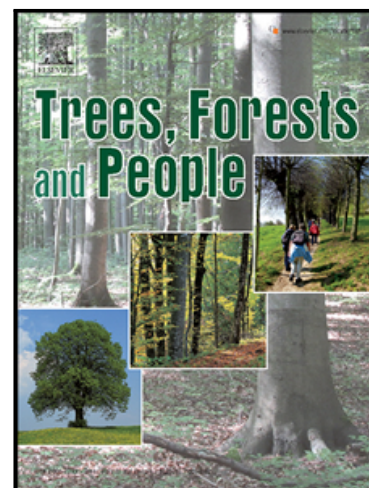


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Pollination and sexual reproduction of key dominant trees of Arid Chaco under different land-use intensities

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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

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

Keywords

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

1.Introduction

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

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

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

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

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

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

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

2. Materials and methods

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-

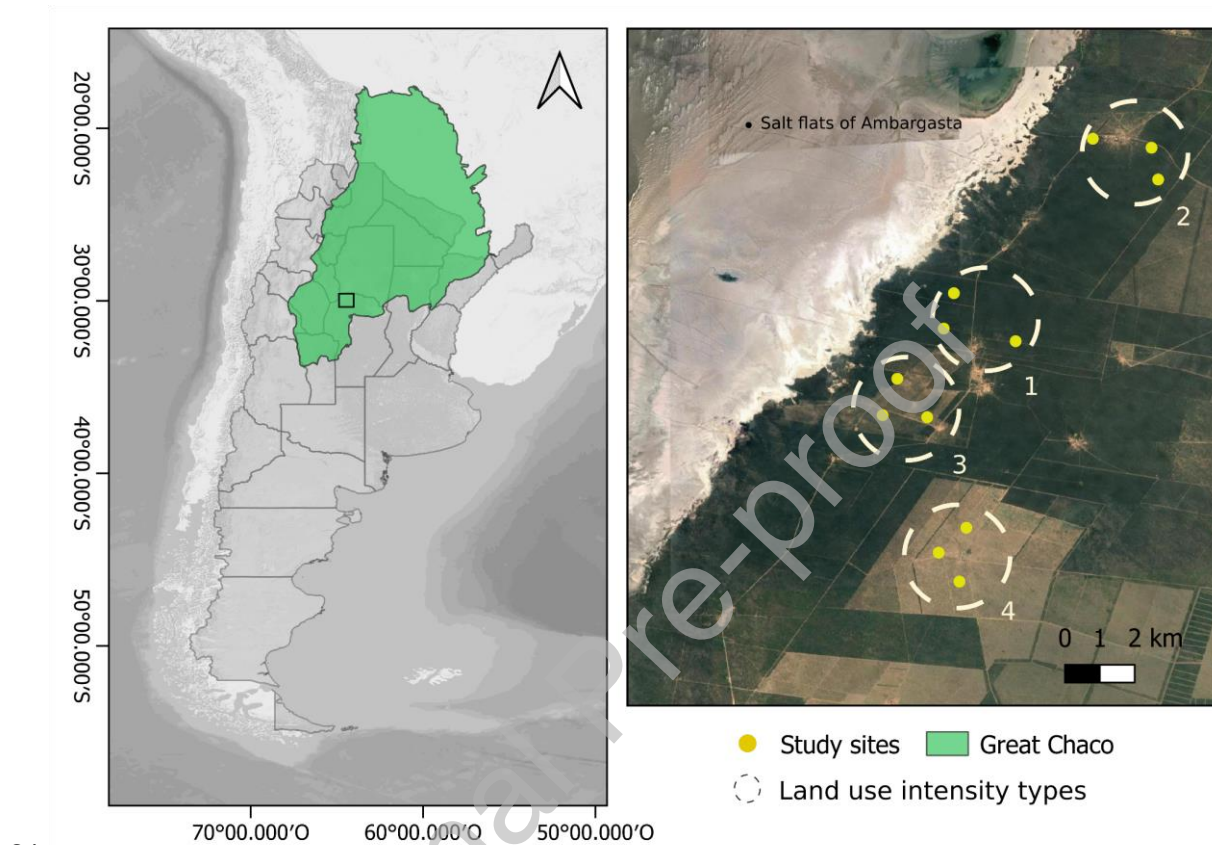
182 incompatible, mostly outcrossing species (Cerino et al., 2015). However, geitonogamy can
183 easily take place at the level of inflorescence and the entire plant (Cerino et al., 2015).

