functional strategies of subtropical climbers

16

17 **Abstract**

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

26 the community level are also responding to vegetation structure change, a much less
27 | addressed topic in [the ecology of climbing plants](#).

28 **Methods:** The study was carried out in the Chaco forest of Córdoba Mountains, central
29 Argentina. We selected 18 patches of "native forests", "shrublands" and "*Ligustrum*
30 *lucidum* forests". We counted and identified climbing plant individuals in each patch,
31 including woody and herbaceous species. For each species, we measured ten functional
32 traits: leaf area, leaf area ratio, leaf dry matter content, leaf tensile strength, specific leaf
33 area, stem density, wood saturated water content, internode length, petiole length and
34 plant cover. We compared climbing plant composition, richness and abundance among
35 the three vegetation types. Then, we assessed trends of functional variation of climbing
36 plant species by performing a principal component analysis. Finally, we investigated
37 whether simple mean, weighted mean and Functional Richness index of PCA axes
38 differed among the climbing plant communities of the three vegetation types.

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

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

55

56 **Keywords:** Vines, functional traits, Chaco Serrano, climbing plant species richness,
57 community weighted means.

58

59 **Introduction**

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

76 conservation of the group and improves our understanding of subtropical climbing plant
77 ecology in the context of global change.

78 It is well known that abundance and species richness of climbers are highest in tropical
79 forests and decrease toward higher latitudes and drier ecosystems (Gentry 1991;
80 Schnitzer and Bongers 2002; Schnitzer 2005). Patterns of climbing plant species
81 richness, at the local scale, have been mostly studied in tropical forests and involved
82 woody climbers (lianas) (Gianoli *et al.* 2010; Durigon *et al.* 2014). Abundance and
83 species richness of climbing plants are mostly determined by the woody species
84 composition and the forest structure (e.g., by different physiognomies, along
85 chronosequences; Putz 1984; DeWalt *et al.* 2000; Laurance *et al.* 2001). Specifically, -
86 abundance and richness of climbers are higher in forest gaps and edges (Putz 1984;
87 Laurance *et al.* 2001; Schnitzer and Carson 2001), as well as in younger forests than in
88 older ones (DeWalt *et al.* 2000). Nonetheless, this pattern is not conclusive, since an
89 increasing number of studies outside of the tropics have shown that climbing plant
90 species increase their richness and abundance in more conserved patches (Carrasco-Urra
91 and Gianoli 2009; Yuan *et al.* 2009; Gianoli *et al.* 2010). These results suggest that
92 patterns of climbing plant species richness may depend on the ecosystems where they
93 occur. Furthermore, some authors agree in the need for re-evaluating the importance
94 that is given to climbers in regions outside the tropics, especially in the southern
95 hemisphere (Gianoli *et al.* 2010; Ladwig and Meiners 2010; Durigon *et al.* 2014). They
96 also suggest that the complete range of climbing plants should be included for a better
97 understanding of this group, since climbing plant communities outside the tropics
98 include a larger proportion of herbaceous species than in the tropics (Durigon *et al.*
99 2014).

100 Other aspect that has been poorly explored in the literature is the functional variability

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

123 The “Gran Chaco” forest, one of the most extensive dry forests in the world (Archibold
124 1995), is suffering a significant fragmentation and degradation process (Vallejos *et al.*
125 2015), as most worldwide forest. Particularly in the Chaco forest of central Argentinean

