Frequent fires do not affect sexual expression and reproduction in *Vachellia caven*

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Abstract   In environments with high fire frequency the impoverishment of abiotic resources may favour male sexual expression in plants as it is less costly than female expression. Also, fire can modify pollinator communities and thus affect plant reproduction. Here we evaluate the effect of frequent fires on sexual expression, pollination and reproductive success of *Vachellia caven* (Leguminosae), an andromonoecious tree that is highly dependent on animal pollination and is abundant in burned sites. We expect that increased fire frequency will favour maleness but it will decrease reproductive success due to abiotic resource depletion in repeated burned sites. To test this, we selected focal plants in three unburned sites and three frequently burned sites and measured their sexual expression, basal diameter, pollination and fruit set. The proportion of male inflorescences per plant was not affected by fire and it was negatively related with the diameter of the plant. The proportion of pollinated flowers was not affected by fire, and fruit set increased with maleness only in frequently burned sites. These results indicate that *V. caven* is adapted to regimes of high fire frequency: not only was there similar fruit set in both burned and unburned sites, but more male plants had higher fruit set in burned sites. Despite the soil impoverishment triggered by repeated fires, *V. caven* is able to maintain its sexual and reproductive functions, allowing it to persist and maintain viable populations in fire-prone environments.

Abstract in Spanish is available with online material.

Key words: andromonoecy, Chaco Serrano, fire frequency, pollination, sexual expression, sexual reproduction.

INTRODUCTION

Sexual plant reproduction is costly in terms of resources required for flowering and fruiting. Plants growing in nutrient-rich environments usually produce more flowers, pollen and seeds than those growing in nutrient-depleted soils (Vasek *et al*. 1987; Lau & Stephenson 1993, 1994; Carbone & Aguilar 2017). For example, some plant species can invest up to 50–60% of all acquired phosphorus into sexual reproduction (Van Andel & Vera 1977; Fenner 1986; Lau & Stephenson 1994; Kerkhoff *et al*. 2006). Because resources are usually limited, plants must deal with resource allocation to male and female functions (Charnov 1982). Sexually polymorphic plant species have different types of flowers (male, female and hermaphrodite) within the same individual, and these types of flowers differ in their relative

production cost. Male flowers are cheaper to produce than hermaphrodite and female ones (Vallejo-Marín & Rausher 2007a), thus, male sexual expression is usually favoured in nutrient-poor environments, whereas female expression prevails in fertile soils (Freeman *et al*. 1980; Policansky 1981; Charnov 1982; Salomon 1985). Changes in sexual expression caused by environmental factors have been observed for several plant species, but they have not been studied in the cosmopolitan genus *Acacia* Mill. s.l. (Leguminosae). Species of this genus show intraspecific variability in sexual expression, but whether such variability is linked to environmental factors is still unknown (e.g. Calviño *et al*. 2014; Correia *et al*. 2014). Thus, species of this genus may represent an interesting model system for investigating intraspecific variability in sexual expression under different or changing environments.

The size of the plant is another factor that can influence resource acquisition and allocation and thus sexual expression and reproduction (e.g. Klinkhamer *et al*. 1997). In animal-pollinated plants the allocation of resources to the female function (ovules

and seeds) usually increases with plant size. Larger plants have higher proportion of female or hermaphroditic flowers and also higher fruit set than smaller ones (e.g. Klinkhamer & de Jong 1997; Calviño & Galetto 2010). In addition to environmental and plant conditions, plant reproductive success also varies widely according to fluctuations in the pollination service. For plant species reproductively dependent on animal pollination, the pollination success is usually linked to the abundance of pollinators (Haig & Westoby 1988; Burkle & Irwin 2009).

