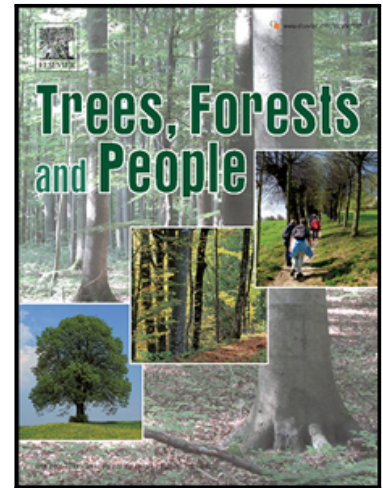


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Pollination and sexual reproduction of key dominant trees of Arid Chaco under different land-use intensities

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1 **Pollination and sexual reproduction of key dominant trees of Arid Chaco under**  
2 **different land-use intensities**

3

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25

## 26 Highlights

- 27 • Fruit production by dominant native trees in arid Chaco is a key ecosystem service
- 28 • Different land use intensity regimes may affect their pollination and reproduction
- 29 • Increased land use intensity reduced fruit-set in pollinator-dependent *Neltuma* spp.
- 30 • *Mistoles*, able to set fruits by geitonogamy, benefited in higher land use intensity
- 31 • Meliponini were key for *Neltuma* spp. fruit-set, while *A. mellifera* favored *Mistoles*

32

33

34 **Abstract**

35 Fruit production by dominant native trees in the arid Chaco of central Argentina  
36 represents a crucial provisioning ecosystem service for local peasant economies. This  
37 region presents gradients of different woody vegetation cover (open forests and shrublands)  
38 along with cattle production systems operating under a variety of management regimens and  
39 socio-environmental degradation conditions. Here, we assess land-use intensity effects on  
40 pollination and reproduction of *Neltuma* spp. and *Sarcomphalus mistol*. The studied species  
41 responded differently to land-use intensity. Pollination service and fruit production in the  
42 strict self-incompatible *Neltuma* spp. tended to decrease with increased land-use intensity. In  
43 contrast, both pollination and reproduction in *S. mistol*, which is able to set fruits with  
44 geitonogamous pollen, increased in the highest land-use intensity sites (silvopastoral  
45 system). In *Neltuma* spp., the highest values of fodder production (fruit set, fruit mass and  
46 total fruit per plant) were found in secondary forests (medium land-use intensity). The  
47 positive effects of land-use intensity on the reproduction of *S. mistol* could be related to the  
48 higher visitation frequency observed in these sites, especially from *Apis mellifera*, but also  
49 with the higher amounts of soil nitrates and light availability in these sites. The only two  
50 stingless bee species present in the region (*Plebeia molesta* and *P. catamarcensis*) played  
51 an important role in the reproduction of *Neltuma* species, increasing fodder production. Our  
52 results highlight the complexity of species response to land-use changes and underline the  
53 importance of thinking beyond the conservation of species to concentrate on preserving

54 ecological interactions. Many key functional aspects of ecosystems functioning and  
55 ecosystem services provision closely depend on plant-animal interactions. Thus, the  
56 promotion of local production systems that allows the preservation of not only provision  
57 services but also plant-pollinator interactions is crucial to conserve these remaining arid  
58 Chaco forests and secure the livelihoods of local communities.

### 59 **Keywords**

60 Ecosystem services, cattle production systems, peasant economies, non-timber forest  
61 products, forage production.

### 62 **1.Introduction**

63  
64 Billions of people in all regions of the world rely on and benefit from the use of natural  
65 ecosystems and wild species for food, medicine, energy, income, and many other purposes  
66 (IPBES, 2022). The benefits that nature provides directly or indirectly to humans are known  
67 as ecosystem services (Díaz et al., 2015). What is more, local rural communities and  
68 indigenous people depend more directly on ecosystem services provided by the forests and  
69 thus they will be most affected than any other social sectors by practices that favor the  
70 degradation of the environment (Silvetti, 2011; IPBES, 2022). The Great American Chaco  
71 holds one of the most extended seasonally dry subtropical forests of the world, historically  
72 used by local communities (Bucher, 1982). Approximately 60% of its total surface is located  
73 in Argentina, where it has been drastically replaced by different productive systems without  
74 multi-scale planification and straightforward state intervention (Frate et al., 2015; Marinaro et  
75 al., 2020; Verga and Lauenstein, 2021). In the driest Chaco region of northwestern Córdoba  
76 province, deforestation has been mainly associated with pasture implantation and increasing  
77 livestock production, in contrast to northeastern regions where soybean cultivation has been  
78 the main driver of deforestation (Hoyos et al., 2013; Frate et al., 2015; Buchadas et al.,  
79 2022). Land management by peasant communities is retracting within the arid Chaco due to

80 the growing demand for large-scale silvopastoral systems that have advanced into territories  
81 historically occupied by peasants with no formal tenure of the land (Altrichter and Basurto,  
82 2008; Cáceres et al., 2010; Cáceres 2015). Large-scale silvopastoral systems initially  
83 eliminate all woody vegetation, leaving only large trees standing. To remove the vegetation,  
84 tractors with heavy cylinders equipped with transverse blades are used to chop and crush all  
85 small and medium-sized woody vegetation. To avoid the proliferation of woody vegetation  
86 ("woody encroachment"), roller chopping must be applied every certain period of time (Kunst  
87 et al., 2012). Therefore, the frequency of roller chopping application determines the intensity  
88 of land use, and is a fundamental factor in sustaining silvopastoral management. For the  
89 Chaco region, silvopastoral systems typically repeat roller chopping every 3 or 4 years  
90 (Casas et al. 1978). As a consequence, the arid Chaco of Córdoba presents gradients of  
91 different woody vegetation cover (open forests and shrublands) along with cattle production  
92 systems operating under a variety of management regimens and socio-environmental  
93 degradation conditions (Hoyos et al., 2013; Fernández et al., 2020; Marquez et al., 2022).