126 | mountains (hereafter Chaco Serrano), human disturbances are, nowadays, the ~~major~~
127 | main mechanisms underlying forests dynamics (Zak and Cabido 2002, Gavier-Pizarro
128 | and Bucher 2004; Hoyos *et al.* 2010; Gavier-Pizarro *et al.* 2012). Cattle grazing,
129 | intentional or accidental fires, urbanization and invasion significantly affect forest
130 | structure, leading to a mosaic of degraded vegetation patches with different
131 | physiognomies and plant species composition (Zak and Cabido 2002; Zeballos *et al.*
132 | 2014). Moreover, previous studies have shown that light availability, soil moisture, soil
133 | nutrients, and vertical structure conditions are different among these vegetation patches
134 | (Hoyos *et al.* 2010; D'Agostino *et al.* 2012; Zeballos *et al.* 2014, Kowaljow *et al.*
135 | unpubl., Whitworth-Hulse unpubl.). This environmental variability may promote a
136 | particular floristic and functional composition of the climbing community in each type
137 | of patch. Accordingly, the subtropical dry forest of Chaco Serrano represents an ideal
138 | system to study how composition of climbing plant communities responds to alterations
139 | of the original forest structure. In addition, we can inquire if functional strategies are
140 | also responding to these changes, a much less addressed topic in climbing plant ecology.
141 | Therefore, the aims of the study were: (1) to describe patterns of climbing plant
142 | community composition, abundance and richness in patches of different vegetation
143 | types (secondary native forest, shrublands and exotic *Ligustrum lucidum* forest) of a dry
144 | forest in Central Argentina; (2) to characterize climbing plant species according to their
145 | functional traits, mainly those related to the acquisition and use of resources; and (3) to
146 | analyse whether functional strategies of the climbing plant communities vary among
147 | different vegetation patches.

148

149 **Materials and methods**

150 The study was conducted in the Reserva Hídrica Natural Parque La Quebrada (31° 09'

151 | 00" S, 64° 20' 44 " W), located on the eastern slope of the Córdoba mountains, Ceentral
152 | Argentina. Climate is subtropical, with highly seasonal precipitations occurring during
153 | the warm season (October-April), and water deficit occurring in the dry season. Mean
154 | annual temperature and mean annual precipitations are 15.6 °C and 750 mm,
155 | respectively (De Fina 1992). Vegetation of the area corresponds to the Chaco Serrano
156 | district (Cabrera 1976), a xerophytic semi-deciduous forest. Some representative species
157 | of the area are the native trees *Lithraea molleoides* (Vell.) Engl., *Zanthoxylum coco*
158 | Gillies ex Hook. f. & Arn. and *Celtis ehrenbergiana* (Klotzsch) Liebm., the native shrub
159 | *Vachellia caven* (Molina) Seigler & Ebinger and the tussock grass *Jarava pseudoichu*
160 | (Caro) F. Rojas. As mentioned earlier, owing to human land use and biological
161 | invasions, the original forest has become a mosaic of three main vegetation cover types
162 | corresponding to different degrees of structure modification (Zak and Cabido 2002;
163 | Gavier-Pizarro and Bucher 2004, Hoyos *et al.* 2010). Secondary native forests (hereafter
164 | “native forests”) are the most preserved vegetation type. They correspond to areas
165 | where disturbance has been low in intensity and frequency (they may be from c.a. 50 to
166 | 120 years old, Whithworth-Hulse unpubl.). Shrublands (and scrubby grasslands)
167 | suffered a significant loss of tree cover and canopy height. They present significantly
168 | higher quantity and quality of light than native secondary forest (D’Agostino *et al.*
169 | 2012). Moreover, it is known that patches that have frequently being exposed to fire
170 | (every two to ten years), which is common for shrublands (Argañaraz *et al.* 2015), have
171 | lower total nutrient stock (consequence of soil loss, Kowaljow *et al.* unpubl.) and water
172 | content (Carbone and Aguilar 2016) in comparison with unburned patches. Since For
173 | the last 30 to 40 years, there has been a rapidly increasing-increase in the cover of the
174 | exotic tree *Ligustrum lucidum* (W.T. Aiton), occupying; nowadays; up to 20% of the
175 | total forest area (Hoyos *et al.* 2010, Gavier-Pizzaro *et al.* 2012). *L. lucidum* dominated

Comment [R11]: Don't you know how old are they (even approximately)?

