

## Fire effects on the reproductive potential of two dominant woody species along an elevation gradient in central Argentina

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### ABSTRACT

Fire and elevation affect reproduction of woody species and, therefore, their distribution in the landscape; however, the effect of both factors are often confounded. In addition, plant size may also influence reproduction. Our objective was to investigate the combined effects of fire, elevation and pre-fire size on woody species reproductive potential in a seasonally dry mountain ecosystem. We tested the predictions that fire and elevation impair reproductive potential and that the negative effects of fire are enhanced at high elevation. Our study was carried out in the mountains of central Argentina, from 800 to 1700 m a.s.l. We selected individuals of two dominant resprouting woody species (*Vachellia caven* and *Lithraea molleoides*) in burned and comparable unburned areas. We estimated pre-fire size and fire damage level in each tree. We monitored parameters related to reproductive potential during four post-fire fruiting seasons in 185 *V. caven* and 78 *L. molleoides* trees. Our main results for *V. caven* show negative fire effects on most reproductive parameters, and on the expected number of germinable seeds per tree, which was estimated as an integrated parameter. The negative fire effects decreased over time until the fourth post-fire fruiting season, when we detected almost no fire effects. Moreover, the negative fire effects were greatly enhanced with elevation, while pre-fire size showed consistently positive effects on most reproductive parameters. For large trees located at low elevation, fire reduced the number of germinable seeds per tree by a factor of nearly six in the third post-fire fruiting season (from 2020 to 358 seeds), while at high elevation fire reduced germinable seeds by a factor of 15 (from 106 to 7 seeds) for similarly large trees. Small trees had a lower reproductive potential than large trees and the negative effects of fire were smaller but noticeable, and were enhanced by elevation, as in the case of large trees. For *L. molleoides* we found similar patterns to those of *V. caven*; however, since few trees produced seeds during the study, we did not compute formal statistics. We conclude that fire reduction should gradually increase reproductive potential, tree density and forest cover at high elevation, even when, according to previous studies, survival is not affected by fire or elevation in the study species.

### 1. Introduction

Some ecosystems climatically suitable for tree growth and forest development are maintained in a long-lasting treeless state due to a positive feedback between vegetation and fire (Pausas and Bond, 2020). Shrubs and herbs, particularly grasses, facilitate fire spread, preventing tree colonization and forest maturation (Tepley et al., 2018; Pausas and Bond, 2020, 2022). If present, the dominant tree species have a small

size, often a shrubby growth form, and most individuals are not able to reach maturity because of recurrent fires (Giorgis et al., 2013; Fairman et al., 2015; Karavani et al., 2018). These feedbacks can be generated after a high-severity wildfire or another kind of disturbance, such as logging, opens the forest canopy, allowing more light to reach the soil surface and favoring smaller and more flammable plants (Tepley et al., 2018; Landesmann et al., 2020). Moreover, since fire is an ancient process on Earth, in some ecosystems the feedback has been operational

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for thousands or even millions of years (Pausas and Bond, 2020; Bond, 2022). For example, in some areas with unsuitable conditions for trees during the last glacial period, a high fire frequency prevented forest or woodland expansion when climatic conditions became suitable, at the onset of the Holocene (Behling et al., 2007; Jeske-Pierschka et al., 2010, 2012).

In mountain ecosystems, the modulating effect of fire on the landscape may be combined, and often confounded, with the effect of climatic variation along the elevation gradient. Mean temperature decreases, the number of days with frost increases, and the growing season is shortened from mountain base to top (Körner, 2012). These changes negatively affect the performance of tall woody species up to the treeline, the elevation after which climatic conditions completely prevent their occurrence (Körner and Paulsen, 2004; Körner, 2012). However, below the treeline, response to elevation may be variable among species; for example, in water-limited systems the most water-demanding woody species may perform better at high elevation until temperature becomes limiting, near the treeline (Lippok et al., 2013; Matías and Jump, 2014; Toledo-Garibaldi and Williams-Linera, 2014). Because of the combined effects of soil moisture, temperature and fire on woody species' reproduction and growth, the causes of vegetation distribution in mountains are not always easily interpreted (Pini et al., 2017). In this context, the study of tall woody species' performance in response to fire along elevation gradients may help to disentangle the role of the different factors in shaping woody cover patterns in mountains.

Wildfires generally produce damage to above-ground tissues of woody species, that may result in plant death (Clarke et al., 2015; Karavani et al., 2018; Giorgis et al., 2021a). In some ecosystems, however, woody plants can survive the fire and recover by resprouting (Pausas and Keeley, 2014), even after losing all their aerial biomass. Yet, their reproduction may be impaired for some years, because the plant needs to recover aerial tissues and reserves before investing in reproduction (Clarke et al., 2015; Gomes et al., 2021). Other factors that can impair post-fire reproductive potential are temporary changes in the biotic and abiotic environment, such as reductions in soil moisture and nutrients, or in the pollinator activity, that may impose limits to parental investment in reproduction (Carbone and Aguilar, 2017). Thus, even in ecosystems adapted to fire through a resprouting strategy of their dominant species, a high fire frequency can limit forest development (Karavani et al., 2018; Nolan et al., 2021). Impaired reproduction can lead to a reduced population density compared with a situation without fire. Woody species can take longer to recover from fire at higher elevation due to the more stressing conditions than at lower elevations (Körner, 2012). This fact may explain the decrease of tall woody communities along elevation gradients, despite the suitable temperatures for tree growth.

Pre-fire tree size also has a strong influence on post-fire recovery in sprouting woody species; large plants have more accumulated underground reserves to be used in post-fire re-growth than smaller plants (Gurvich et al., 2005; Wigley et al., 2009; Herrero et al., 2016). At high elevation, the slower growth rate may result in smaller plants with fewer reserves; therefore, post-fire biomass accumulation may be further reduced, magnifying the differences in the effects of fire between low and high elevation. Although the separate effects of fire, elevation and plant size on woody species performance have been widely documented (e.g. Wang et al., 2012; Pollice et al., 2013; Karavani et al., 2018), the combined effects of those factors on reproductive potential are poorly understood. This is the case of the mountains in central Argentina, where both fire and elevation, as well as plant size, have effects on woody plant performance and distribution (Gurvich et al., 2005; Torres et al., 2014; Marcora et al., 2008, 2013). However, those effects have been scarcely studied in combination (e.g. Argibay and Renison, 2018).

The mountains of central Argentina (500–2790 m above sea level) have a Chaco flora at low elevation, shifting to a Sub-Andean flora as elevation increases (Giorgis et al., 2021b; Cingolani et al., 2022). The

two dominant tall woody species of low mountain Chaco forests and successional shrublands are *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae) and *Vachellia caven* (Molina) Seigler & Ebinger (Fabaceae), respectively. They have the potential to live up to 1700 m (Giorgis et al., 2017, 2021b; Alinari, 2017), but the cover of Chaco forests and shrublands shows a sharp decrease after ~1100–1300 m. At this elevation, woody physiognomies are largely replaced with grasslands (Giorgis et al., 2013; Cingolani et al., 2022), while Sub-Andean high-mountain forests reach their optimal conditions at ~1700–1800 m (Marcora et al., 2008, 2013; Argibay and Renison, 2018). Giorgis et al. (2013, 2017) proposed that anthropogenic wildfires are one of the main factors limiting the expansion of Chaco forests at elevations above ~1100–1300 m. A higher fire incidence between 900 and 1700 m than at lower or higher elevations (see details in the study area section) supports this hypothesis (Argarañaz et al., 2020). However, this factor alone cannot explain the decrease in population densities of Chaco tall woody species as elevation increases. For example, at 600–700 m, even in areas with high local fire frequency, successional shrublands are the dominant physiognomy, with high densities of potentially tall woody species in the form of small or medium-sized individuals, in contrast to the notorious scarcity of Chaco woody plants above ~1100–1300 m under a similar fire frequency (Argañaraz et al., 2015; Kowaljow et al., 2019; Cingolani et al., 2022). Most individuals of the two dominant species survive fire, and elevation does not influence mortality up to 1700 m (Torres et al., 2014; Alinari et al., 2019). Hence, a differential post-fire mortality would not be the cause of the low population density of Chaco woody species in the upper part of their distribution. Instead, we hypothesized that a differential post-fire reproduction plays a role in shaping this pattern, since fire and cold temperatures can impair seed production and germination capacity (Ne'eman and Dafni, 1999; Caignard et al., 2017; Gomes et al., 2021).