94 In this arid region of central Argentina, non-timber forest products such as fruit  
95 production by native trees represent a crucial provisioning ecosystem service for local  
96 peasant economies since one of the main productive activities of the local inhabitants is  
97 extensive breeding of domestic livestock (goats and cows; Cáceres, 2015). Some of the  
98 most iconic and dominant native tree species in the arid Chaco, such as Algarrobos  
99 (*Neltuma* spp, Fabaceae) and Mistol (*Sarcomphalus mistol*, Rhamnaceae), produce large  
100 quantities of fruits with high content of sugar, protein and minerals, representing a suitable  
101 fodder resource that can meet grazing requirements of livestock (Abdalla et al., 2014).  
102 These fruits are not only important forage resources as they can be stored to be used in  
103 fodder gap winter time, but they are also widely used as human food and medicine by local  
104 rural communities (e.g., Scarpa, 2007; Saur Palmieri et al., 2022; Joseau et al., 2023). In  
105 addition, these species are widely used as firewood as well as for the production of charcoal

106 (Martínez, 2015; Rueda, 2015). Thus, they play a relevant role in maintaining and enhancing  
107 ecosystem service provision of timber and non-timber products, cultural relevance and key  
108 ecological functions, including resilience to climate change and tolerance to soil degradation  
109 conditions (Verga and Lauenstein, 2021). Importantly enough, these tree species are mostly  
110 self-incompatible, which makes them highly dependent on insect pollinators for successful  
111 seed and fruit production (Neff et al., 1977; Aizen and Feinsinger, 1994; Aguilar et al., 2012;  
112 Cerino et al., 2015).

113 Land-use changes imposed by human activities currently represent the most  
114 important driver of biodiversity loss worldwide (Jaureguiberry et al., 2022). In particular,  
115 large-scale agricultural intensification that result in the loss and fragmentation of native  
116 habitats, along with the increase use of pesticides, have been signaled as one of the main  
117 factors of the global insect pollinator decline (e.g., Powney et al., 2019; Zattara & Aizen,  
118 2021). In the case of bees, the most important pollinator group of terrestrial angiosperms,  
119 consistent overall declines have been observed in their richness and abundance in highly  
120 fragmented and land-use intensified ecosystems (e.g., Winfree et al., 2009). Such declines  
121 are related to habitat alterations that reduce nesting sites (Steffan-Dewenter et al., 2006;  
122 Winfree et al., 2009) as well as floral and non-floral resources for bees (e.g., Kaluza et al.,  
123 2018; Requier and Leonhardt, 2020). Furthermore, increased cattle stocking rates can alter  
124 floral diversity as well as plant community composition, negatively affecting bee abundance,  
125 richness and floral visitation frequency (e.g., Xie et al., 2008; Tadey, 2015; Thapa-Magar, et  
126 al., 2020; Cutter et al., 2021; Chen et al., 2022). A recent meta-analysis found that grazing  
127 decreases sexual reproduction in herbaceous species by decreasing plant-pollinator network  
128 diversity and resource allocation to reproductive structures such as reproductive branches  
129 and flowers; however, the effects on woody plants is much less studied (Wentao et al.,  
130 2023).

131 Because more than 80% of terrestrial flowering plants depend on animal pollination  
132 for successful reproduction (Ollerton et al., 2011), decreased diversity of pollinator fauna  
133 implies a reduction in pollination ecosystem service and thus in the sexual reproduction of  
134 most angiosperms (Aguilar et al., 2006). Furthermore, land-use changes can also reduce the  
135 number of available mating individuals in plant populations, decreasing the number of  
136 compatible pollen donors for successful reproduction (e.g., Quesada et al., 2013; Aguilar et  
137 al., 2006). In highly pollinator-dependent plants, such as self-incompatible species,  
138 decreased pollinators and mating partners will likely have a much stronger negative effect on  
139 the quantity and quality of fruits and seeds produced than in less pollinator-dependent  
140 species (Aguilar et al., 2006, 2019; Bennett et al., 2020). Thus, understanding the pollination  
141 ecology and sexual plant reproduction of key native tree species and how land-use intensity  
142 may affect them is crucial to guarantee ecosystem function sustainability and to ensure the  
143 continued provisioning of non-timber forest products to local rural communities. No study has  
144 yet assessed the effects of land-use intensity on pollinators and native tree reproduction in  
145 the arid Chaco.

146 The aim of this study was to evaluate the effects of land-use intensity on pollination  
147 and sexual reproduction of economically important, native, dominant, self-incompatible tree  
148 species of the arid Chaco: *Neltuma* spp. and *Sarcomphalus mistol*. We hypothesize that  
149 increased land-use intensity reduces floral frequency of visitation, which results in decreased  
150 pollination and sexual reproduction in these tree species. As a consequence, land-use  
151 intensity will decrease their fruit production affecting the provisioning of fodder, medicine and  
152 raw material for food production.

153

## 154 **2. Materials and methods**

155

### 156 *2.1. Study system and species*

157

158           The study was conducted in the Sobremonte Department, in the north of Córdoba  
159 province (Argentina). This area belongs to the driest region of the Great Chaco forests with a  
160 strong hydric deficit due to the combined high mean temperature (34 °C) and low mean  
161 annual precipitation (300-500 mm), during the summer growth season, from November  
162 through March. The upper layer of the original vegetation reaches up to 10m height and is  
163 constituted by the dominant trees *Aspidosperma quebracho-blanco*, *Neltuma flexuosa*,  
164 *Neltuma torquata*, *Sarcomphalus mistol* and the cacti *Stetsonia coryne*. The shrub layer  
165 varies between 3-4m height with *Mimozyanthus carinatus*, *Larrea divaricata*, *Senegalia*  
166 *gilliesii* and *Parkinsonia praecox* as the dominant species (Cabido and Zak, 1999).