176 | patches (hereafter “*L. lucidum* forests”) present a ~~simplification of the simpler~~ vertical
177 | structure, and a meaningful reduction of light availability (because of the dense canopy)
178 | and soil water content, in comparison with native forest (Hoyos *et al.* 2010, Zamora
179 | Nasca *et al.* 2014; Whitworth-Hulse unpubl.).

180

181 Climbing plant species surveys

182 | To characterize composition, abundance and species richness of climbing plants, we
183 | selected 18 patches (between 770 and 890 m a.s.l.): seven corresponding to "native
184 | forests", seven to "shrublands" and four to "*L. lucidum* forests" (see detailed information
185 | of each patch in Appendix S1). Patches were separated for at least 100 m from the
186 | nearest patch. Given the degree of degradation of the study area, patches were

187 | heterogeneous in size, although all of them were at ~~at least~~ 100 × 100 m. ~~So Thus~~, to
188 | homogenize sampling units, in each patch we established three 3 × 15 m plots parallel
189 | to the slope where we sampled climbing plants. We counted and taxonomically
190 | identified sexually mature climbing individuals with their roots inside the plots. We
191 | defined “climber” as any climbing plant that has its roots in the soil, regardless of its
192 | climbing mechanism, and included both woody and herbaceous ones. Sexual maturity
193 | was determined by the presence of flowers or fruits, or evidence that these processes
194 | had occurred (e.g. traces of flowers, fruits or seeds). **We could apply this criterion**

195 | **because sampling was carried out during flowering and fruiting season.** We consider
196 | genets as one individual plant. When it was unclear whether stems were connected or
197 | not, we treated them as distinct individuals (according to DeWalt *et al.* 2000 and Yuan *et*
198 | *al.* 2009).

199

200 Measurements of functional traits

Comment [R12]: Please, elaborate on this description a bit further as to satisfy Reviewer 2’s concern regarding the timing of the surveys. Your writing is still somewhat ambiguous in this regard.

201 For each climbing plant species recorded in the surveys, we studied ten vegetative
202 functional traits (Pérez-Harguindeguy *et al.* 2013, see Appendix S2). We measured traits
203 related to resource-use strategy (mainly nutrients and $\delta^{13}\text{C}$ Carbon) and associated to growth
204 rate: leaf area (LA), leaf area ratio (LAR), leaf dry matter content (LDMC), leaf tensile
205 strength (LTS), specific leaf area (SLA), stem density (SD) and wood saturated water
206 content (Wsat) (Westoby *et al.* 2002; Wright *et al.* 2004). We also measured internode
207 length (IL) and petiole length (PL) due to their relationship with plant light-foraging
208 strategies (Tekena 1994; Gianoli 2001). Finally, we measured plant size, which is
209 related to species competitive ability (Westoby *et al.* 2002, Pérez-Harguindeguy *et al.*
210 2013). All traits were measured on six healthy (without any damage due to herbivory or
211 diseases), sexually mature individuals of each climbing species that were in well-lit
212 environments (following Pérez-Harguindeguy *et al.* 2013 handbook for standardised
213 measurements of functional trait). Individuals were selected at any vegetation patch
214 provided they fulfil the standard criterions for trait determination. For each plant, we
215 took one or two stem segments ca. 70 cm long, with all leaves expanded and sun-
216 exposed. Techniques for trait measurements were made following protocols of Ackerly
217 (2004), Pickup *et al.* (2005) and Pérez-Harguindeguy *et al.* (2013). To determine plant
218 size, we measured mean cover of individuals as absolute area occupied by the plant,
219 since we assume that climbers can spread horizontally (and not vertically)
220 independently of support size. Therefore, we took one measurement in the direction of
221 the longest extension of the crown and another one perpendicular to that measurement,
222 and then calculated the cover area of the individual. In this way, we determined one
223 mean value of each trait for each climbing plant species under standard conditions.