Our objective was to analyze how fire affects reproductive potential, evaluated through reproductive parameters related to seed production and germination capacity, of *V. caven* and *L. molleoides* along an elevation gradient from 800 to 1700 m in the mountains of Córdoba (central Argentina). We predicted that: (1) reproductive potential of both species will show a negative response to fire damage and elevation; (2) reproductive potential will show a positive relationship with plant size, and (3) the impairment of reproductive potential after fire damage will be stronger at high than at low elevation.

## 2. Materials and methods

### 2.1. Study area and species

The study was carried out in the Córdoba mountains (central Argentina), which consist of three main ranges that span 430 km from north to south and 110 km from east to west. These mountains have two elevation belts differing in floristic composition, with a transitional belt between them. The lowest belt (500–1300 m) is dominated by a Chaco flora, the upper belt (1700–2800 m) is dominated by a Sub-Andean flora, while the transitional belt (1300–1700 m) shows a gradual turnover between both floras (Giorgis et al., 2021b; Cingolani et al., 2022).

The study area (central point at 32°02'39'' S; 64°58'37'' W) was located on the western slope of the central range (Sierras Grandes), along an elevation gradient between 800 and 1700 m. Vegetation is a mosaic of forests, shrublands, grasslands and rocky outcrops (Giorgis et al., 2017; Cingolani et al., 2022). In the upper zones along the study gradient, woody cover is low, with small patches of tall shrublands, forests or isolated woody individuals, including *Lithraea molleoides* and *Vachellia caven* (Giorgis et al., 2013, 2017). Above our study area, in the Sub-Andean belt, tall shrublands and forests occupy a low proportion of the area, with *Polylepis australis* being the dominant tree (Cingolani et al., 2022).

The climate is mainly driven by elevation. At 530 m, in Villa Dolores (21.5 km to the west of our study area), mean annual temperature is

18.9°C, while at 1800 m, on the eastern slope (10 km from the study area), mean temperature is 11.2°C. At 2700 m, close to the mountaintop, annual mean temperature is about 7.4°C (INTA, 2007; Marcora et al., 2008; Argañaraz et al., 2020), indicating that our whole mountain range is below the global treeline (Körner and Paulsen, 2004). Rainfall is highly seasonal along the whole elevation gradient and is concentrated in the warmest months (October–March); the dry period spans from autumn to spring (April–September, Colladon and Pazos, 2014). At 530 m, the historical precipitation average is 682 mm (1961 – 2006, INTA, 2007); this value increases with elevation, reaching 900–1000 mm in the upper belt of the mountains. Temperature and precipitation patterns lead to more humid soils at higher elevation (Giorgis et al., 2017; Tecco et al., 2016; Argañaraz et al., 2020).

At present, most wildfires are human-ignited, and they burn 0.1–5.3% of the total mountain area every year (average 1.9%), mainly between August and September, when temperatures begin to rise and vegetation is highly flammable after 3–5 dry months (Argañaraz et al., 2015, 2016, 2020). The average return interval for the whole mountain area is 52 years, but it is variable with elevation. At 900–1300 m it was estimated in 32 years, and at 1300–1700 m in 37 years, from a 1999–2017 fire data base. In turn, at a lower or higher elevation the estimated intervals were longer: 80, 53 and 59 years at < 900 m, 1700–2100 m and > 2100 m, respectively (Argañaraz et al. 2020). However, these estimations represent averages across large areas; at more local scales, in some sectors close to human settlements, fire frequency can be much higher, up to one fire every three or four years (Argañaraz et al., 2015; Kowaljow et al., 2019). In our study area, the fire return interval is shorter than the average, and decreases with elevation, from 43 years below 900 m to 15 years above 1300 m (see details in Appendix A).

Studies on dominant Chaco and Sub-Andean woody species have shown that fire damage is more severe in small individuals with more herbaceous biomass below their canopy than in taller individuals surrounded by rock or bare soil (Renison et al., 2002; Alinari et al., 2019). Since woody species in our study area have slow growth (around 5–10 cm in height per year when not recently burned, Renison et al., 2005; Torres and Renison, 2015, 2016; Capó et al. 2016), individuals are usually affected by fire when they are less than 3–4 m in height (Gurvich et al., 2005; Alinari et al., 2015, 2019; Herrero et al., 2016). Therefore, recurrent fires prevent the maturation of forests, maintaining shrublands with average height of 1–2 m and emergent individuals of 4–5 m (Renison et al., 2011; Cingolani et al., 2022). Two wildfires occurred on the western slope of Sierras Grandes in July and August 2007: one close to San Javier town, which extended from 1100 to 1700 m (353 ha), and the other close to La Población town, which burned from 800 to 2700 m (552 ha). Both wildfires were ignited in the lowest part and spread up-slope. For this study, we merged both areas as a continuum, since they were less than 6 km apart and similar in topography and vegetation (shrublands, grasslands and small Chaco forest patches, Giorgis et al., 2017). Cattle were present in similar densities along the whole study gradient (Alinari et al., 2019).

We worked with the two dominant tall woody species of the Chaco low mountain forests and successional shrublands: *Lithraea molleoides* and *Vachellia caven*. Both species have a high post-fire survival, recover mostly through basal resprouting (Gurvich et al., 2005; Herrero et al., 2016; Torres et al., 2014) and can produce fruits even when they are 70–100 cm tall.

*V. caven* is a semi-deciduous tree or shrub (hereafter "tree" for simplicity) up to 5–6 m tall; it is dominant in successional shrublands but is also present in grasslands and open forests (Giorgis et al., 2017; Cabido et al., 2018). This species is absent in closed forests, because it is intolerant to shade (Giorgis et al., 2017; Cabido et al., 2018). *V. caven* is an andromonoecious species pollinated by insects; each inflorescence has 20–60 small yellow staminate and/or perfect flowers (Ashworth and Martí, 2011, Marquez et al., 2019). The flowering period usually lasts from August to October, with presence of immature fruits in November

and December, and of mature fruits from January to March (Ferreras et al., 2023).

*L. molleoides* is an evergreen, shade-tolerant, dioecious tree up to 12–15 m tall (Demaio et al., 2002). It is dominant in closed and open forests, being also present as small and medium-sized individuals in successional shrublands and in some grasslands (Cingolani et al., 2022). This species has ambophilous flowers pollinated by both wind and insects (Galfrascoli and Calviño, 2020). The flowering period begins in September or October, and mature fruits are found from December to May. Flower and fruit production is highly variable among years. During some years, entire populations of *L. molleoides* do not flower nor produce fruits (Ferreras et al., 2023).

## 2.2. Study design

Two to three months after the fires (October 2007), before the onset of the growing season, we selected a total of 198 and 85 individuals of *V. caven* and *L. molleoides*, respectively, distributed in the burned areas and in a comparable unburned area. To stratify the selection of individuals, we divided the elevation gradient (800–1700 m) into nine sections of about 100 m elevation each. We selected and tagged 11–21 *V. caven* trees per section in the burned area, and 5 trees in the unburned area (except for the upper two sections, where no individuals were found in the unburned area). In the case of *L. molleoides*, we selected 11–13 and 7–10 individuals per section in the burned and unburned areas, respectively, but only in the lowest four sections (800–1200 m), since on the upper sections we were not able to find enough trees. We selected trees of either sex, since we were not able to distinguish between males and females, but we assumed a sex ratio of about 0.5 that did not vary with the environment where the tree was growing (Chiapero et al., 2021).

We measured the size (height and two perpendicular crown widths) of the selected trees in the unburned area, and estimated pre-fire tree size in the burned area from remnant stems. After surface fires, the woody tissues of almost all trees remain standing, either scorched or not, including relatively fine branches (Gurvich et al. 2005). In general, non-scorched branches maintain their green leaves, while scorched branches show dead leaves or no leaves at all. Only very small individuals may occasionally lose all their aerial tissues. All selected trees of both species had a pre-fire height greater than 80 cm. During the selection process, for each tree we visually assessed the proportion (%) of the remaining woody tissue that was scorched, which was considered an estimator of fire damage (Renison et al., 2002; Alinari et al., 2015). In the unburned area, fire damage was recorded as zero. In the burned areas, we aimed to select, within each elevation section, individuals within the entire range of fire damage (from < 25% to > 75%). This was possible for *V. caven*, but not for *L. molleoides*, since trees were mostly 100% damaged, while only a small proportion showed a partial escape from fire (i.e., damage less than 100%). Thus, for *L. molleoides* we classified the selected burned trees in two categories: total (100%) and partial damage (5–80%).