167           Tree species from the genus *Neltuma* (disintegrated of *Prosopis*, Fabaceae; Hughes  
168 et al., 2022) are one of the most iconic and representative trees in the arid and semi-arid  
169 Chaco (Verga and Lauenstein, 2021). All *Neltuma* species are strictly self-incompatible,  
170 obligately exogamous, and are thus highly dependent on pollinators for sexual reproduction  
171 (Neff et al., 1977; Aguilar et al., 2012). Bees are the most important group of pollinators of  
172 *Neltuma* species and highly attracted to its flowers for both pollen and nectar resources  
173 (Simpson et al., 1977). Interspecific hybrids occur between the different *Neltuma* species  
174 and create intermediate phenotypes, as a result, delimitation of different species through  
175 morphological characters is difficult (Vega et al., 2021). The most abundant *Neltuma* species  
176 in the study area are *N. nigra*, *N. flexuosa* and *N. pugionata*. Given the uncertainty for  
177 precise species identification, we used a complex of these species, that is *Neltuma* spp., as  
178 the taxonomic unit in our samplings. Another dominant tree species in the arid Chaco is  
179 *Sarcomphalus mistol* (Rhamnaceae). As most species in the genus, *S. mistol* has  
180 hermaphrodite flowers that exhibit intrafloral dichogamy (protandry) that prevents  
181 autonomous self-pollination. Experimental studies have proposed that *S. mistol* is a self-



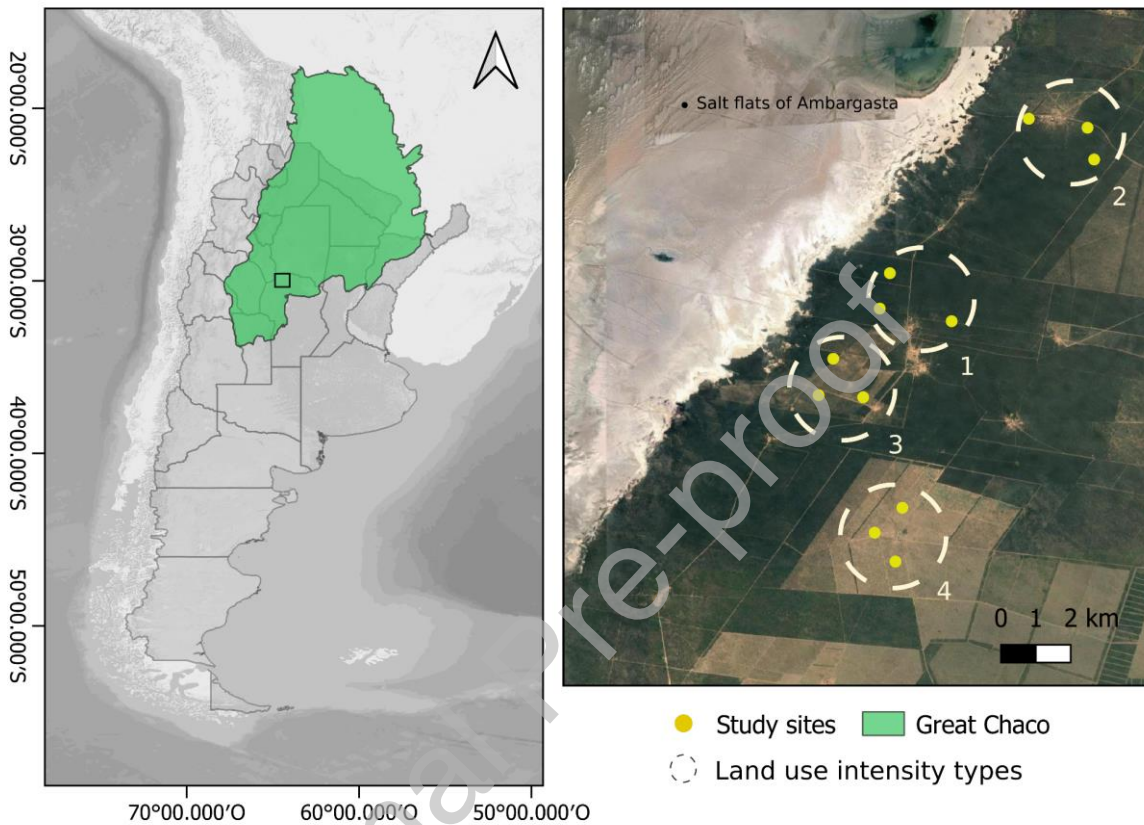
182 incompatible, mostly outcrossing species (Cerino et al., 2015). However, geitonogamy can  
183 easily take place at the level of inflorescence and the entire plant (Cerino et al., 2015).

184

## 185 2.2. Sampling design

186 Within an area of 14 km<sup>2</sup> (29° 27' 38" S, 64° 14' 47" W and 29° 34' 51" S, 64° 18'  
187 36" W) we selected twelve sites located in four different land-use intensity types (3 sites per  
188 condition; Fig. 1). Each site was located at a minimum distance of 1km from any other site.  
189 All selected sites correspond to the arid Chaco ecoregion, sharing the same climate, rainfall  
190 regime and soil type but having experienced different combinations of historic and present  
191 livestock grazing, logging and deforestation processes (Marquez et al., 2022). None well-  
192 preserved, intact native forest is present in the study area. The land-use intensity levels were  
193 classified as follows, in increasing order of intensity: 1) *Conserved secondary forests* (CSF),  
194 representing the more conserved expressions of the forest in this area. These forests  
195 present high woody cover (at least 30% of tree), low stocking rate of primary goats (0.037  
196 cow equivalent) and minor selective logging, and they are under peasant land-use  
197 management; 2) *Secondary forests* (SF), which are also under local peasant land-use-  
198 management and preserve woody cover (~30% of trees), but the goat stocking rate is higher  
199 than in CSF (0.095 cow equivalent); 3) *Closed shrublands* (CS), these land-use types  
200 represent a semi-abandoned silvopastoral systems with a high percentage of shrub cover  
201 (~80%) produced by shrub encroachment after >8 years of roller chopper use, poor tree  
202 cover (15 %) and higher stocking rate (primary cows; 0.138 cow equivalent); 4) *Silvopastoral*  
203 *systems* (SS), are implanted grassland ecosystems, which are subjected to roller chopping  
204 every 4-6 years, thus maintaining a very low cover of understory woody vegetation to  
205 increase herb production and the only standing tree layer is represented by isolated  
206 individuals of *Neltuma* spp. and *S. mistol*. This latter system allows high stocking rate  
207 production of mostly cattle (0.403 equivalent cow) and represents the most intense land-use

208 type. Within each site, we marked 7 adult individuals of *Neltuma* spp. (84 individuals across  
 209 all sites) and 5 individuals of *S. mistol* (60 individuals across all sites) separated by at least  
 210 50 m.