Fire is an ecological and evolutionary factor shaping the distribution, structure and dynamic of biomes around the world (Bond & Keeley 2005). The fire regime (frequency, intensity and seasonality) is mainly influenced by climate as it determines the productivity of the system and the natural ignition frequency (Davies 2013). However, anthropogenic activities can affect the regime of fire in synergy with the climatic conditions, drastically modifying the natural fire frequency of a region (Pausas & Keeley 2009; Keeley et al. 2011). Fire generates significant changes in soil properties, affecting the availability and dynamics of water and nutrients (Certini 2005; Pellegrini et al. 2015; Carbone & Aguilar 2017). High fire frequencies increase the impermeability of the substrate, leading to a lower water retention capacity of soils (Certini 2005). Recurrent fires cause mineralisation of the organic matter, modifying soil structure and decreasing carbon and nutrient storage (Carbone & Aguilar 2016; Pellegrini et al. 2018). The more open vegetation structure driven by recurrent fires also increases insolation and light availability. Post-fire changes on these abiotic resources can affect the sexual expression and reproduction of surviving plant species (Wolfe 1998; Pedroso-De-Morales et al. 2016; Abdusalam et al. 2017; Buide et al. 2018).

Fire can also modify pollinator's communities by direct effects of the flames and lethal temperatures, or indirectly by modifying the composition and structure of vegetation and therefore the quantity and quality of nesting and feeding resources used by pollinators (Dafni et al. 2012; Koltz et al. 2018). Although there are studies that report negative effects of fire on pollinator richness and abundance, especially in Mediterranean scrublands (Ne'eman et al. 2000; Potts et al. 2003), there are several studies showing increased abundance of floral visitors due to an increase flower availability triggered by fire (e.g. Potts et al. 2001; Campbell et al. 2007; Van Nuland et al. 2013; Carbone & Aguilar 2017). The Gran Chaco is the most extensive dry forest of South America (Moglia & Giménez 1998), and fire has been historically present as part of the natural dynamic of this environment. The southernmost limit of the Gran Chaco is known as the Chaco Serrano, a region of woodlands growing in the slopes of the hills between 500 and 1300 m

above sea level (Giorgis et al. 2011). This region holds the highest frequency of fires in central Argentina (Argañaraz et al. 2015). In the Chaco Serrano region, the main strategy of woody species to persistence after fire is basal resprouting (Gurvich et al. 2005; Torres et al. 2014). However, beyond the capacity of individual persistence, sexual reproduction is a key process that determines the long-term viability of plant populations, as it allows genetic recombination and progeny dispersal in space and time (Wilcock & Neiland 2002). Moreover, studies assessing the effects of anthropogenic fire frequency on pollinator communities in the Chaco Serrano are still incipient (Carbone & Aguilar 2017).

To assess the hypothesis that fire may indirectly shape the sexual expression and reproduction of plants through its negative effects on abiotic resources, pollination service and/or by decreasing the size of surviving individual plants (Alinari 2017; Carbone & Aguilar 2017), we studied Vachellia caven (Molina) Seigler & Ebinger (ex Acacia caven (Molina) Molina), a dominant species of the native flora and a main component of the post-fire communities in the Chaco Serrano (Herrero et al. 2015). This species is andromonoecious, having hermaphrodite and male flowers in the same plant (Peralta et al. 1992), so its sexual expression may change according to the availability of resources. Vachellia caven is a strict self-incompatible species and unable to self-pollinate autonomously. Because it depends obligatory on animal pollination to set fruits (Peralta et al. 1992; Ashworth 2004), its sexual reproductive success will reflect both pollination service and resources availability. Finally, it has been shown that maleness in V. caven increases female reproductive success (Calviño et al. 2014). Such counterintuitive effect of staminate flowers increasing female success has been observed in several other plant species and it may be the consequence of reduced sexual interference, among other factors (Podolsky 1992; Vallejo-Marín & Rausher 2007b; Calviño et al. 2014).