224

225 Data analysis

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

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

246 We explored the possibility of association between functional strategies of the climbing
247 plant community and their spatial distribution among patches of Chaco Serrano, by
248 considering functional traits of the complete set of climbing plant species present in
249 each patch (Cingolani *et al.* 2007). We calculated the simple and weighted mean value
250 of each PCA axis for the climbing plant community of each patch. Simple mean can be

251 interpreted as the result of a filter that determines which species are present and which
252 are not (species occurrence). Weighted mean based on species abundance (i.e. each
253 species is assigned a "weight" according to its relative abundance in each patch) can be
254 interpreted as the result of the previously described filter plus a second level filter that
255 determines which species may become more abundant (Keddy 1992; Cingolani *et al.*
256 2007). In order to measure variability of functional strategies of the climbing plant
257 communities, we calculated the Functional Richness index proposed by Mason *et al.*
258 (2005) for each one of the PCA axes. This index shows the proportion of the total
259 functional variability (i.e. considering all the patches together) that is present in each
260 patch community. It is calculated as:

$$FR_{ci} = \frac{Max_{ci} - Min_{ci}}{Max_c - Min_c} \quad \begin{array}{l} c = 1, 2, 3 \\ i = 1, \dots, 17 \end{array}$$

262 where FR_{ci} is the Functional Richness index of PCA axis "c" in the climbing plant
263 community of patch "i", $Max_{ci} - Min_{ci}$ is the difference between maximum and minimum
264 species score on the PCA axis "c" of the climbers in the community of patch "i", and
265 $Max_c - Min_c$ is the difference between maximum and minimum species score on PCA
266 axis "c" considering the climbing plant communities of the complete set of sampled
267 patches. FR_{ci} values range from 0, when there is no variability in functional strategies
268 among climbers of a community (i.e. minimum and maximum species scores of PCA
269 axis in a patch have the same value) to 1, when a community includes all the functional
270 variability (i.e. minimum and maximum species scores in the patch match with the
271 minimum and maximum of all the communities together). Finally, statistically
272 significant differences in the simple and the weighted mean were evaluated by
273 performing general linear models with patch type as a factor and adding a variance
274 function to cope with heteroscedasticity, when it was necessary. We tested differences

275 in Functional Richness index among patches using a Kruskal-Wallis test.
276 For statistical analysis, we considered only three *L. lucidum* forests because one of them
277 hosted only one climbing individual, causing important distortions in data analysis. The
278 climbing species *Passiflora mooreana* Hook. f. was also excluded because it occurred in
279 only one patch. Statistical analyses were performed using Infostat (version 2013, Grupo
280 InfoStat, FCA, Universidad Nacional de Córdoba, Argentina); NMDS ordination and
281 PERMANOVAs were done using the R statistical software, package “vegan:
282 Community Ecology Package” (version 2.3–1, [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)
283 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan)).

284

285 **Results**

286 Composition and diversity patterns of climbing plants

287 A total of 1409 climbing adult individuals, representing 24 climbing plant species, of 19
288 genera and 12 families were recorded (see Appendix S3). The families with the highest
289 number of species were Fabaceae (5) and Apocynaceae (4), and those with the highest
290 number of individuals were Fabaceae (51.0%), Apocynaceae (13.3%) and Bignoniaceae
291 (12.3%). The most abundant species were the herbaceous climbers *Rhynchosia edulis*
292 Griseb. and *Cologania broussonetti* (Balb.) DC., representing 25.8% and 17.5% of all
293 individuals recorded, respectively. Two climbing plant species were exotic in the area:
294 *Asparagus setaceus* (Kunth) Jessop (which is native to Africa) and *Vigna caracalla* (L.)
295 Verdc. (which is native to subtropical South America but not to the study area). Only
296 one of the recorded species, *Dolichandra cyanchoides* Cham., was a woody climber
297 (i.e. liana growth form), whereas the other climbers were herbaceous or present
298 | ~~scarcely~~ little lignified stems. Out of the 24 climbing plant species recorded, eight were
299 present in the three types of patches. One species, *P. mooreana*, was exclusive to