211  
 212 **Fig.1** Spatial location of the sampling sites in the arid Chaco Forest of Central Argentina.  
 213 The green area in the map represents the Chaco region and the rectangle the study area in  
 214 Córdoba province. Yellow circles indicate the 12 study sites and the numbers indicate the  
 215 land-use intensity types: 1) Conserved secondary forest, 2) Secondary forest, 3) Closed  
 216 shrubland and 4) Silvopastoral systems.

217

### 218 2.2.1 Floral visitation frequency and pollinator assemblage

219

220 We conducted diurnal observations between 8:00 and 17:00 hs, avoiding cold and  
 221 windy days to ensure pollination activity. Four-five observers recorded simultaneously all

222 insects visiting open flowers for 5-minute-periods on 5-3 focal trees per site (N= 60 for  
223 *Neltuma* spp. and N= 36 for *S. mistol*). We considered as potentially legitimate pollinators  
224 those insects that contacted fertile floral whorls. At the beginning of each observation, we  
225 counted the number of open flowers in *S. mistol*, and the number of inflorescences with open  
226 flowers in *Neltuma* spp. to use them as a covariate. Then, we counted the number of visited  
227 flowers/inflorescences by floral visitors in 5-min period. Given the difficulty of taxonomic  
228 identification of pollinators at the species level during field work or through photographs, in  
229 most cases we identified them as morphospecies. Moreover, we grouped them into the  
230 following broad functional/taxonomic categories: honeybees (*Apis mellifera*), Halictidae  
231 bees, stingless bees (*Plebeia molesta* and *Plebeia catamarcensis*), other bees (non-*Apis*,  
232 non-Halictidae bees, non- stingless bees, primarily solitary bees), wasps, flies (Diptera),  
233 butterflies (Lepidoptera), and beetles (Coleoptera). The frequency of pollinator floral  
234 visitation per individual tree was calculated as the total number of visited flowers per 5 min.  
235 Pollinators observations were made during the flowering periods of two years (2018 and  
236 2019) in *S. mistol*, and only in 2018 in *Neltuma* spp., as bad weather conditions preclude  
237 observations in the flowering period of 2019. The flowering period of *Neltuma* spp.  
238 comprises the months of September, October and November, whereas *S. mistol* flowers  
239 during the months of November and December. (Demaio et al. 2015). With these  
240 observations we were able to determine: the total frequency of floral visitation (all pollinators)  
241 per tree; the relative frequency of floral visitation of each functional/taxonomic category, total  
242 pollinator richness of morphospecies at each sampling site for each tree species, and  
243 pollinator assemblage composition per site.

244

245 2.2.2. Plant reproduction

246

247 In each focal tree we measured the basal diameter and the number of conspecifics in  
248 a ratio of 30 meters (conspecific density). We assessed sexual reproduction through open  
249 pollination treatment across two consecutive reproductive periods, 2018-2019 and 2019-  
250 2020. In each *Neltuma* spp. tree, we counted and marked 50-200 inflorescences in two  
251 randomly selected branches and we left them exposed to natural pollination. The length of  
252 the marked branch was also measured to relativize the number of inflorescences produced  
253 within 100 cm branch length. To exclude pollination by insects and to assess wind  
254 pollination, we bagged inflorescences at the bud stage on an extra branch with a tulle net. In  
255 *S. mistol* we counted and marked 100-350 flowers in one selected branch per tree. Similarly,  
256 the length of the marked branch was measured to relativize the number of flowers produced  
257 within 50 cm length. In this species we also bagged two extra branches, one with tulle net to  
258 exclude pollinators and to check seed production by wind pollination, autonomous self-  
259 pollination and apomixis. The other branch was bagged with a voile bag to prevent animal  
260 and wind pollination to determine the ability to produce seeds by autonomous self-pollination  
261 and by apomixis. This last treatment was only performed for *S. mistol* because it is already  
262 known that *Neltuma* spp. do not produce seeds by apomixis and they need exogamous  
263 pollen to produce seeds (e.g., Neff et al., 1977; Golubov et al., 1999; Aguilar et al., 2012).  
264 We quantified the number of mature fruits in the tagged branches and calculated the fruit set  
265 as: number of mature fruits/number of inflorescences (flowers for *S. mistol*) marked for each  
266 of the treatments. At least 10 mature fruits per focal tree produced under open pollination  
267 were collected to weigh them.

268 Finally, to quantify total fruit production in each of the land-use intensity types, we  
269 estimated the total fruit number per tree in each site. Given the large amount of fruit  
270 production per tree, we divided the crown into 4–8 equally-sized quadrants, depending on  
271 the size of the crown and counted the total number of fruits in two of these quadrants. We

272 calculated an average number of fruits per quadrant, which was then multiplied by the  
273 number of quadrants to estimate total fruit production per tree (Aguirre-Acosta et al., 2014).

274

### 275 2.3. Statistical analysis

276

277 Analyses were performed using the R environment (R development Core Team,  
278 2022). To test the effects of land-use intensity on plant reproductive variables, pollinator  
279 richness and frequency of floral visitation, we employed generalized linear mixed models  
280 (GLMM). We used land-use intensity as the fixed effect with four levels (conserved  
281 secondary forest, secondary forest, closed shrubland and silvopastoral systems), site  
282 identity as a random effect (N=12) nested within each land-use intensity level and focal trees  
283 as a random effect (N=84/60) nested within the site, when appropriate. According to the  
284 error distribution of each response variable, we performed different GLMM extensions:  
285 Poisson distribution was used for count data (pollinators richness), negative binomial error  
286 distribution was used for number of inflorescences (flowers for *S. mistol*) produced in 100  
287 and 50 cm, respectively, and total fruit production, as these variables showed  
288 overdispersion. For proportions (fruit set), we used binomial error distribution (`glmer.nb` and  
289 `glmer` functions from the `lme4` package) and gaussian error distribution for fruit mass (`lmer`  
290 function from the `lme4` package). Tree diameter and the conspecific density within each site  
291 were not included in the models as covariates because the independence assumption for the  
292 inclusion of a covariate was not met (Table 1S). After checking assumptions and fit of the  
293 model, significance of fixed effects was assessed with Wald-Z statistics. To evaluate the  
294 significance of random effects we compared nested models (one with and one without  
295 random effects) with a global model using a likelihood ratio test (LRT). Model parameters  
296 were estimated with restricted maximum likelihood methods. Overdispersion was found in  
297 binomial models so we used `glmmPQL` function to correct it (`nlme` package).