After three years, in the winter of 2010, 13 and 7 individuals of *V. caven* and *L. molleoides* were dead, representing 6.6 and 8.2% of the selected trees, respectively. Mortality was not affected by fire damage or elevation (reported in Alinari et al., 2019). Here, we used only individuals that survived; thus, the total number of *V. caven* study trees was 185 (150 in the burned and 35 in the unburned areas), while the total number of *L. molleoides* trees was 78 (44 in the burned and 34 in the unburned areas). Of the 44 *L. molleoides* trees in the burned areas, 34 were completely damaged and only 10 were partially damaged.

## 2.3. Fruit and seed production

During the first fruiting season after the fire (January to April 2008), very few trees in the burned areas produced fruits and we did not record the information for each tree. During the second, third and fourth post-

fire fruiting seasons (January to April 2009, 2010 and 2011, respectively), we recorded fruit production for each individual of both species as a binary variable (presence or absence of fruits). For simplicity, we will refer to 2009, 2010 and 2011 fruit production, although the fruits recorded on those dates were the result of the processes occurring during the whole reproductive period, which started in the flowering season of the previous calendar year.

In the case of *V. caven*, in the 2010 summer we collected and counted the number of fruits per tree ( $N = 60$  fruiting trees). When fruit abundance was excessively high ( $N = 4$  trees), we collected and counted only those fruits present in a quarter of the individual, visually estimated, and we multiplied the value by four. Since this species produces a partially dehiscent legume, with more than one seed, we opened the fruits and counted the total number of seeds; then we calculated the average number of seeds per fruit, for each tree.

In the case of *L. molleoides*, only the same four trees produced fruits during the three study seasons (see results), and we were not able to count the fruits per tree, since many had already fallen to the ground when we visited the area. This species produces one seed per fruit; therefore, we did not estimate the number of seeds per fruit.

#### 2.4. Germination capacity

For each tree, we randomly selected 120 seeds in suitable conditions to be germinated (i.e., we discarded seeds predated by Bruchids or stuck to each other or to the legume). In some cases we had to discard the complete individual, because the number of seeds in suitable conditions was not enough; thus, we kept 43 individuals. Discarded individuals ( $N = 17$ ) did not differ from non-discarded individuals ( $N = 43$ ) in their fire damage, elevation or pre-fire height (test-t,  $P > 0.29$  for the three variables). Then, for each tree, we distributed the 120 seeds, not subjected to pre-germination treatments, in four trays filled with soil, which were randomly placed in germination chambers under controlled optimal conditions of light and temperature (25/15°C, 12 light and 12 dark hours, Funes et al. 2009). After 30 days, we counted the total number of germinated seeds per sample of 120 sowed seeds, to estimate the germination proportion as an indicator of the germination capacity of the seeds produced by each tree.

In the case of *L. molleoides*, we did not estimate seed germination proportion because the few trees that produced seeds were in the unburned area. Thus, it was not possible to evaluate the effects of fire on those parameters.

#### 2.5. Data analyses

To obtain a one-dimensional estimator of tree volume, we calculated the cubic root of the height multiplied by both crown widths. Then we correlated pre-fire height with the estimator of pre-fire volume for both species. Since the correlation was high in both cases (see results), we used only height for further analyses. For trees in the unburned area, height measured at the start of the study (October 2007) was considered equivalent to the pre-fire height (i.e. height in July 2007) estimated for trees in the burned areas, since the growing season had not started yet.

Additionally, to aid in the interpretation of results we performed pair-wise Pearson correlations among the three independent variables (fire damage, elevation and pre-fire height; hereafter, these variables will be named generically as "covariates") and among the three non-binary reproductive parameters estimated in 2010 (fruits per tree, seeds per fruit and germination proportion).

##### 2.5.1. *Vachellia caven*

We analyzed the effects of fire damage (%), elevation (m) and pre-fire height (cm) on six reproductive parameters: fruit production (presence-absence) in 2009, 2010 and 2011 fruiting seasons; and, for the 2010 fruiting season only, the number of fruits per tree; number of seeds per fruit; and germination proportion (number of germinated seeds in relation to the number of sowed seeds). We analyzed the data using

Generalized Linear Models (GLMs) in R version 4.1.2 (R Core Team, 2021). For fruit production ( $N = 185$  trees) and germination ( $N = 43$ ), we assumed a binomial (Bernoulli for fruit production) distribution with a logit link function. For fruit production we fitted a separate model for each fruiting season. Since germination proportion data showed overdispersion, we used a quasi-likelihood approach via the dispmmod R package (Scrucca, 2018). For the number of fruits per tree, we only considered the individuals that had produced at least one fruit ( $N = 60$ ). Thus, we assumed a zero-truncated negative binomial distribution with a log link function, using the VGAM package (Yee, 2020). For the number of seeds per fruit ( $N = 60$ ), we used a gamma distribution with a log link function. We did not assume a discrete distribution because we used the average by individual, computed from the sampled fruits, as response variable. We assessed each model fit by plotting the DHARMA residuals (i.e. the randomized estimated cumulative distribution function evaluated at each data point; Dunn and Smyth, 1996; Hartig, 2022), as a function of the predicted values and of each covariate. To evaluate whether interaction terms were needed, we plotted the DHARMA residuals as a function of each pair-wise product of the covariates; since we found no patterns we did not include interaction terms in the models. However, because of the non-linearity of the link functions used in GLMs, the models already impose some degree of interaction between covariates (McElreath, 2020). In the case of the fruit production models for 2010 and 2011, the DHARMA residuals suggested a unimodal relationship with elevation; therefore, we included the quadratic term of elevation in these models. The analyses of the remaining DHARMA residuals plots did not justify further changes in the models for the other response variables. To assess the proportion of explained variability, we computed the Nagelkerke  $R^2$  for the models with Bernoulli distribution (binary data, i.e. fruit production for 2009, 2010 and 2011). For the remaining models, we calculated the  $R^2$  from the linear regressions between predicted and observed values in their original scales.

Once the models were obtained, we explored the combined effects of fire damage, elevation and plant height on each reproductive parameter. For this, we calculated and plotted the models' predictions under contrasting values of these covariates. The contrasting values consisted in the 12 combinations of short (15% percentile) and tall (85% percentile) plant height, low (15% percentile), medium (different criteria depending on the model) and high (85% percentile) elevation, and null (0%) and total (100%) fire damage. For each reproductive parameter, covariate percentiles were obtained from the data set used for the respective model.

Finally, we obtained the expected number of germinable seeds per tree, as an integrated estimator of reproductive potential, under the 12 combinations of low, medium (in the case of elevation) and high values of the covariates. In this case, we used the 15% and 85% percentiles from the whole data set ( $N=185$ ) for all models. To obtain the integrated estimation, we multiplied the predicted values of the four reproductive parameters evaluated in 2010:

$$GST = FP \times FT \times SF \times GP \quad (1)$$

where GST is the expected number of germinable seeds per tree, FP is the 2010 fruit production probability, FT is the number of fruits per tree, SF is the number of seeds per fruit, and GP is the germination proportion. Fruit production probability and germination proportion are expressed in a 0–1 scale for this estimation. To obtain approximate 95% confidence intervals, we computed the same predictions using 30,000 draws of coefficient vectors for each model sampled from multivariate normal distributions, with the maximum likelihood estimates as the mean vector and the variance-covariance matrix of the estimates (Bolker, 2008).

##### 2.5.1. *Lithraea molleoides*

For this species we only reported descriptive information. We tabulated the data about fire damage, elevation and pre-fire height of the

four trees that produced fruits and of the remaining 74 trees that did not produce fruits during the three study fruiting seasons.