We hypothesise that decreased soil moisture and fertility, as a consequence of increased fire frequency in the Chaco Serrano (Carbone & Aguilar 2016), will bias sexual expression of resprouting individuals growing in frequently burned sites to maleness as it is less expensive than the hermaphrodite expression (Vallejo-Marín & Rausher 2007a). Secondly, because V. caven is completely dependent on insects for pollination, and the pollinator community in the Chaco Serrano recovers relatively quickly after fire (Carbone & Aguilar 2017), we expect that pollination service will not be affected. Nevertheless, regardless of unchanged pollination services and reduced sexual interference, we expect to find decreased reproductive success in individuals growing in frequently burned conditions because of soil resource depletion.

METHODS

Study area and species

The study area corresponds to the Chaco Serrano district, in the southernmost portion of Chaco phytogeographical province (Cabrera 1971). The predominant vegetation is a montane xerophytic subtropical forest currently formed by compound mosaics of forest, shrubland and grassland as a consequence of human land use changes and recurrent fires (Luti *et al.* 1979; Gavier & Bucher 2004). The climate is warm continental type, with minimum and maximum temperatures averaging between 10 and 25°C (Capitanelli 1979). Precipitation ranges between 500 and 1200 mm per year (Cabrera 1971), and it is concentrated mainly on the warm season (October–March), delimiting a clear period of water deficit during autumn and winter (from April to September). The soil in general presents a dark superficial horizont, with a moderate tenor of organic matter (Giorgis *et al.* 2013). In this region, wildfires typically occur at the end of the dry season, when temperatures begin to increase, fuel moisture is low and winds reach their maximum speeds (Bravo *et al.* 2001). Particularly, for the Sierras Chicas from central Argentina, the estimated average fire frequency was one fire every 5 or 6 years for the 1999–2011 period (Argañaraz *et al.* 2015).

Vachellia caven is one of the most widespread shrub or tree species of subtropical South America; in Argentina it occurs mainly in lowland and mountain arid and semi-arid forests from central to northern regions (Aronson 1992; Zuloaga & Morrone 1999). It is a semi-deciduous small tree (2–6 m high), flowers are yellow and nectar-less and they are arranged in globular fragrant inflorescences (Peralta *et al.* 1992). The pollen is grouped in polyads, containing approximately 32 grains of pollen and each flower contains an average of 30 ovules. The cup-shaped stigma of *V. caven* only allows the deposition of a single polyad. Therefore, only one polyad is needed to fertilise all the ovules of an ovary (Baranelli *et al.* 1995).

Vachellia caven is an andromonoecious species and each inflorescence can display between 20 and 60 small flowers with a variable percentage of perfect and staminate flowers (Peralta *et al.* 1992; Baranelli *et al.* 1995). Thus, three inflorescence types can be distinguished: male (i.e. those with staminate flowers only), hermaphrodite (perfect flowers only) and mixed, with both flower types (Calviño *et al.* 2014). It is pollinated by a wide variety of native insects including bees, flies and wasps, but its most frequent pollinator is the exotic bee *Apis mellifera* (Ashworth 2004; Aguilar 2005). *Vachellia caven* can only reproduce by seeds, which are dispersed by goats, guanacos and domestic cattle (Ashworth 2004).

It is a very common pioneer species in disturbed sites (Giorgis *et al.* 2011; Ashworth *et al.* 2015), and like many woody Leguminosae species, it is capable to fixing atmospheric nitrogen in root nodules formed by the symbiotic association with bacteria (Brewbaker *et al.* 1990; Frioni *et al.* 1998).