298 Pollinator visits exhibited an excess of zero observations (no pollinators registered);  
299 therefore, we performed a GLMM with a poisson family distribution (flower visitation  
300 frequency of *Neltuma* spp.) or negative binomial family distribution (flower visitation  
301 frequency of *S. mistol* in both years) and zero-inflation (glmmadmb function of the  
302 glmmADMB package, Bolker et al., 2012). After checking assumptions for the inclusion of a  
303 covariate, we added the number of open flowers as a covariate in these models to test the  
304 effect of floral offer per plant on frequency of pollinator visits. Significance of the fixed and  
305 random effects were performed with likelihood-ratio tests of nested models. Pollinator  
306 assemblage composition was compared among land-use intensity levels through a one-way  
307 non-parametric similarity analysis, ANOSIM (999 permutations). For this analysis, we used a  
308 matrix with Bray-Curtis distance from pollinator visitation frequency of morphospecies, using  
309 the vegan package (Oksanen et al., 2016).

310

### 311 **3. Results**

312

#### 313 *3.1. Tree diameter and conspecific density*

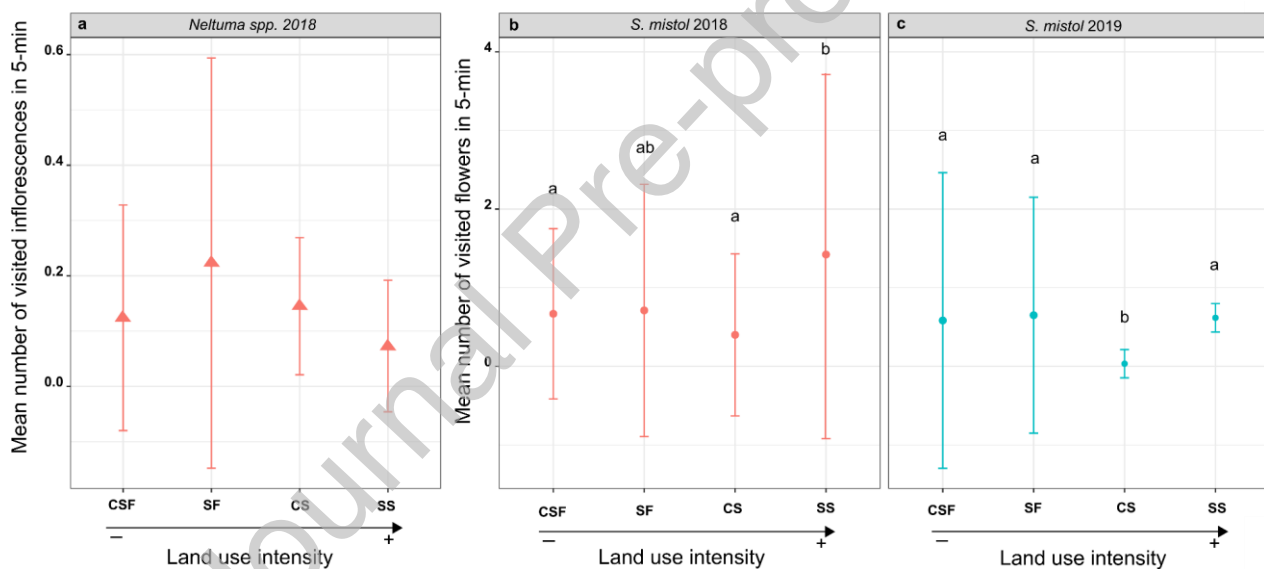
314 In *Neltuma* spp. tree diameter was higher in silvopastoral systems (SS), whereas in  
315 *S. mistol* tree diameter was similar across land-use types, except in secondary forests (SF)  
316 that presented the lowest diameters (Table.1S). The lowest conspecific density of *Neltuma*  
317 spp. was observed in silvopastoral system (SS) whereas the lowest conspecific density of *S.*  
318 *mistol* was observed in closed shrubland (CS; Table 1S).

319

#### 320 *3.2. Floral visitation frequency and pollinator assemblage*

321 There was no evidence that land-use intensity has an effect on total floral visitation  
322 frequency in *Neltuma* spp. (Fig 2a; Table. 2S). In *S. mistol*, there was evidence that land-use  
323 intensity affected total floral visitation frequency in both years (Fig.2b; Table 2S). The highest

324 value of floral visitation frequency in 2018 was found in the most intense land-use condition  
 325 (silvopastoral system, SS; Fig 2b). In 2019, the lowest visitation frequency was observed in  
 326 the CS condition, whereas the rest of land-use types showed similar values (Fig.2c). We  
 327 found similar values of pollinators richness across all the study conditions for both study tree  
 328 species (Table 3S). Regarding the pollinator assemblage we found moderate evidence of  
 329 differences in pollinators composition across the land-use intensity levels for *Neltuma* spp.  
 330 ( $R= 0.41$ ,  $P= 0.01$ , Fig. 1S). For *S. mistol* there was no evidence of differences in pollinator  
 331 assemblage composition in 2018 ( $R= 0.32$ ,  $P= 0.17$ ) but in 2019 a moderate evidence was  
 332 found ( $R= 0.46$ ,  $P=0.01$ , Fig. 1S).



333  
 334 **Fig. 2** Floral visitation frequency of pollinators for *Neltuma* spp. (triangles) and  
 335 *Sarcomphalus mistol* (circles) in each land-use intensity type: conserve secondary forest  
 336 (CSF), secondary forest (SF), closed shrubland (CS) and silvopastoral system (SS). Study  
 337 years are represented by color, red for 2018 and blue for 2019. Values are mean  $\pm$  SD.  
 338 Different letters indicate statistically significant differences ( $P < 0.05$ ) among land-use  
 339 intensity levels, according to GLM analysis. The arrow indicates the intensity of the land-use  
 340 intensity gradient.