### 3. Results

#### 3.1. *Vachellia caven*

The pre-fire height of *V. caven* trees varied between 95 and 450 cm and was strongly correlated with the estimator of volume ( $R = 0.84, P < 0.001, N = 185$ ). Height was slightly and negatively correlated with elevation ( $R = -0.21, P = 0.004, N = 185$ ), but not with fire damage, nor was fire damage correlated with elevation ( $R < 0.01, P > 0.93$  in both cases).

In the summer of 2009 (the second fruiting season after the fire), only 6.5% of the trees produced fruits, whereas in 2010 and 2011, overall fruit production was 32.4% and 25.9%, respectively. The three non-binary reproductive parameters estimated in 2010 (number of fruits per tree, number of seeds per fruit and germination proportion) were positively, although weakly, correlated with each other.  $P$ -values were not always significant, but they were low ( $P < 0.105$ , Table 1).

##### 3.1.1. Response of reproductive parameters to covariates

Fire damage significantly decreased fruit production probability in 2009 and 2010, and produced a similar but non-significant response in 2011. Elevation showed negative effects on fruit production in 2009, but in 2010 and 2011 the response to this covariate was unimodal. Pre-fire tree height produced positive effects, significantly increasing fruit production probability in 2009 and 2010, and exhibited a similar trend, but not significant, in 2011 (Fig. 1, Table 2). According to the model prediction, in 2009 the probability of fruit production was almost null for completely damaged trees of any pre-fire height and along the whole elevation gradient, whereas for undamaged trees it reached ~50% only if they were tall and located at low elevation (Figs. 1 and 2a,b). In 2010, fruit production probability varied between ~4 and 32% for damaged trees, and more than doubled for undamaged trees, being maximum for tall trees at low to intermediate elevation (~70–75%, Fig. 2c,d). In 2011, fruit production probability varied between ~9% for short, damaged trees at high elevation and ~55% for tall, undamaged trees at intermediate elevation (Fig. 2e,f).

In the case of trees that produced at least one fruit in 2010, the predicted number of fruits was highest for tall individuals located at low elevation (~170–200 fruits per tree) and lowest for short individuals at high elevation (~55–70 fruits per tree). The effects of both elevation and pre-fire height were significant, whereas the effect of fire damage was negligible and non-significant (Table 2, Fig. 3a-c, Fig. 4a,b).

The number of seeds per fruit decreased with elevation and fire damage, and increased with pre-fire height, but only the effect of elevation was significant (Table 2, Fig. 3d-f). Fire damage and pre-fire height were not significant, although the trends were clear (Fig. 3d,f). According to the model predictions, at low elevation undamaged trees, either short or tall, produced ~24 seeds per fruit, whereas totally damaged trees produced ~19 seeds per fruit. In contrast, at high elevation each fruit contained on average ~13–17 seeds, depending on the damage level (Table 2, Fig. 3d-f, Fig. 4c-d).

Germination proportion significantly decreased with fire damage and elevation of the parental tree, whereas it was almost constant across different pre-fire heights (Fig. 3g-i, Table 2). Predicted germination for

undamaged trees varied between 65% and 90% for those located at high and low elevation, respectively, whereas for damaged trees it varied between 25% and 65% (Fig. 4e-f).

#### 3.1.2. Germinable seeds per tree

When most parameters were integrated in an estimator of the expected number of germinable seeds per tree in the third fruiting season after the fire (2010), differences between contrasting conditions of the covariates were largely magnified. We estimated  $> 2000$  germinable seeds in the case of undamaged tall trees at low elevation and  $< 1$  in the case of short damaged trees at high elevation (Fig. 5). Elevation had an overall larger effect than pre-fire height or fire: the number of germinable seeds per tree was reduced by a factor of 19–51 from low to high elevation, by a factor of 6–15 from no damage to total fire damage, and by a factor of 6–9 from tall to short height (Fig. 5, Appendix B).

Moreover, the effect of fire on germinable seeds per tree was stronger at high than at low elevation. For example, if only tall trees are considered (Fig. 5b, Appendix B), at low elevation total fire damage reduced the number of germinable seeds by a factor of nearly six (from 2020 to 358 seeds), whereas at high elevation this factor was 15 (from 106 to 7 seeds). Likewise, the effect of elevation was stronger for completely burned than for unburned trees (Fig. 5 and Appendix B).

### 3.2. *Lithraea molleoides*

The pre-fire height of *L. molleoides* study trees varied between 80 and 390 cm and was strongly correlated with the estimator of volume ( $R = 0.85, P < 0.001, N = 78$ ). Height was slightly and negatively correlated with elevation ( $R = -0.20, P = 0.084$ ) and with fire damage ( $R = -0.22, P = 0.049$ ), whereas fire damage was not correlated with elevation ( $R = 0.08, P = 0.47$ ). In all post-fire summers (2009, 2010 and 2011) only the same four trees (5.1%) produced fruits.

The four *L. molleoides* trees that produced fruits were located in the unburned area, whereas the 74 remaining trees, which did not produce fruits, were distributed in the unburned and burned areas, and when burned, they experienced total or partial damage. Additionally, the trees that produced fruits were tall, while trees that did not produce fruits varied from short to tall. The distribution of the four trees that produced fruits along the elevation gradient was similar to that of the 74 which did not produce fruits (Table 3).

## 4. Discussion

Our results support the predictions that fire and elevation affect reproduction of low-mountain Chaco woody species. Altogether, our findings indicated that both factors limit *V. caven* reproductive potential, and that the negative effects of fire were enhanced at high elevation. Plant size also showed the expected effects; trees that were large before the fire had better reproductive potential during most of the study period than smaller trees. In the case of *L. molleoides*, although the effects were not conclusively demonstrated, the observed trends were in line with our hypothesis. Based on our results, we suggest that a reduction in fire frequency would gradually increase Chaco shrubland and forest cover in the upper part of their distribution.