300 shrublands, and two were exclusive to the native forest (*Cardiospermum halicacabum*
301 *L.* and the alien *V. caracalla*). *L. lucidum* forests did not have any exclusive climbing
302 plant species (Fig. 1). Shrublands and native forests shared most of their climbing plant
303 species (Fig. 1). Along NMDS axis 1, climbing plant communities present in the native
304 forest patches were segregated from those found in the shrublands and *L. lucidum*
305 forests, which were more similar (at the negative extreme of the axis) (Fig. 1). Results
306 of PERMANOVA confirmed this trend (complete model pseudo- $F=37.09$; $p = 0.001$):
307 climbing species composition of the native forests significantly differed from that of the
308 shrublands ($p = 0.04$) and *L. lucidum* forests ($p = 0.02$). Composition of shrublands and
309 *L. lucidum* forests did not differ significantly ($p = 0.33$). Finally, there was a significant
310 effect of patch type on species richness ($p = 0.0059$). *L. lucidum* forest presented the
311 lowest mean species richness (5.25 ± 1.15 SE), while native forest (11.00 ± 1.25 SE)
312 and shrublands (8.86 ± 1.12 SE) did not differ between them. The three types of patches
313 did not differ in climbing individuals abundance ($p = 0.0983$); however, a tendency of *L.*
314 *lucidum* forest to have fewer mean climbers abundance (43.25 ± 14.98 SE) than
315 shrublands (99.71 ± 17.19 SE) and native forest (76.86 ± 15.10 SE) was observed.

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317 Functional characterization of climbing plant species

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

325 smaller individuals (Fig. 2).

326

327 Relationship between climber community functional strategies and distribution

328 Regarding simple means, significant differences were only found in PC3 ($p = 0.0102$).

329 The climbing plant community of native forests presented species with larger size

330 individuals (i.e. larger PC3 simple mean) than communities of shrublands and *L.*

331 *lucidum* forests, which did not differ between them (Fig. 3). Concerning weighted

332 means, there were significant differences among patches in PC2 and PC3 and

333 marginally significant differences in PC1. PC1 weighted mean was marginally ($p =$

334 0.0581) higher in the climbing plant community of native forests than in those of

335 shrublands and *L. lucidum* forests (Fig. 3). Climbing plant communities of shrublands

336 had significantly lower weighted mean values of PC2 than native forests and *L. lucidum*

337 forest. The latter vegetation types did not differ between them, although there was a

338 tendency ~~effor~~ for the climbing community of *L. lucidum* forests to have larger mean

339 values. PC3 weighted mean was significantly higher in climbing plant communities of

340 native forests than in those of shrublands and *L. lucidum* forests (Fig. 3). These results

341 for weighted means indicated that the most abundant climbing species in the native

342 forest presented more acquisitive functional strategy and larger size than those of

343 shrublands and *L. lucidum* forests. In addition, the most abundant species of shrublands

344 had shorter internodes and petioles and higher SLA than those occurring in the native

345 and invaded forests patches (Fig. 3). Finally, Functional Richness of PC1 was

346 significantly higher in climbing plant communities of native forest than in those of

347 shrublands and *L. lucidum* forests, whereas functional richness of PC2 did not differ

348 among patches (Table 1). Functional richness of PC3 was marginally higher in native

349 forest and shrublands than in *L. lucidum* forests (Table 1). Therefore, the community of

350 the native forests was more heterogeneous in terms of resource acquisition strategy and
351 the communities of both the native forests and the shrublands were marginally more
352 heterogeneous regarding the size strategy than that of the *L. lucidum* forests.

353

354 **Discussion**

355 Our study provides important information about the ecology of climbing plant species
356 in a subtropical dry forest biome. We also included herbaceous species, which are an
357 important component of climbing plant diversity outside the tropics (Durigon *et al.*
358 2014). We found an important effect of the vegetation structure and composition on
359 climbing plant community composition, richness and functional characteristics. The
360 observed patterns contradict some commonly reported results for tropical forests,
361 highlighting the importance of addressing the study of climbers in other environments.
362 This research is, to our knowledge, one of the few studies that address climbing plant
363 ecology from a functional strategy approach (*sensu* Reich *et al.* 2003; Díaz *et al.* 2004).
364 We found climbers spreading along the main functional axes described in the literature
365 for plants (i.e. the resource-use and the size specialization axes; Westoby *et al.* 2002;
366 Wright *et al.* 2004). Finally, we were also able to relate these functional strategies, at the
367 community level, to climbing plant species spatial distribution among patches.