341

342 In *Neltuma* spp. the stingless bees were the most frequent floral visitor in the less  
343 intensive land-use types (conserve secondary forest and secondary forest; Fig. 2S). As land-  
344 use intensity increases, the relative frequency of stingless bees decreases and the relative  
345 frequency of honeybees and other bees tend to increase. For *S. mistol*, in 2018, stingless  
346 bees and honeybees were the most frequent pollinators in the two lower land-use intensity  
347 conditions (conserve secondary forest and secondary forest), whereas in the two higher  
348 land-use intensity conditions (closed shrubland and silvopastoral system) halictidae bees  
349 and honeybees were the most frequent pollinators (Fig. 3S). In 2019, stingless bees were  
350 the most frequent pollinator in almost all the conditions except in CS, where wasps were the  
351 only pollinators registered (Fig. 3S).

352

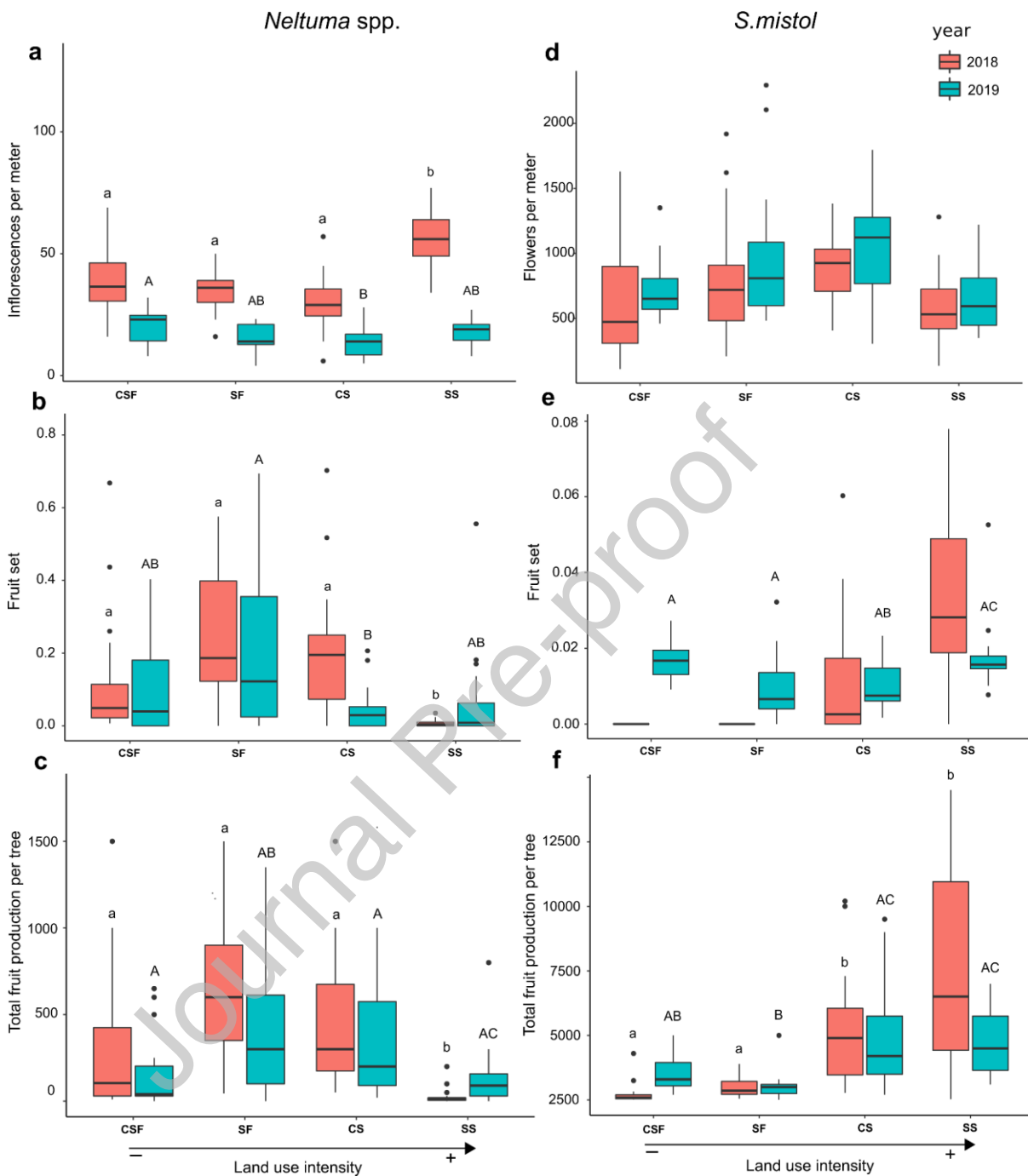
### 353 3.3. Plant reproduction

354 In *Neltuma* spp. trees no fruits were produced after excluding pollinators, indicating  
355 the high dependence on insects for successful pollination. The data revealed moderate  
356 evidence that the number of inflorescences produced were affected by land-use intensity in  
357 both years (Table 4S). In 2018, the highest number of inflorescences was found in SS, the  
358 most intense land-use type (Fig. 3a; Table 5S), where trees produced at least 34% more  
359 inflorescences than trees from the other land-use intensity levels. However, for the same  
360 2018 period, we found strong evidence that the fruit-set of open pollination treatment was  
361 lowest in SS, as compared to the other land-use intensity levels (Fig. 3b; Table 5S). In 2019,  
362 we found moderate evidence that the number of inflorescences produced were only different  
363 between the conserved secondary forest and the closed shrubland (Fig.3a; Table 5S), where  
364 the maximum and minimum number of inflorescences were produced, respectively. Similar  
365 to 2018, in 2019 fruit-set tended to be higher in the secondary forest (intermediate intensity  
366 use) lower in the conditions with the higher use intensity (CS and SS, Fig. 3b; Table 5S). We



367 found a similar trend in total fruit production in 2018 as the lowest values were found in SS in  
368 comparison with the other land-use intensity levels (Fig. 3c; Table 5S). Similarly, fruit mass  
369 presented the lowest values in SS (Table 4S, Table 5S).