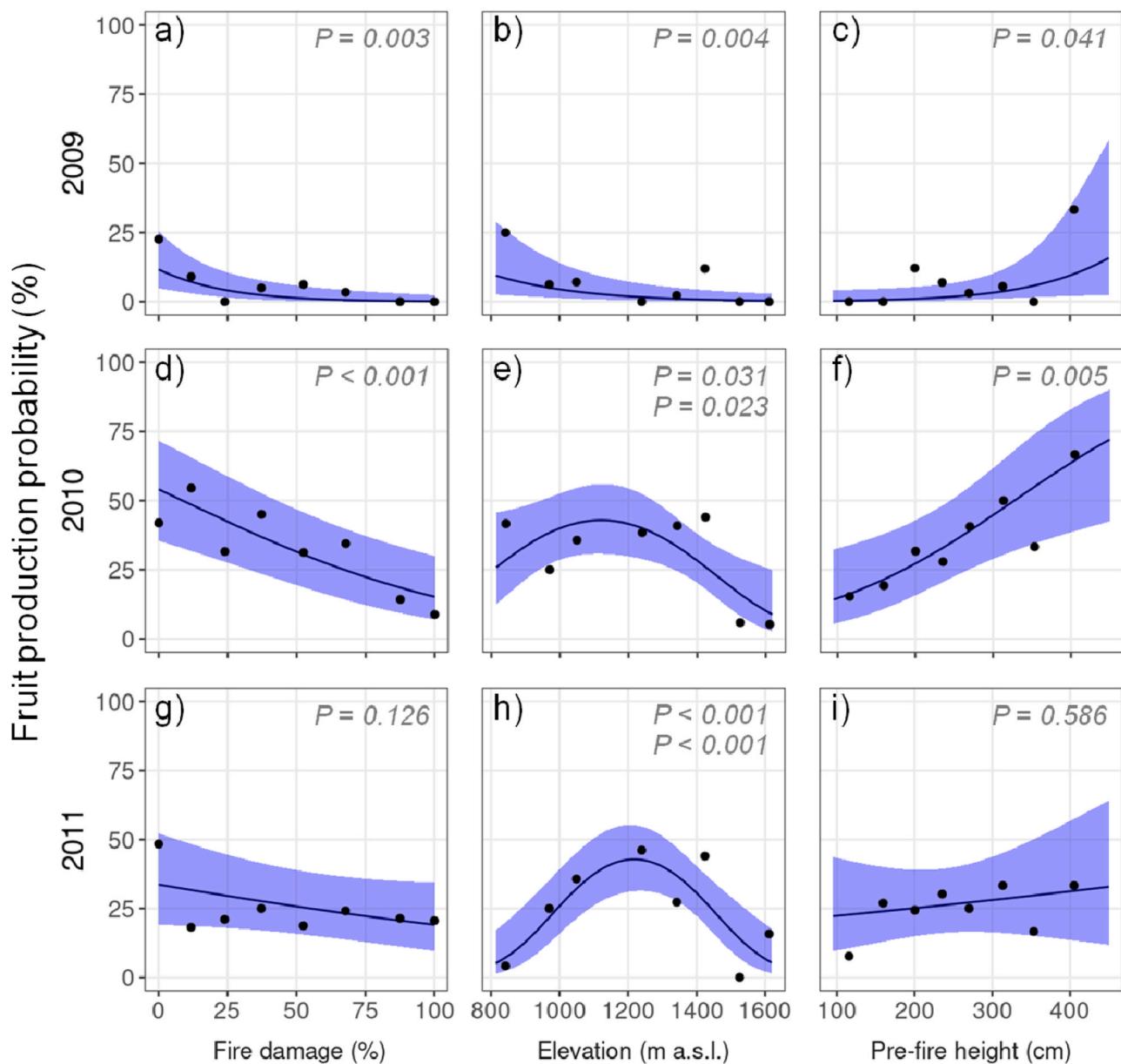
#### 4.1. Fire effects

Fire damage reduced fruit production probability of *V. caven* up to the third post-fire fruiting season, whereas in the fourth season (2011), the effect of fire was negative but not significant, suggesting an important recovery of the capacity to produce fruits. Since only the presence/absence of fruits was evaluated in that season, the total post-fire recovery of reproductive potential cannot be conclusively asserted from our data. However, a previous study showed that the proportion of *V. caven* trees that produced fruits (69–95%) and the number of fruits per inflorescence (0.001–0.179) were similar or even lower in unburned

**Table 1**

Pair-wise Pearson correlations among reproductive parameters of *V. caven* trees that produced at least one fruit in the 2010 fruiting season.

		N	R	P
Fruits / tree (No.)	Seeds / fruit (No.)	60	0.26	0.041
Fruits / tree (No.)	Germination (%)	43	0.26	0.089
Seeds / fruit (No.)	Germination (%)	43	0.25	0.105



**Fig. 1.** Partial predictions for fruit production probability (%) in *V. caven* as a function of fire damage, elevation and pre-fire height for three post-fire fruiting seasons. Black circles represent averages of data binned into 8 similar-width categories for each covariate (only for illustrative purposes). Curves were plotted from the respective logistic models, fixing the values of the non-plotted covariates at their means (tree height 231 cm, fire damage 48%, elevation 1264 m) or at the elevation that predicts average probabilities (885 m and 1001 m, for d-f and g-i, respectively). The P-values of the slopes either of the single first-order term (in a-d, f-g, i) or the first-order and quadratic terms (e, h) are indicated at the upper right corner of each panel. All model coefficients are shown in Table 2.

sites than in frequently burned sites evaluated in the sixth post-fire fruiting season (Marquez et al., 2019; L. Carbone pers. comm.). Based on both studies, we can infer that the reproductive potential of *V. caven* recovers in about four to six years after a fire. Our results agree with those of Gomes et al. (2021) for the Brazilian savanna; the authors reported a reduction in reproductive potential of woody species until at least the third fruiting season after fire, particularly in totally burned plants that resprouted from the base. The delay of four to six years to completely recover the reproductive potential may be caused by the high energetic costs of regenerating the aerial vegetative structures killed by fire (Obeso, 2002; Marquez et al., 2019; Gomes et al., 2021). *V. caven* starts flowering in late winter, before the onset of vegetative growth (Alinari, 2017; Ferreras et al., 2023); hence, the availability of underground reserves may play a key role in triggering the flowering processes (Loescher et al., 1990). In burned plants that are using their

reserves for shoot regrowth, resources may not be enough to be allocated to reproduction (Wigley et al., 2009).

In trees that had produced at least one fruit in 2010, fire did not affect the number of fruits, whereas pre-fire tree size showed a strong effect on this reproductive parameter. These results are surprising, since the most immediate effect of fire is the reduction in size due to the elimination of live biomass (Gomes et al., 2021; Giorgis et al., 2021a), and size is usually related to the total amount of fruits produced by a tree (e.g. Pollice et al., 2013; Minor and Kobe, 2019; Ouédraogo et al., 2020). The lack of a fire effect on the number of fruits may be explained by the rapid regrowth after the fire (Alinari, 2017). In *V. caven*, as well as in other resprouting species, regrowth is facilitated by a large pre-fire size, since large plants have high amounts of stored carbon (Gurvich et al., 2005; Sala et al., 2012; Herrero et al., 2016; Moris et al., 2023). This fast regrowth may be an adaptation to escape, at least partially, future fire

**Table 2**

Generalized linear models for *V. caven* reproductive performance parameters as functions of fire damage (D), elevation (E) and pre-fire height (H). The response variable (for fruit production a separate model was fitted by year), the distribution assumed in the models, the function to calculate the mean or probability, the equation to calculate the linear predictor (LP), the N used in each analysis and the R<sup>2</sup> (Nagelkerke in the case of Bernoulli distributions) are indicated. The P-value associated with each regression term is shown in the plots (Figs. 1 and 3).

Response variable	Distribution	Function for the mean or probability (p)	Equation for the linear predictor LP =	N	R <sup>2</sup>
Fruit production					
2009	Binomial	$p = 1/(1+e^{-LP})^*$	0.736 - 0.0451 x D - 0.00429 x E + 0.01152 x H	185	0.35
2010	(Bernoulli)		-11.47 - 0.0188 x D + E terms <sub>10</sub> + 0.00772 x H	185	0.23
2011			-24.11 - 0.0076 x D + E terms <sub>11</sub> + 0.00151 x H	185	0.17
Fruits per tree	Zero-truncated negative binomial	$\text{mean} = e^{LP} / (1 - p_0)^{\dagger}$	4.856 - 0.0015 x D - 0.00302 x E + 0.00982 x H	60	0.24
Seeds per fruit	Gamma	$\text{mean} = e^{LP}$	3.662 - 0.0023 x D - 0.00070 x E + 0.00048 x H	60	0.18
Germination	Binomial	$p = 1/(1+e^{-LP})^*$	4.827 - 0.0159 x D - 0.00289 x E - 0.00039 x H	43	0.22

\*In the plots, p was multiplied by 100 to express the results as percentage.

† E terms<sub>10</sub> = 0.01840 x E - 0.000008213 x E<sup>2</sup>, E terms<sub>11</sub> = 0.00391 x E - 0.00001607 x E<sup>2</sup>

‡ In the case of fruits per tree, the function for the mean is different from a typical log-link model because of the truncation. Here, p<sub>0</sub> is the probability of finding zero in a non-truncated negative binomial distribution, defined as p<sub>0</sub> = [θ/(θ+e<sup>LP</sup>)]<sup>0</sup>, where θ is the (inverse) dispersion parameter, estimated as 0.6923.

injury by rapidly attaining a large size (Wigley et al., 2009; Alinari et al., 2019). As a result, in 2010, completely burned *V. caven* trees in our study were only ~30–36% smaller than unburned trees of similar pre-fire size, since the latter grew at a slower rate (Alinari, 2017). This relatively small difference did not appear to influence the number of flowers or the proportion that sets fruits once the plant had enough stored resources to invest in reproduction.

Besides consuming biomass, fire can reduce fruit production by depleting soil resources or changing the pollinator community (González et al., 2004; Marquez et al., 2019). However, *V. caven* is a nitrogen-fixing Fabaceae, and fruit set did not differ between sites with high and low nutrient availability (Marquez et al., 2019). Additionally, Carbone and Aguilar (2017) reported that unburned and frequently burned sites did not differ in the richness and identity of pollinators visiting two characteristic plant species of our study area. In the same line, Giorgis et al. (2021a) did not find consistent fire effects on invertebrate abundance and diversity between recently burned ( $\leq 3$  years) and unburned sites in a meta-analysis across South America. These results suggest that in this area and species, the most important fire effect on fruit production is induced by the removal of plant biomass and not by a reduction in nutrient availability or in pollinator visits.