368

369 Composition and diversity patterns of climbing plant species

370 Climbing plant species composition differed among native forests and shrublands and
371 invaded *L. lucidum* forests patches. These results suggest that changes in forest original
372 structure are associated with changes in climbing plant species composition, as
373 previously reported (e.g. DeWalt *et al.* 2000; Yuan *et al.* 2009). Since most species are
374 shared among patches (see Venn diagrams in Fig. 1), differences among climbing plant

375 communities are mainly determined by species abundances. Therefore, at the patch
376 scale, environmental conditions seem to affect the species dominance (i.e. second level
377 filter; Cingolani *et al.* 2007) but not the presence-absence of each species (i.e. first level
378 filter).

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

390 Climbing plant species richness and abundance did not differ between native forests and
391 shrublands. This result disagrees with other studies, mainly of tropical rainforest, which
392 reported an increase in climbing species richness and abundance at plots where tree
393 canopy has been lost (i.e. early successional stages, forest gaps) and that attributed it to
394 an increase in light availability (e.g. DeWalt *et al.* 2000; Laurance *et al.* 2001).

395 However, several studies have found that climbers proliferate equally well in patches
396 with different levels of original canopy opening, and even became more abundant and
397 diverse in more conserved plots. Some of these results have been reported for temperate
398 and subtropical forests (e.g. Carrasco-Urra and Gianoli 2009; Yuan *et al.* 2009; Gianoli
399 *et al.* 2010; Ladwig and Meiners 2010). Consequently, a possible explanation of such

400 pattern is that the effect of disturbance on the climbing plant community may depend on
401 ecosystem type. For example, light is the major limiting resource in rainforest
402 ecosystems (Chazdon 1988), hence, a disturbance that produces a canopy opening
403 reduces stress on climbers. As mentioned before, canopy open in shrublands increase
404 radiation (D'Agostino *et al.* 2012) and, consequently, soil evaporation may be increased
405 (Magliano *et al.* 2016). Then, opposite to tropical forests, in the Chaco Serrano
406 xerophytic forest where water is one of the major limiting resources (Zeballos *et al.*
407 2014), forest structure degradation, may reduce water availability in the soil profile,
408 increasing stressing conditions for vines and likely preventing greater proliferation.
409

410 Functional characterization of climbing plant species

411 We were able to describe three functional axes for climbers. To our knowledge, this is
412 the first study that explicitly assesses intra-group functional variation in climbing plants,
413 including non-woody and non-tropical climbers. Along PC1, we observed a shift from
414 acquisitive climbing plant species with large specific leaf area, and low wood density
415 and leaf tensile strength to climbers having the opposite attributes. PC1 is related to the
416 resource-use strategy axis-whichaxis, which has been consistently found in diverse plant
417 groups across regions and is amply accepted in the literature (Díaz *et al.* 2004; Wright *et*
418 *al.* 2004; Reich *et al.* 2014). ~~This~~ represents a trade-off between species with
419 acquisitive use, retention and release of resources, mainly nutrients (N, P) and
420 cCarbone, to species that have the opposite conservative resources-use syndrome. PC2
421 separated climbing plant species with long internodes and petioles and large leaves from
422 climbing species with the opposite attributes. One possible interpretation of trait
423 variation described by PC2 is in relation to light-foraging strategies. Attributes at the
424 positive extreme of PC2 match with descriptions of species that grow successfully in the