370 In *S. mistol*, after excluding insects, no fruits were produced by either wind pollination  
371 or by apomixis, similarly indicating the importance of animal pollinators for successful sexual  
372 reproduction of this species. There was no evidence that flower production was affected by  
373 land-use intensity neither in 2018 nor 2019 (Table 4S; Fig. 3d). In 2018, fruit set under  
374 natural pollination was very low in *S. mistol*, especially in the less land-use intensity types,  
375 where the values were zero. We found moderate evidence that the fruit-set differed only in  
376 2019 between SS and CS, where the maximum and minimum fruit-set values were found,  
377 respectively (Fig. 3e; Table 4S; Table 5S). Total fruit production was strongly affected by  
378 land-use intensity in both studied years (Table 4S). In 2018, we found very strong evidence  
379 that total fruit production was lower in the less intensive land-use types (CSF and SF) in  
380 comparison with the more intensive ones (CS and SS; Fig. 3f; Table 4S; Table 5S). A similar  
381 trend was found in 2019, as the highest values were found in CS and SS (Fig.3f; Table 5S).  
382 Fruit mass was also strongly affected by land-use intensity, with lowest fruit mass values  
383 found in SF and the highest values in the most land-use intense condition (SS; Table 4S;  
384 Table 5S).



385  
 386 **Fig. 3** inflorescences/flower produced (a-c), fruit set (d-f) and total fruit production per tree  
 387 (e-f) of *Neltuma* spp. and *Sarcomphalus mistol* in each land-use intensity type: conserve  
 388 secondary forest (CSF), secondary forest (SF), closed shrubland (CS) and silvopastoral  
 389 system (SS) in two studied years. Red boxes represent the values obtained in 2018 and blue  
 390 boxes the ones obtained in 2019. Different letters indicate statistically significant differences

391 ( $P < 0.05$ ) in parameter value among land-use intensity levels, according to GLM analysis.

392 The arrow indicates the intensity of land-use gradient

393

#### 394 **4. Discussion**

395 In this study we assessed pollination and sexual reproduction of important tree species  
396 under different land-use intensity levels in the arid Chaco. Our results contribute to  
397 understanding the provisioning of non-timber forest products such as fodder, medicine and  
398 food, provided by these tree species to local rural communities in different production  
399 systems. Given that these tree species are highly dependent on pollinators to set fruits, we  
400 expected that land-use intensity would negatively affect plant reproduction in both species.  
401 However, the studied species showed contrasting responses. Pollination service and fruit  
402 production in *Neltuma* spp. tended to decrease with increased land-use intensity whereas  
403 both pollination and reproduction in *S. mistol* increased in the highest land-use intensity sites  
404 (silvopastoral system). Below, we discuss possible causes for the response patterns found.

405

##### 406 *4.1. Frequency of floral visitation and pollinators composition*

407 Our results do not support the initial hypothesis that increased land-use intensity negatively  
408 affects floral visitation frequency of pollinators. In the case of *Neltuma* spp., we found similar  
409 values of pollinator richness and frequency of floral visitation across all different land-use  
410 intensities. However, the composition of pollinator assemblages did change across the study  
411 sites, meaning that land-use intensity may differentially affect floral visitors. While stingless  
412 bees were one of the most frequent pollinators in all land-use intensity levels, their relative  
413 visitation frequency decreased as land-use intensity increased and as the relative frequency  
414 of other bees (mainly solitary bees) and honeybees increased. Such responses could be  
415 related to different functional traits (morphological, physiological and behavioral attributes) of  
416 these stingless bee species that determine their sensibility to environmental changes (McGill

417 et al., 2006). Thapa Magar et al. (2020) found that grazing altered bee species composition  
418 in a semiarid steppe of Colorado and that sites with higher stocking rates were associated  
419 with lower abundance of above-ground nesting bees, while supporting a higher abundance  
420 of below-ground nesting bees (mainly solitary bees). It is possible that decreased tree cover  
421 and increased livestock rates might be reducing the abundance of dominant stingless bee  
422 species by changing vegetation structure and reducing their nesting sites (Marquez et al.,  
423 2022). Such changes could release interspecific competition and enhance the abundance of  
424 other non-dominant species (Tadey 2015). Stingless bees are key pollinators of tropical and  
425 subtropical regions (Bueno et al., 2023) and *Plebeia catamarcensis* and *P. molesta*  
426 (Meliponini tribe) are the only two species present in central Argentina (Alvarez et al., 2016).  
427 These bees are social and generalist pollinators that collect nectar and pollen from a vast  
428 array of plants, nevertheless individuals tend to have high flower constancy meaning that  
429 they specialize on a single floral species for a certain amount of time (Slaa, et al. 2003). This  
430 foraging pattern decreases the likelihood of heterospecific pollen transfer making them more  
431 efficient pollinators (Waser, 1983). We found that higher relative floral visitation frequency of  
432 stingless bees in secondary forests correlated with higher fruit set, total fruit production per  
433 tree, and fruit mass in *Neltuma* spp. individuals. Thus, these *Plebeia* species can be  
434 considered important pollinators of *Neltuma* spp., potentially enhancing fruit quality and  
435 production. In contrast, the visits from *Apis mellifera*, observed in larger abundance in the  
436 highest land-use intensity conditions, might have been partially responsible for decreasing  
437 fruit set in these sites. *Apis mellifera* is known to increase geitonogamous crosses, which  
438 can have negative effects on fruit-set of strict self-incompatible species such as *Neltuma*  
439 spp. (e.g., Aguilar et al., 2012; Debani et al. 2002; Sáez et al., 2022).

440 In the case of *S. mistol*, pollinator richness and pollinator assemblages were similar  
441 across land-use types, while frequency of floral visitation was highest in the sites under  
442 highest land-use intensity (SS) in 2018, where the most frequent pollinator was *A. mellifera*.