Fire reduced not only post-fire fruit production probability, but also the germination capacity of seeds. Fire produce changes in the biotic and abiotic environment surrounding the tree, which can last a few years (Torres et al., 2014; Giorgis et al., 2021a). In consequence, the soil water-balance, as well as the light and temperature conditions during the seed production process may be altered, affecting seed-coat hardness, seed dormancy and germination capacity (Penfield and MacGregor, 2017; Menegat et al., 2018).

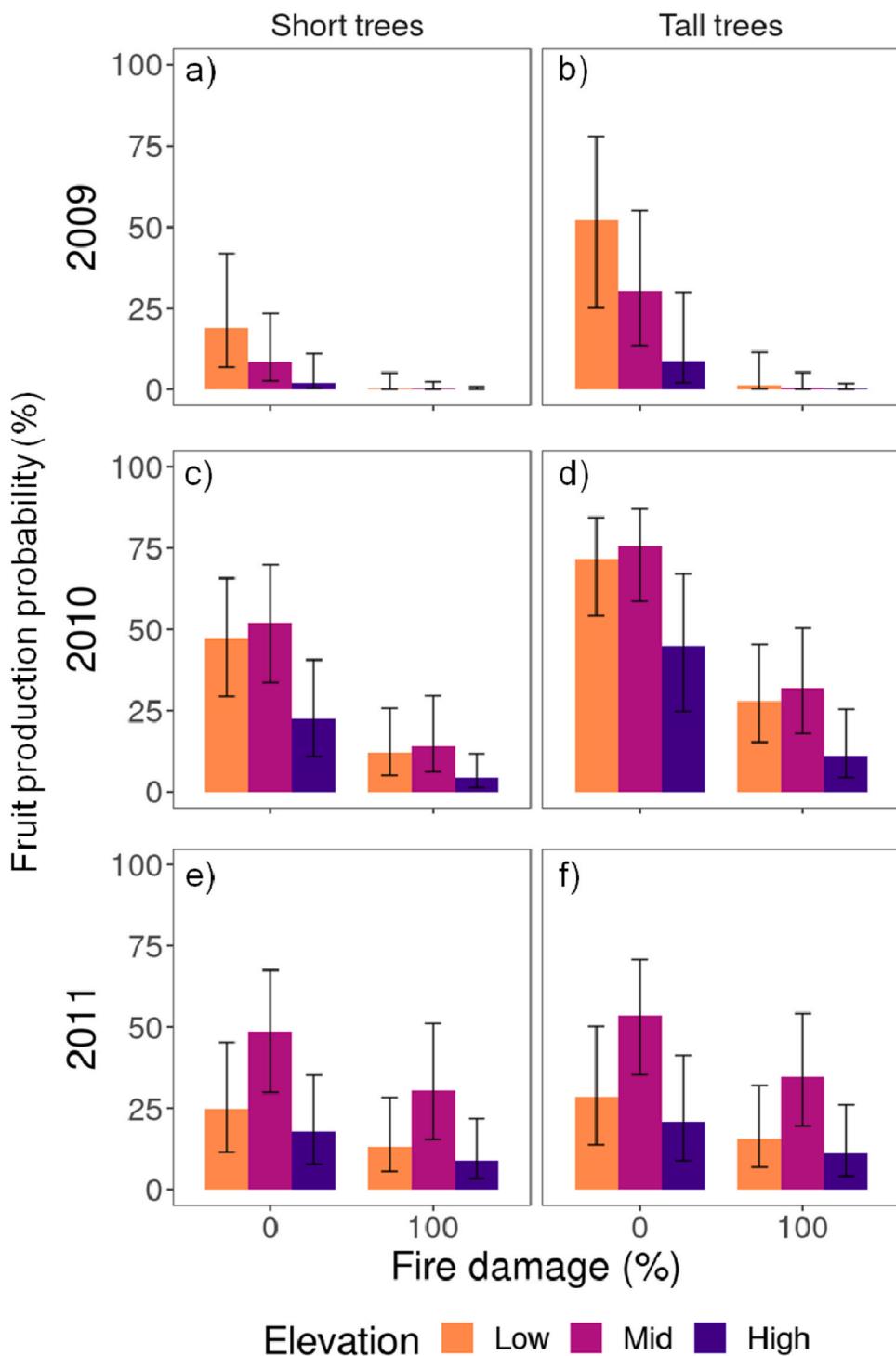
In the case of *L. molleoides*, the four trees that produced fruits were located in the unburned area, while trees of similar pre-fire size in the burned area did not produce fruits at all. Assuming that the sex ratio is not related to our study covariates, these observations suggest that fire damage is detrimental to fruit production at least until the fourth post-fire fruiting season. Since we did not extend our study for more than four years, we cannot speculate about how much longer it would take to recover *L. molleoides* reproductive potential. The low fruit production in *L. molleoides*, even in the unburned area, is in line with other reports. Chiapero et al. (2021) found that only 30–50% of male and female trees > 3 cm DBH (i.e. ~1.7 m height) produced flowers across two growing seasons, and Ferreras et al. (2023) found that only 42% (averaged across four years) of large female trees produced fruits, with high variability among years (0–100%). We found that only 17% of the unburned trees higher than 1.7 m produced fruits (data not shown); assuming that about half of our individuals may be males, our values (i.e. 34% for large female trees) are within the range of those in the literature.

#### 4.2. Elevation effects

Although in 2010 fruit production of *V. caven* showed a unimodal response to elevation, other reproductive parameters responded in a decreasing fashion. As a consequence, for large and undamaged trees, the expected number of germinable seeds, as an integrated parameter, decreased from more than 2000 per tree at low elevation to fewer than 110 at high elevation. The shorter growing season at high elevation may reduce the investment of maternal energy into the offspring and limit the time available to complete the reproductive cycle. Furthermore, pollinators may lower their activity due to progressively shorter periods of suitable temperatures, which can reduce the proportion of flowers bearing fruit (e.g. Ma et al., 2023). In our study, reproductive potential at high elevation was also reduced because of a lower germination capacity of the seeds, which may be a direct consequence of colder temperatures during seed development and maturation (Penfield and MacGregor, 2017). An additional and more indirect effect of elevation on reproduction may occur through the reduction in vegetative growth rate (Alinari, 2017). As a consequence of slower growth rates, large plants, which have the best reproductive potential, are less common at high than at low elevation, which in turn contributes to a reduced regeneration.

Fruit production was the only parameter evaluated in *V. caven* during more than one year. It showed a notorious inter-annual variability independent of fire, both in absolute terms and in the response to elevation. This is not surprising, since the effect of elevation is mainly associated with changes in temperature and evapotranspiration, which are also affected by inter-annual climatic variations. Total fruit production for undamaged trees peaked in 2010 after an extremely dry and warm flowering season in spring, and the minimum occurred in 2009 after a cold and unusually rainy spring (Appendix C). Our results suggest that warm springs benefit pollinator activity and/or plant investment in reproduction, which is in line with results obtained by Ferreras et al. (2023). The role of water stress is more difficult to interpret, as it seems to limit fruit production at low elevation, as compared to mid-elevation, during dry springs (2010 and 2011); but when comparing among years, the highest fruit production was obtained after the most extreme dry spring (2010), even at low elevation. Further studies covering longer periods would be necessary to elucidate the role of water stress on fruit production.

In the case of *L. molleoides*, the effect of elevation was not evident, since the four trees that set fruits were distributed along the whole elevation range studied for this species, up to 1200 m. However, an effect was implicit in our study, as we did not find enough trees above 1200 m. Additionally, Vera (2016) and Alinari (2017) found a reduction in *L. molleoides* vegetative growth rate up to 1300 and 1500 m, respectively. In our study, that phenomenon was reflected in the slightly



**Fig. 2.** Combined effects of fire, elevation and pre-fire height on *V. caven* fruit production probability (%) in three post-fire fruiting seasons. Bars represent the predicted probability (%) and 95% confidence intervals for undamaged (0%) and completely damaged (100%) trees of tall (300 cm) and short (165 cm) pre-fire height, located at low (957 m), mid (1169 m) and high (1525 m) elevation. The low and high values for plant height and elevation were fixed at the 15% and 85% percentiles of the 185 study trees. The mid elevation was fixed at the average between 1120 m and 1218 m, which predicted the maximum fruit production in 2010 and 2011, respectively.