425 | understory (Reich *et al.* 2003; Valladeres and Niinemets 2008). Long internodes,
426 | petioles and large leaf area would maximize light interception in shady environments by
427 | minimizing self-shading and maximizing light interception (Gianoli 2001; Falster and
428 | Westoby 2003; Niinemets and Sack 2006). Since we found differences among
429 | vegetation types in relation to this axis, we assumed that the associated trait syndromes
430 | have an ecological importance that deserves further exploration. PC3 is related to the
431 | size functional axis (Westoby *et al.* 2002; Pérez-Harguindeguy *et al.* 2013). Large
432 | plants are considered better competitors and more resistant to some stress than small
433 | ones (Grime 1977; Westoby *et al.* 2002; Pérez-Harguindeguy *et al.* 2013). Therefore,
434 | among climbers, a larger size would provide them with some benefits, such as greater
435 | leaf exposure to light, greaterbetter access to available support structures, and better
436 | resistance to physical stress and likely to some biological stress (i.e. diseases, parasites
437 | and insect attack) than smaller climbers.

438

439 | Relationship between community functional strategies and distribution patterns

440 | Forest structure showed an effect on functional strategies and Functional Richness of
441 | climbing plant communities. The main differences in functional strategies were related
442 | to dominant species (represented by weighted means) and, to a lesser extent, to the
443 | variety of functional strategies presented in the patches (represented by Functional
444 | Richness index). With respect to resource-use strategies (described by PC1), climbing
445 | plant communities of native forest patches presented the highest functional diversity
446 | (i.e. higher Functional Richness index) with a tendency of dominant species to be more
447 | acquisitive than in the other patches. Lebrija-Trejos *et al.* (2010), Lohbeck *et al.* (2013)
448 | and Bhaskar *et al.* (2014) proposed two processes acting consecutively in the assembly
449 | of plant communities along succession in a tropical dry forest. At early successional

450 stages, when the forest is less structured and environmental conditions are more
451 restrictive (limited water supply, high solar irradiance and high evaporative demand;
452 Lebrija-Trejos *et al.* 2010), there is a strong effect of abiotic environmental filters that
453 leads to a convergence towards few “successful” functional strategies (i.e. low
454 functional richness). At advanced successional stages, when forests are more structured,
455 the abiotic conditions become less stressful but the increase of stand biomass results in
456 greater biological competition for resource access. This situation promotes a divergence
457 of functional strategies as a way to avoid competitive exclusion, which translates into
458 greater functional richness. Similar processes may explain patterns of resource-use
459 strategy in our study system. Patches of native forests provide benign abiotic conditions
460 and resources for climbers (i.e. intermediate light availability, high support availability,
461 higher humidity; Hoyos *et al.* 2010; D'Agostino *et al.* 2012; Withworth-Hulse unpubl.).
462 However, high stand biomass would imply strong competition. Then, on the one hand, ~~it~~
463 ~~is expected that~~ the climbing community of native forest patches is expected to exhibits
464 greater functional richness in order to avoid competitive exclusion. On the other hand, it
465 is still expected that the more abundant species have acquisitive functional strategy,
466 which allows them to capture resources more rapidly and to grow faster, conferring an
467 advantage in a benign environment (Díaz *et al.* 2004). On the contrary, *L. lucidum*
468 forests and shrublands offer harsher environmental conditions for climbers (very low or
469 high irradiance, lower support availability and lower soil humidity; Hoyos *et al.* 2010;
470 D'Agostino *et al.* 2012; Withworth-Hulse unpubl.), which would explain the occurrence
471 of climbing plant communities with lower functional richness and the convergence
472 towards a more conservative strategy that ensures survival under stress conditions (Díaz
473 *et al.* 2004).
474 The dominant climbing plant species of both native and *L. lucidum* forests had longer