Sampling design

To select the sampling sites, we compiled the fire history of the last 25 years from the entire study area using different databases and covering approximately 40 km^2 (31°5′38.53″ to 31°9′11.73″S and 64°24′10.49″ to 64°20′40.35″W). We used fire records registered by Civil Defence of Rio Ceballos city (Giorgis *et al.* 2013) and Landsat TN and ETM satellite images (Argañaraz *et al.* 2015) for 1991–2016 period. We selected three 'unburned' sites and three frequently 'burned' sites (3–4 fires) in the 1991–2016 period. All sites were selected with the criteria of relative closeness (average distance between sites of 1530 m), and comparable topographical characteristics such as elevation (820–1200 m a.s.l.), slope (middle slope) and exposure (mostly N). The unburned sites had a physiognomy of open forest while burned sites had an open shrubland physiognomy (Carbone *et al.* 2017). Previous studies conducted in the exact same sampling sites have empirically verified that the elevation of the sites is not related to the quality of the soil (Carbone & Aguilar 2017) and that the livestock load does not affect the floristic composition of the plant community (Carbone *et al.* 2017).

Seven adult individuals were selected per site (total *N* = 42) in August 2016 and followed up until February 2017, covering the flowering and fruiting periods of the species. To quantify the sexual expression, 20 inflorescences were randomly collected per plant and were classified as male, hermaphroditic and mixed, depending on the presence of staminate, perfect or both types of flowers respectively. This classification was conducted in the laboratory with the help of a stereoscopic microscope. The proportion of male inflorescences per plant was determined as the number of male inflorescences/total number of inflorescences (male, hermaphrodite and mixed).

To determine the proportion of pollinated flowers per plant, 14 senescent inflorescences were randomly collected per individual. Three flowers were taken at random from each inflorescence (42 flowers per plant), and were observed under a stereoscopic microscope to determine the presence/absence of pollen (polyad) deposited on the stigma.

Female reproductive success was quantified as fruit set. Three branches per individual plant were randomly selected and the total number of inflorescences produced in 50 cm of length of each branch was quantified and the branch was tagged. In February, the number of mature fruits produced in the tagged branches was quantified. The fruit set was calculated as the summation of mature fruits per plant/ number of inflorescences, correcting by the proportion of hermaphrodite and mixed inflorescences estimated for each plant, since only hermaphrodite flowers present in that inflorescences can set fruits. To estimate the size of the plants the basal diameter of the stem was measured. In the case that a plant had multiple stems from the base, all the living stems were measured and the diameters were summed.

Data analysis

To assess whether sexual expression, proportion of pollinated flowers and fruit set differed between unburned and burned conditions, we used generalised linear mixed

models with binomial distribution of errors as these three response variables were proportions. Fire was considered a fixed factor with two levels (unburned and burned) and site was a random factor nested within condition (three replicates per condition). When analysing the effect of fire on sexual expression, pollination and fruit set, the diameter of the plants was used as a covariate, after having reviewed the assumptions for the inclusion of this covariate in the model. In order to test specifically whether the effect of fire on the fruit set of *V. caven* is better explained when considering the level of pollination and sexual expression, these two variables were used as covariates. The individuals that did not produce fruits were excluded from these analyses. The interaction between the fixed factor 'fire' (burned, unburned) and pollination and sexual expression was significant, so a bifactorial mixed model was used to compare the fruit set between burned and unburned conditions. To perform these analyses, we used *lmer* function of the *lme4* package (Bates *et al.* 2015). To evaluate the assumption of homogeneity of variances, we estimated overdispersion by calculating the parameter of scale, $\hat{c} = \Sigma(\text{Pearson residuals}^2)/\text{degrees of freedom}$. Overdispersion ($\hat{c} > 3$) was observed in the explanatory models of all response variables (Burnham & Anderson 2002). This lack of homogeneity of variances between conditions was corrected using selection of models by the information criterion of Akaike for overdispersed data, correcting also for small sample size (QAICc, function *dredge* of the *MuMIn* package; Bartoń 2016). The best-fitting model was the one presenting the lowest value of QAICc. For the comparison between nested models, the ΔQAICc was calculated as the difference between a given model and the model with the best fit. The significance of the fixed factor was determined by the Wald Z statistic, the P value and confidence intervals based on averaging the multiple models according to their relative weight (*model.avg* function of the *MuMIn* package; Bartoń 2016). This method (conditional GLMM) considers the variability attributed to both fixed and random factors. All analyses were performed in R version 3.3.1 (R Core Team 2017).