184

185 2.2. Sampling design

186 Within an area of 14 km² (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.



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.

218 2.2.1 Floral visitation frequency and pollinator assemblage

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

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

2.2.2. Plant reproduction

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

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

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

2.3. Statistical analysis

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

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

3. Results

3.1. Tree diameter and conspecific density

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

3.2. Floral visitation frequency and pollinator assemblage

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

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

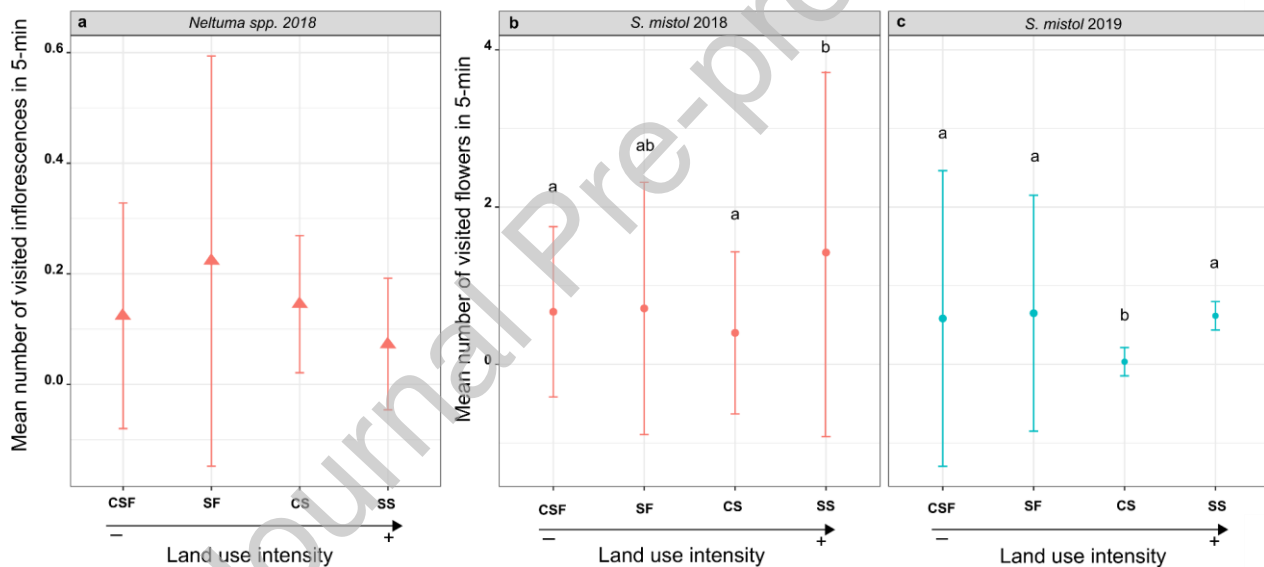


Fig. 2 Floral visitation frequency of pollinators for *Neltuma* spp. (triangles) and *Sarcomphalus mistol* (circles) in each land-use intensity type: conserve secondary forest (CSF), secondary forest (SF), closed shrubland (CS) and silvopastoral system (SS). Study years are represented by color, red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