443 As proposed by Tadey (2015), increased livestock rate along with decreased richness and  
444 abundance of floral resources could increase the pollinator visitation frequency by  
445 concentrating on the few floral resources available in such conditions. What is more, *A.*  
446 *mellifera* can usually thrive in highly grazed and disturbed sites as is not limited by a narrow  
447 range of suitable ecological factors, providing pollination services in such degraded  
448 environments (e.g., Kearns et al., 2009; Winfree et al., 2009). *Sarcomphalus mistol* has a  
449 self-incompatible system and its intrafloral dichogamy prevents autonomous self-pollination;  
450 however, floral sexual phases overlap among flowers within the same branch, which implies  
451 geitonogamy mediated by pollinators can easily occur (Cerino et al., 2015). The populations  
452 of *S. mistol* studied here seem to be in reproductive advantage in silvopastoral systems,  
453 benefiting from an increased frequency of visitation by *A. mellifera*. In line with this, a study  
454 conducted in Brazil found that *Apis mellifera* was an efficient and frequent pollinator of  
455 *Sarcomphalus joazeiro* (Tarcila de Lima et al., 2007). Our findings suggest that wasps are  
456 also efficient pollinators of *S. mistol*, since in 2019 wasps were the only observed pollinators  
457 in CS sites where high fruit set and total fruit production were observed. Interestingly, in  
458 2019 the relative visitation frequency of *A. mellifera* in the same SS sites was nearly zero,  
459 while stingless bees presented the highest abundances. This trend suggests that stingless  
460 bees may be displaced when the abundance of *A. mellifera* is high in these more intensive  
461 land-use sites (Cairns et al., 2005; Layek et al., 2021). Stingless bees are highly dependent  
462 on forests as they use tree cavities for nesting and require and exploit non-floral resources  
463 (e.g., resins) provided mainly by trees and woody vegetation (Requier and Leonhardt, 2020;  
464 Shanahan and Spivak, 2021; Campbell et al., 2022). Also, woody vegetation provides higher  
465 structural complexity and diversity of plant species, thus offering shelter as well as important  
466 floral resources for wild and managed bees (Rollin et al., 2013; Requier et al., 2015). Hence,  
467 we highlight the importance of preserving the last remaining tracts of native forests in the

468 region, to guarantee the conservation of *P. catamarcensis* and *P. molesta*, the only two  
469 Meliponid bees present in the arid Chaco of central Argentina.

470

#### 471 4.2. Plant reproduction

472 Increased land-use intensity positively affected the number of inflorescences  
473 produced in *Neltuma* trees, but it did not translate into a higher fruit set, fruit mass or overall  
474 fruit production (i.e., quantity and quality of fodder production). On the contrary, fruit set, fruit  
475 mass and total fruit production were significantly lower in the most intensive land-use type in  
476 both years, indicating that a large number of the flowers produced were not pollinated or  
477 were pollinated with incompatible pollen. A similar response was observed in isolated  
478 *Neltuma caldenia* trees that produced more flowers than trees in continuous forests but they  
479 set a similar proportion of fruits (Aguilar et al., 2012). While greater light availability in  
480 silvopastoral systems could favor a higher investment in floral production, reduced fruit-set  
481 implies pollen limitation of *Neltuma* trees in high intensity land-use sites (silvopastures).  
482 Thus, pollen limitation could be related to a reduction of pollen quantity and/or quality as well  
483 as a reduction of mate availability due to decreased population density (Aizen and  
484 Feisenger, 1994; Ghazoul and McLeish, 2001; Aguilar et al., 2012). In line with this, we  
485 found significantly larger *Neltuma* trees and a lower number of conspecifics in silvopastoral  
486 systems. Low population density and large floral displays typically increase duration of  
487 pollinator visits within individuals, reducing outcrossing and increasing geitonogamy,  
488 particularly affecting strict self-incompatible species (e.g., Mustajarvi et al., 2001; Grindeland  
489 et al., 2005). Contrary to our expectation, the highest values of fruit production (fruit set, fruit  
490 mass and total fruit production) were found in sites subjected to intermediate land-use  
491 intensity (SF). As we mentioned before, this could be related with the higher relative  
492 frequency of stingless bees in secondary forest, but also with a reduction in competition by

493 soil resources and light in comparison with more conserved secondary forests, which had  
494 higher tree cover (Marquez et al., 2022).

495 Contrary to our initial hypothesis, we found that *S. mistol* reproduction was positively  
496 affected by increased land-use intensity. In 2018, the higher fruit production per tree in  
497 silvopastoral sites, is probably related to the higher pollinator visitation frequency observed,  
498 especially of *Apis mellifera*. In 2019, fruit set, total fruit production, and fruit mass were also  
499 significantly higher in the closed shrubland and silvopastoral system (CS and SS) but  
500 pollinator visits were lowest in the CS. Such decoupling between pollination and  
501 reproduction in 2019, could be indicating that abiotic factors are also playing an important  
502 role in *S. mistol* reproduction in the more intensive land-use types. Higher light availability  
503 and less competition for soil resources in more intensive land-use sites might allow higher  
504 resource allocation to reproduction (Fuchs et al., 2003; Herrerías-Diego et al., 2006). In  
505 addition, we observed that soils in the more intensive land-use types presented higher  
506 amounts of nitrates (Marquez et al., 2022), which is the most important form of available  
507 nitrogen for plants (Lui et al., 2022). Such edaphic conditions may favor plant reproduction in  
508 *S. mistol*, which is a non-nitrogen fixing species.

509 Our results imply that obligately outcrossing species with a strict self-incompatible  
510 system, such as *Neltuma* spp., will be more vulnerable to increased land-use intensity. In  
511 contrast, *S. mistol* that can also set fruits by geitonogamous crosses may be benefited in  
512 scenarios of high land-use intensity, provided there are managed honeybees nearby (Sáez  
513 et al., 2022). However, because *S. mistol* has a predominantly outcrossing mating system  
514 (Cerino et al. 2015), increased geitonogamy may clog stigmas with self-pollen, reducing  
515 pollen competition and resulting in the expression of inbreeding depression in the progeny.  
516 Thus, the fitness and survival probability of progeny produced in more intensive land-use  
517 types may be seriously compromised (Aguilar et al. 2019). Stingless bees played a key role  
518 in the pollination of *Neltuma* species that need more efficient cross pollination, increasing

519 non-timber resources such as fodder production and reproduction in less intensive land-use  
520 sites. Our results highlight the complexity of species response to land-use changes and  
521 underline the importance of thinking beyond the conservation of species to concentrate on  
522 preserving ecological interactions (Valiente-Banuet et al., 2015). Because many key  
523 functional aspects of ecosystems closely depend on plant-animal interactions, their loss  
524 could decay ecosystem functions, collapsing the derived ecosystem services provided to  
525 humans (Díaz et al., 2013). Thus, the promotion of local production systems that allow the  
526 preservation of not only provision services but also plant-pollinator interactions is crucial to  
527 conserve these remaining arid Chaco forests and secure the livelihoods of local  
528 communities.

529

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536

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**808 Declaration of interests**

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810 The authors declare that they have no known competing financial interests or personal rela-  
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812

813 The authors declare the following financial interests/personal relationships which may be  
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