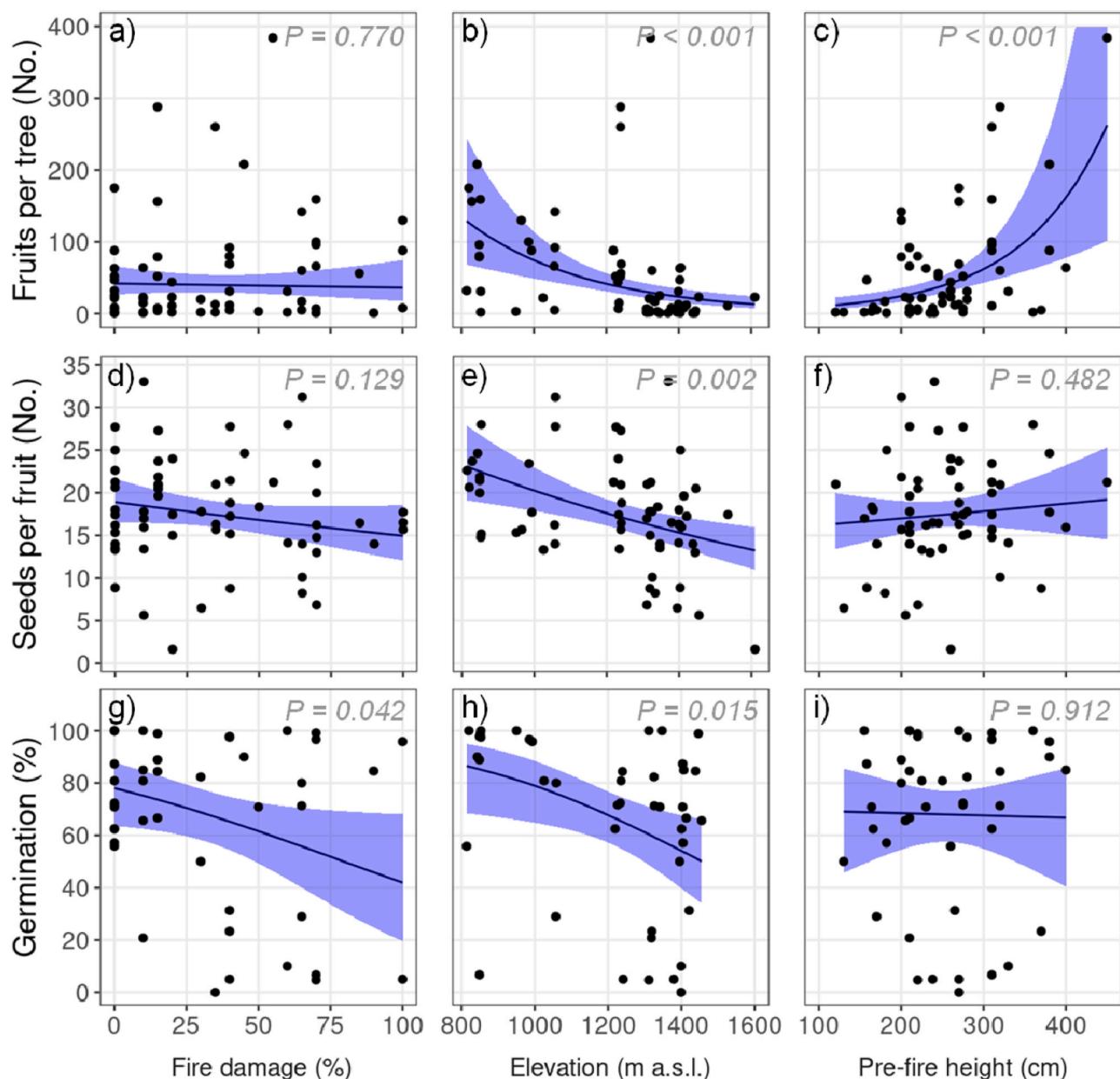
negative correlation between elevation and size. Since size was related to fruit production, elevation indirectly influences reproductive potential by reducing vegetative growth.

For both species, the low tree density at high elevation contributes to an overall low seed rain, slowing population growth and feeding back on the low tree density. Additionally, it is known that isolation at high elevation may generate inbreeding depression effects (Hensen et al.,

2012). However, previous work on the study species did not find effects of isolation on seed production and germination (Ashworth and Martí, 2011; Chiapero et al., 2021).

#### 4.3. Size effects

As expected, *V. caven* trees that were large before the fire had a better

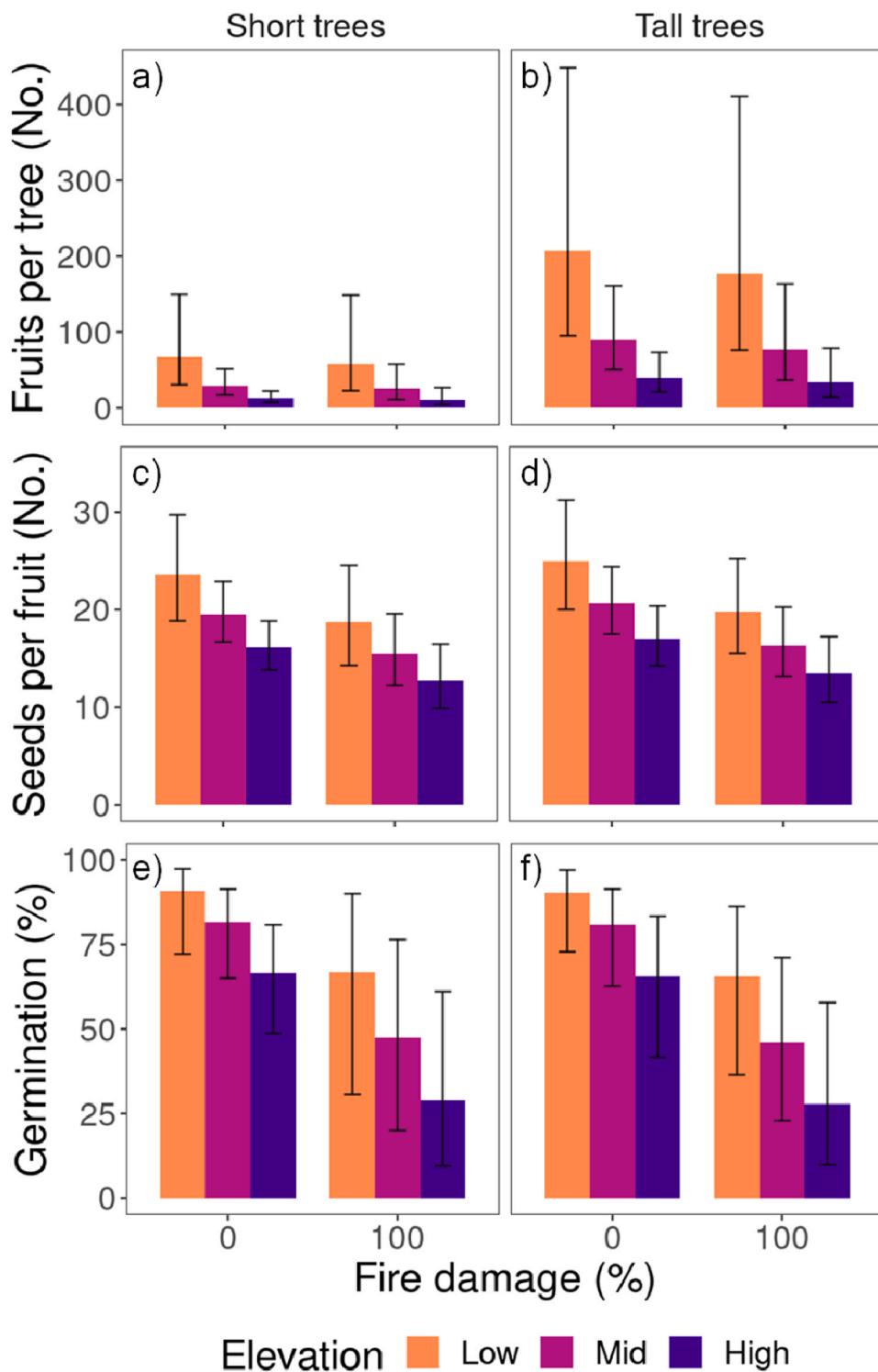


**Fig. 3.** Partial predictions for *V. caven* number of fruits per tree, number of seeds per fruit and germination proportion as functions of fire damage, elevation and pre-fire height. Black circles represent the observed values. Curves represent the predicted values, plotted from the respective models; the values of the non-plotted covariates were fixed at the means in their respective data set (tree height 253 cm for a, b, d, e and 254 cm for g, h; elevation 1214 m for a, c, d, f and 1195 m for g, i; fire damage 34% for b, c, e, f and 32% for h, i). The *P*-value for the regression coefficient corresponding to each covariate and model is shown in the upper right corner of each panel. All model coefficients are shown in Table 2.