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

3.3. Plant reproduction

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

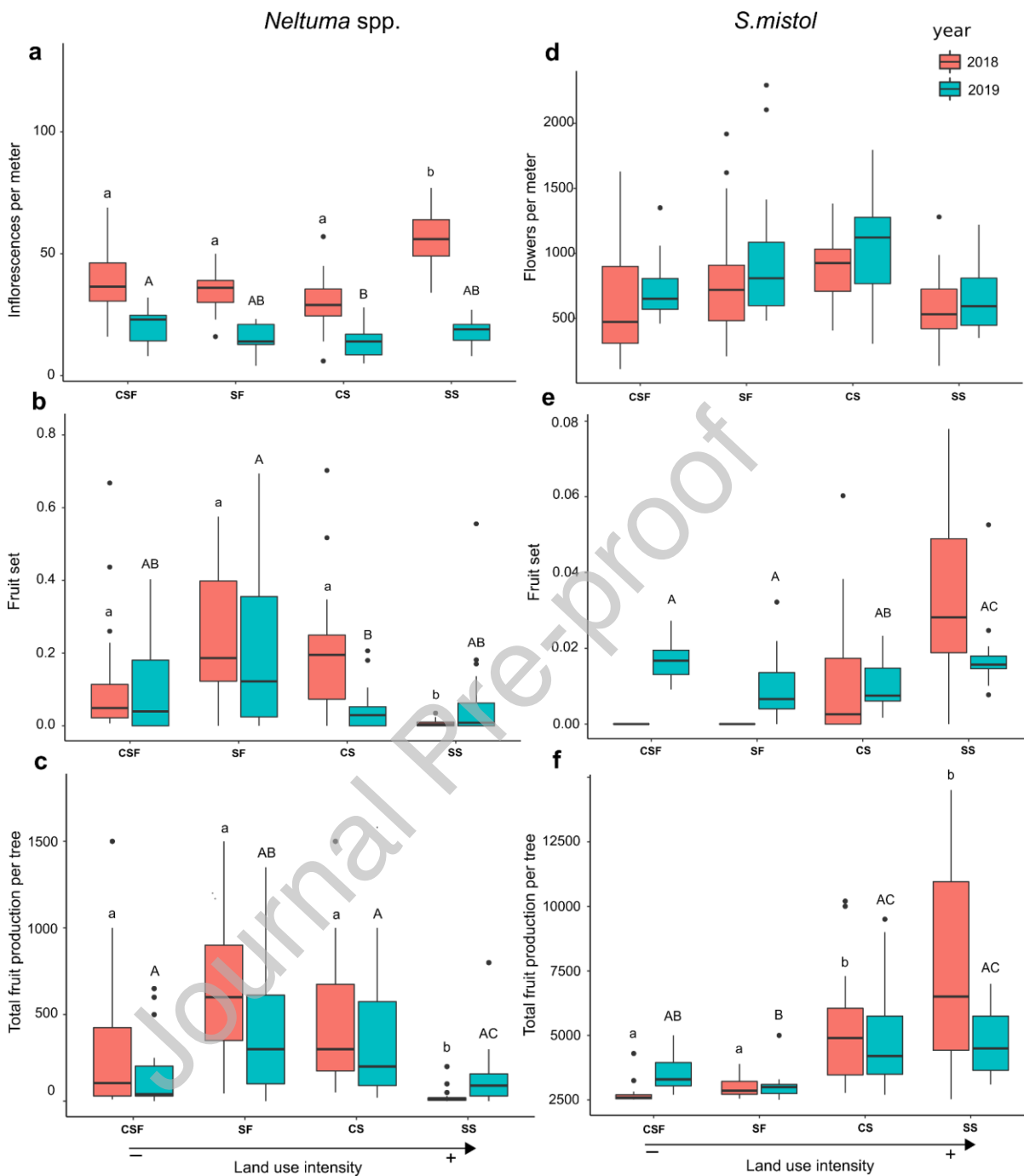


Fig. 3 inflorescences/flower produced (a-c), fruit set (d-f) and total fruit production per tree (e-f) of *Neltuma* spp. and *Sarcomphalus mistol* in each land-use intensity type: conserve secondary forest (CSF), secondary forest (SF), closed shrubland (CS) and silvopastoral system (SS) in two studied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

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

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

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

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

4.2. Plant reproduction

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

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

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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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