RESULTS

Sexual expression and pollination

The proportion of male inflorescences per plant (i.e. maleness) varied from zero to 0.70, and it did not differ between unburned and burned conditions ($Z = 0.838$, $P = 0.402$). Interestingly, the basal diameter of the individuals significantly explained the variations in sexual expression ($Z = 2.718$, $P = 0.007$, Appendix S1), where maleness decreased as the basal diameter increased, independently of the fire condition (Fig. 1). The proportion of pollinated flowers per plant varied from 0.1 to 0.6 and it was neither affected by fire ($Z = 1.497$, $P = 0.134$, Appendices S1 and S2), nor by the size of the plants ($Z = 0.544$, $P = 0.586$).
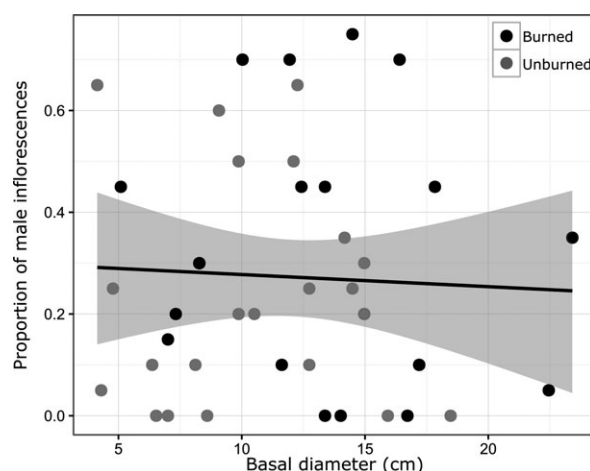

Fig. 1. Relationship between basal diameter and the proportion of male inflorescences of *Vachellia caven* in burned (black) and unburned (grey) conditions. The relation is significant (Estimate = −0.06, $Z = 2.718$, $P = 0.007$, $N = 42$) and independent of the fire condition according to AICc for small samples, corrected by the value of overdispersion.

Fruit set

We established two categories, 'more female plants' (i.e. plants with less than 50% of male inflorescences) and 'more male plants' (i.e. plants with more than 50% of male inflorescences). Among more female plants, 29% and 31% did not set fruits in unburned and burned conditions, respectively. Among more male plants, 14% and 5% failed to set fruits in unburned and burned conditions respectively. Among the individuals that yielded fruits, fruit set (fruits/inflorescences) per plant varied from 0.001 to 0.179. Notably, fruit set was low in both conditions, but it was more variable among individuals in the burned condition (Fig. 2). Fruit set was positively related to the basal diameter of the plants in both conditions ($Z = 2.081$, $P = 0.038$, Fig. 3; Appendix S1). Moreover, fruit set differed between conditions depending on sexual expression (interaction fire*sexual expression, $Z = 6.160$, $P < 0.001$, Fig. 2). Fruit set did not differ between fire conditions when maleness was low; however, as maleness increased, so did fruit set but only in the burned condition (Fig. 2). Moreover, fruit set differed between conditions depending on the pollination level (interaction fire*pollination, $Z = 4.325$, $P < 0.001$). Fruit set was similar between fire conditions when pollination was high, but as pollination decreased, fruit set increased only in the burned condition (Fig. 4).