post-fire fruit production than smaller trees. Pre-fire height strongly influenced post-fire height, both in burned and of unburned trees. Unburned trees continued to grow at an average rate of 9 cm/year, resulting in a strong correlation between pre- and post-fire height of the following three winters (Alinari, 2017). In the case of burned trees, the higher amount of accumulated reserves in larger and older individuals promotes a faster regrowth and recovery of above and underground biomass (Gurvich et al., 2005; Sala et al., 2012; Herrero et al., 2016; Alinari, 2017). Given that the investment in reproduction may depend on accumulated reserves, when trees of different pre-fire size that have undergone the same fire damage are compared, the largest trees are expected to show a better reproductive potential. The observations made in *L. molleoides* are in line with the results for *V. caven*, since no tree smaller than 279 cm produced fruits, even in the unburned area.

#### 4.4. Germinable seeds per tree

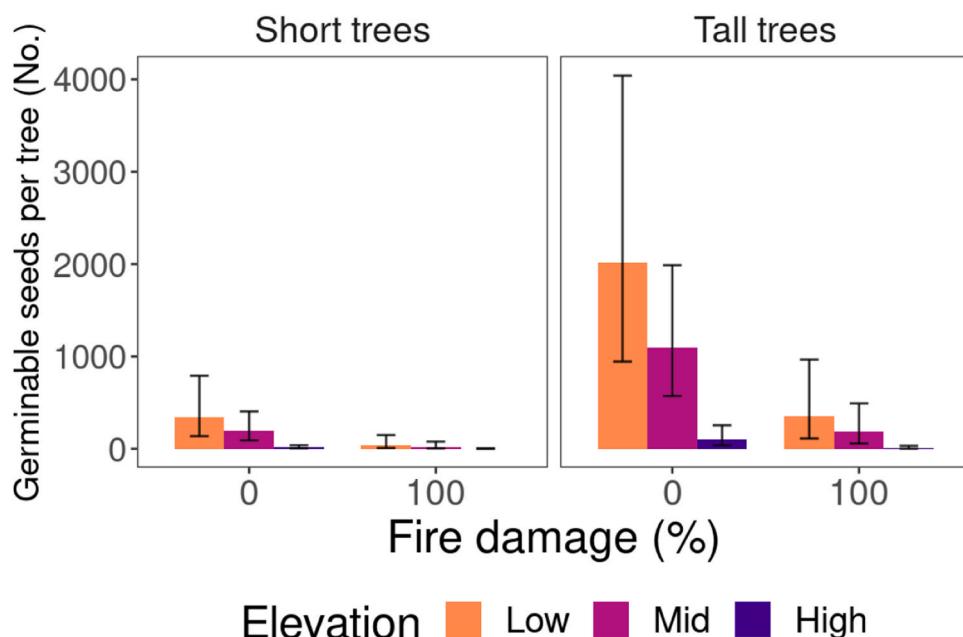
The integrated results for *V. caven* showed that, in the third post-fire fruiting season, fire damage, elevation and pre-fire size had overwhelmingly large effects on the expected number germinable seeds per tree. Despite the fast recovery of aerial biomass during the first three post-fire growing seasons (Alinari, 2017), fire strongly reduced the number of germinable seeds per tree by a factor of 6–15, depending on size and elevation. Besides the effects on reproductive potential, fire can affect the actual post-fire germination, survival and growth of plants in the field, which we have not evaluated here. Those effects may be positive or negative, since fire can enhance or impair the environment for germination and recruitment (Giorgis et al., 2021); however, some previous studies suggest that these effects are not important in our study area (Torres et al. 2014, 2015).



**Fig. 4.** Combined effects of fire, elevation and pre-fire height on *V. caven* number of fruits per tree, number of seeds per fruit and germination proportion. Bars represent the predicted values of each reproductive parameter and 95% confidence intervals for undamaged (0%) and completely damaged (100%) trees of tall and short pre-fire height, located at low, mid and high elevation. The low and high values for plant height (197/311 cm for a, b, c, d and 187/320 cm for e, f) and elevation (~853/1404 m for all panels) were fixed at the 15% and 85% percentiles of the data set used in each analysis; the mid elevation at the average between the low and high elevation (~1128 m).

Our results, together with results reported in Alinari (2017), evidence that at the highest elevation, potential reproduction of *V. caven* is directly limited due to low seed production and germination capacity, and indirectly through the reduction in vegetative growth rate. Actual reproduction of low-mountain woody species at the highest elevation is further reduced by fewer days with optimal warm temperatures for

germination and seedling survival (Funes et al., 2009; Pais Bosch et al., 2012; Torres et al., 2023). Fire represents an additional factor that impairs reproduction, with stronger effects at high than at low elevation. The impairment in reproduction caused by fire may last three years or more. In the upper portion of the Chaco vegetation distribution, in the transition belt (1300–1700 m), fires occur every year, burning from



**Fig. 5.** Combined effects of fire, elevation and pre-fire size on *V. caven* expected number of germinable seeds per tree (an integrated parameter) evaluated in 2010. Bars represent the expected number of germinable per tree and 95% confidence intervals for undamaged (0%) and completely damaged (100%) trees of tall (300 cm) and short (165 cm) pre-fire height, located at low (957 m), mid (1120 m) and high (1525 m) elevation. The low and high values for plant size and elevation were fixed at the 15% and 85% percentiles of the covariates for the 185 study trees. The mid elevation was fixed at the value that predicted the maximum fruit production probability in 2010 (1120 m).

**Table 3**

Fire damage (in three categories), elevation and pre-fire tree height for *L. molleoides* trees with presence and absence of fruits in three post-fire fruiting seasons (2009, 2010 and 2011). The proportion (%) of trees in each fire damage category is indicated for each group, and in the following rows, the mean and range for elevation and tree height.

	Presence of fruits	Absence of fruits
	N=4	N=74
Fire damage categories		
Totally damaged (%)	0	45.9
Partially damaged (%)	0	13.5
Undamaged (%)	100	40.5
Elevation (m a.s.l.)	966.5 (820–1145)	1005.8 (817–1207)
Tree height (cm)	318.5 (279–390)	188.9 (80–390)

0.1% to 10% of the area (3.2% on average; but in the case of our particular study area this average is 6.8%, Appendix A), whereas below this elevation fire incidence is lower (Argañaraz et al., 2020). Thus, above 1300 m fires not only have a stronger negative effect on reproduction than at lower elevation, but also affect a larger proportion of the area per year, which also implies that at a given local point the fire return interval is shorter. In summary, fire impact on reproduction may be a main cause of the decreasing pattern of woody plants cover and density with elevation in the Chaco and transition belts.

#### CRediT authorship contribution statement

**Julieta Alinari:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Axel R. von Müller:** Writing – original draft, Methodology, Investigation. **Ana Cingolani:** Writing – review & editing, Writing – original draft, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Daniel Renison:** Writing – review & editing, Conceptualization. **Marcelo Cabido:** Writing – review & Investigation, Funding acquisition.

editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Iván Barberá:** Writing – review & editing, Software, Methodology.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data are available in CONICET repository (<https://ri.conicet.gov.ar/handle/11336/210957>).

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:[10.1016/j.foreco.2024.121844](https://doi.org/10.1016/j.foreco.2024.121844).

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