475 internodes and petioles, larger leaves and lower SLA than dominant climbers in
476 shrublands (significant differences of PC2 weighted means). Although not significant,
477 there is also a tendency of the climbing community of *L. lucidum* forest to have a
478 greater weighted mean than the climbing communities of native forests (Fig. 3). This
479 pattern can be understood considering that *L. lucidum* forests are environments where
480 light can be a limiting resource in the understory (Hoyos *et al.* 2010, Withworth-Hulse
481 unpubl.) and shrublands, on the contrary, are subject to high irradiance (D'Agostino *et*
482 *al.* 2012). Thus, having a strategy to search for light in the understory would mean an
483 advantage for dominant species, mainly at *L. lucidum* forests, but also at native forests.
484 The functional attributes found in the dominant climbing plant species of the studied
485 patches support the interpretation of PC2 related to light capture strategies.
486 Climbing species in native forests patches were, on average, bigger than species of
487 shrublands and *L. lucidum* forests. A greater cover ensures access to light and support,
488 making climbing species that occupy a large area better competitors than climbers
489 occupying smaller areas. For instance, DeWalt *et al.* (2000) and Yuan *et al.* (2009)
490 found that liana size increases with forest age and structure. In the case of *L. lucidum*
491 forests, despite their high tree cover, the simplification of vertical structure and the fast
492 growth of *L. lucidum* (Lichstein *et al.* 2004; Hoyos *et al.* 2010) would limit the
493 proliferation of larger climbing plant species capable of reach the top of the canopy.
494 Here, we showed floristic and functional differences among climbing plants
495 communities in patches of three vegetation types of the subtropical dry forest biome. In
496 general, the more conserved secondary native forest patches were floristically and
497 functionally different from the more degraded shrublands and *L. lucidum* forest patches.
498 Particularly, we observed that invaded forests involve a serious impoverishment of the
499 climbing plant community. Regarding functional variation, we found climbing plant

500 species spreading along three functional axes associated with the resource-use strategy,
501 the size strategy and also a “new” spectra of variation, which we related to light-
502 foraging. Moreover, we found that the three functional axes were directly related to
503 climbing plant community distribution among the different patches, highlighting their
504 ecological importance. We were able to observe climbers as a diverse ecological group,
505 adapted to different environmental conditions, even at the small patch scale. We
506 emphasize the need of further exploring functional strategies of climbers, especially
507 regarding the light-foraging axis in order to assess its importance. It is also necessary to
508 continue the study of climbing plant ecology in non-tropical ecosystems, as a way to
509 detect the influence of different biotic and abiotic factors in this group of plants.

510

511 **Supplementary Data**

512 **Appendix S1.** Vegetation characteristics of the sampling patches.

513 **Appendix S2.** Description of ten measured functional traits and their scores on PCA.

514 **Appendix S3.** Complete list of recorded climbing plant species and their abundances.

515

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527

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700 **Tables and Figure legends**

701 **Table 1.** Median values of Functional Richness index of different Chaco Serrano patch
 702 types and *H*-value and *p*-value of the Kruskal-Wallis test. Different letters indicate
 703 significant differences ($p < 0.05$).

PCA axis	Functional Richness index			<i>H</i> -value	<i>p</i> -value
	Native forest	Shrubland	<i>L. lucidum</i> 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

704

705

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

713

714 **Figure 2.** Biplot of principal component analysis (PCA) based on a correlation matrix
 715 of 10 functional traits measured in 23 climbing species. Left: PC1 vs PC2. Right: PC1
 716 vs PC3. LA: leaf area, LAR: leaf area ratio, LDCM: leaf dry matter content, LTS: leaf
 717 tensile strength, IL: internode length, PL: petiole length, SD: stem density, SLA:
 718 specific leaf area, Wsat: wood saturated water content. Scientific names are abbreviated
 719 using the first three letters of the genus and species (see full names in Appendix S3).

720

721 **Figure 3.** Mean and standard errors of simple (left) and weighted (right) averages of
722 PCA axes of different Chaco Serrano patch types. Different letters above bars indicate
723 significant differences between means (LSD-Fisher test, $p < 0.05$). On the right of the
724 graph, the functional strategies related to each PCA axis are described to help with
725 interpretation of the means.

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727