DISCUSSION

From previous studies conducted at the same sites, we know that fire significantly reduced water content,
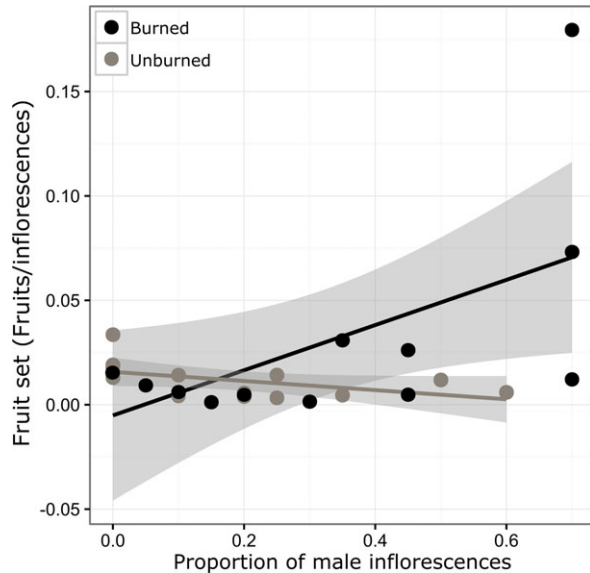
Fig. 2. Relationship between the proportion of male inflorescences and fruit set of *Vachellia caven* in burned (black) and unburned (grey) conditions. Individuals producing no fruits were excluded from the analyses. Fruit set differed between conditions depending on sexual expression (interaction fire*sexual expression, $Z = 6.160$, $P < 0.001$, $N_{burned} = 13$, $N_{unburned} = 13$) according to AICc for small samples, corrected by the value of overdispersion.
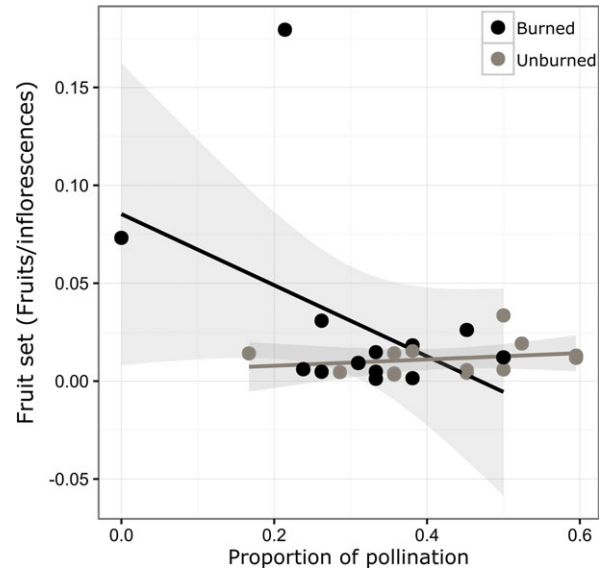

Fig. 4. Relationship between the proportion of pollinated flowers and fruit set of *Vachellia caven* in burned (black) and unburned (grey) conditions. Individuals producing no fruits were excluded from the analyses. Fruit set differed between conditions depending on the pollination level (interaction fire*pollination, $Z = 4.325$, $P < 0.001$, $N_{burned} = 13$, $N_{unburned} = 13$) according to AICc for small samples, corrected by the value of overdispersion.
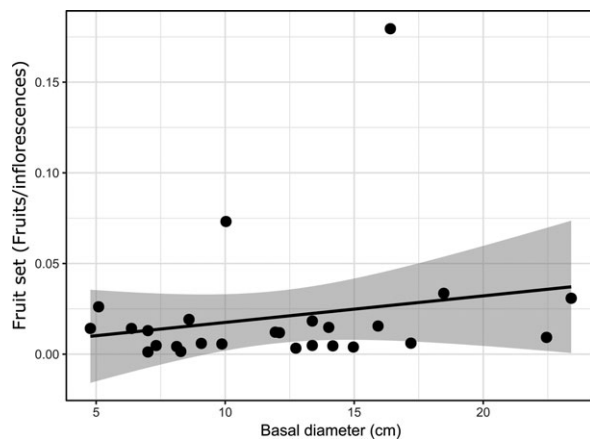

Fig. 3. Relationship between basal diameter and fruit set of *Vachellia caven*. Individuals producing no fruits were excluded from the analyses. The relation is significant (Estimate = 0.03, $Z = 2.081$, $P = 0.038$, $N = 26$) and independent of the fire condition according to AICc for small samples, corrected by the value of overdispersion.

nitrates and electric conductivity in the soils (Carbone & Aguilar 2017). However, these changes in soil fertility did not affect the sexual expression in *V. caven*. Moreover, our results show that femaleness was favoured in larger plants (Fig. 1), suggesting that female sexual expression is, as expected, more expensive than male expression. This finding does not agree with the results of previous studies that found significant effects of soil nutrients on sexual expression for several plant species (e.g. Freeman *et al.* 1980; Policansky 1981; Charnov 1982; Salomon 1985). Our results suggest that *V. caven* presents mechanisms to deal with the limitation of abiotic resources generated by high fire frequency.

Vachellia caven is able to fix atmospheric nitrogen (N_2) from the symbiotic association with bacteria hosted in root nodules (Frioni *et al.* 1998). Atmospheric nitrogen fixation is usually favoured in sites with high stress levels (Raison 1979). Such capability may explain the fact that sexual expression in *V. caven* was independent of soil fertility across sites. The resprouting strategy also implies a great energetic cost of reinvestment in the aerial vegetative structures that were eliminated by the fire (Bond & Midgley 2001). Thus, *V. caven* may tolerate soil nutrients limitation, especially nitrates, and be able to allocate resources not only to reset its vegetative biomass but also to maintain its sexual and reproductive functions in soils impoverished by high fire frequency. In the same way, previous studies have shown that biological N_2 fixation allows legume species to overcome nutrient limitation caused by high fire frequencies, maintaining or even increasing the amount of N in their tissues (Carreira & Niell 1992; Goergen & Chambers 2009;

Carbone & Aguilar 2016). Thus, the effect of soil nutrients on sexual expression may not apply to nitrogen fixing legumes in general, and therefore despite the variable sexual expression, *Vachellia* may not be the best group for exploring the effects of nutrient availability on sexuality.

Regarding pollination levels, no significant differences were found in the proportion of pollinated flowers between burned and unburned conditions (Appendix S2). As pollen can only be deposited during an insect visit, this result indicates that the frequency of effective visits by pollinators is not affected by the fire frequency of our studied system (one fire every 5 or 6 years, Argañaraz *et al*. 2015). In contrast to our results, Brown *et al*. (2016) found differences in pollinator visitation between burned and unburned conditions to an orchid species with a highly specialised pollination system. Factors such as size, intensity and patchiness of the fire may explain different results among these studies (Watson *et al*. 2012; Brown *et al*. 2017). Unfortunately, we do not have such detailed information on these other fire aspects in our study system to contrast our results. However, previous research conducted in the same sites found no changes in the pollinator assemblages of two herbaceous legume species with more specialised pollination assemblages than *V. caven* (Carbone & Aguilar 2017). At the landscape scale, the recovery of the pollination service after a fire event would imply either the restoration of pollinator populations at disturbed sites or a sink effect mobilising pollinators from unburned source sites (Ponisio *et al*. 2016; Brown & York 2017). Recolonisation of burned areas by insects may depend mainly on the size of the fire, on the availability of unburned refuges and on the time elapsed from the last fire (García *et al*. 2018). Moreover, local-scale processes such as facilitation between co-flowering plants may increase pollinator attraction maintaining the pollination service (Brown *et al*. 2016). Because pollination is one of the critical processes involved in the regeneration of plant populations that is most threatened by human disturbances (Neuschulz *et al*. 2016), our results provide novel knowledge about pollination resilience and its effects on the reproductive dynamics of Chaco Serrano plants subjected to fire. However, more studies are needed to understand the effects of the several fire aspects (frequency, size and patchiness) on pollinator communities and sexual plant reproduction in order to design managing strategies in the Chaco Serrano.

Contrary to our initial expectation, a particularly interesting result is the negative relationship between the proportion of pollinated flowers and fruit set. When the proportion of pollinated flowers was high, fruit set did not differ between burned and unburned conditions, but when the pollination level decreased,

fruit set was higher in the burned condition (Fig. 4). This result can be explained by a combination of two factors: pollination quality and abiotic resources. In self-incompatible species, pollination efficiency depends not only on the quantity of pollen deposited on the stigma but also on the quality of pollen. *Vachellia caven* has massive flowering and its most frequent pollinator is *A. mellifera*, which is known to favour geitonogamous pollination when plants have large floral display. Under such situation, it is possible that as the proportion of visited flowers increases (pollinated flowers), the proportion of flowers receiving self (incompatible) pollen also increases. As a result, there would be more flowers receiving pollen from the same plant that will fail to set fruits (Augspurger 1980). If this is correct, the lower the pollination levels to *V. caven* the higher the probability of receiving outcrossed compatible pollen, and thus the probability of setting fruits. For the unburned condition, however, fruit set was always low regardless of the pollination level. Higher vegetation cover and more complex vegetation structure in unburned communities increases interspecific competition for soil and light resources. Thus, although the quality of the pollination might be improved also in unburned conditions, the fruit set may still be limited in *V. caven* by increased competition for resources.

In this study, we observed that fruit set of more female plants did not differ between burned and unburned conditions. In contrast, we only observed differences in more male plants, which had a higher fruit set in burned sites (Fig. 2). Our results show that maleness increase female fitness (fruit set) in burned but not in unburned condition. Similarly, results from Calviño *et al*. (2014) conducted on *V. caven* in different sites and seasons, and those found for the andromonoecious *Solanum carolinense* (Vallejo-Marín & Rausher 2007b), *Capparis spinosa* (Zhang & Tan 2009) and *Anticlea occidentalis* (Tomaszewski *et al*. 2018) showed the same pattern. Several non-mutually exclusive mechanisms have been proposed to explain the benefit of female success supplied by increasing male flowers: (i) producing cheaper male flowers saves resources that can be reallocated to seed production (e.g. Emms 1993); (ii) male flowers are more attractive for pollinators than hermaphrodites, then increased male flower production may enhance pollination and seed set (Vallejo-Marín and Rausher (2007b); (iii) male flowers produce more pollen and/or larger pollen grains with faster pollen tube growth and thus higher potential to produce seeds (e.g. Zhang & Tan 2009; Peruzzi *et al*. 2012); and (iv) reduced or non-functional pistils from male flowers fail to remove pollen from pollinator's body, thus increasing the likelihood of outcrossing when functional pistils from hermaphrodite flowers are contacted (Podolsky 1992;

Vallejo-Marín & Rausher 2007b). We did not evaluate the mechanisms behind the positive relationship between maleness and female fitness, but given that *V. caven* is self-incompatible, it is likely that the latter mechanism is the main responsible of this result, that is, maleness increases outcrossing rates (Calviño *et al.* 2014). Furthermore, we show here for the first time that the positive relationship between maleness and female fitness can be modified by environmental factors. But, why did this relationship only occur in burned sites? One possible explanation is that plants growing under high fire frequency regimes experience lower competitive pressure for abiotic resources and thus increased outcrossing rates would better and readily translate into increased fruit set.

In conclusion, the results of this study indicate that *V. caven* is adapted to the effects of high fire frequency, especially boosting the reproductive success of more male plants in burned conditions. The species is not only able to regenerate its vegetative biomass but it can also maintain its sexual and reproductive functions after repeated fires, allowing it to persist and maintain viable populations in burned scenarios.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Selection of explanatory models of the proportion of male inflorescences (a), proportion of pollinated flowers (b), and fruit set per plant (c) in *Vachellia caven* based on the Akaike Information Criterion for small samples, corrected by the value of overdispersion (QAICc).

Appendix S2. Proportion of pollinated flowers of *Vachellia caven* in burned and unburned conditions.