

Differential pollinator response underlies plant reproductive resilience after fires

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• **Background and aims** Assessing the resilience of plant–animal interactions is critical to understanding how plant communities respond to habitat disturbances. Most ecosystems experience some level of natural disturbance (e.g. wildfires) to which many organisms are adapted. Wildfires have structured biotic communities for millennia; however, the effects of fire on interactions such as pollination have only recently received attention. A few studies have shown that generalist plants can buffer the impact of fires by pollinator replacement, suggesting that the resilience to disturbance could depend on the level of specialization of the interactions. Here, we hypothesize that (1) fires could impose negative effects on plants with specialized pollination systems, and (2) in large wildfires, these negative effects will be stronger with increasing distance inside the burnt area because pollinators will need more time to recolonize.

• **Methods** These questions were tested in the specialized pollination system of a widespread Mediterranean palm, *Chamaerops humilis*. The post-fire pollination resilience was assessed in replicated wildfires representing three post-fire ages by measuring the abundance of beetle pollinators and by estimating fruit set (i.e. the proportion of flowers setting fruits) in burnt and unburnt areas. To test for distance effects, plants were sampled along transects inside the burnt area.

• **Key Results** Despite a marked post-fire decline in the specialist pollinator, exacerbated by the distance from the fire's edge, the palm's fruit set was barely affected. The temporary replacement by a sap beetle at burnt sites – an effective pollinator that had not been previously recognized – provided post-fire reproductive resilience.

• **Conclusions** Differential pollinator responses to disturbance can ensure plant success even in plants with only two functionally similar pollinators. This highlights the importance of pollinator replacement and dynamics for the resilience of interactions and ultimately of plant reproduction in disturbance-prone ecosystems.

Keywords: Arecaceae, *Chamaerops humilis*, *Derelomus chamaeropsis*, entomophily, fire-prone ecosystems, interaction resilience, *Meligethinus pallidulus*, palm, pollinator replacement, sap beetle, weevil, wildfires.

INTRODUCTION

One of the main challenges in community ecology is to get a better understanding of how plant–animal interactions respond to disturbance. Specifically, mutualistic interactions such as pollination play an essential role in the maintenance of biodiversity (Herrera and Pellmyr, 2002). There is evidence of negative impacts on plant fitness by the disruption of pollination interactions linked to recent human-induced disturbances such as habitat fragmentation (Aguilar *et al.*, 2006), pesticides (Stanley *et al.*, 2015) or species invasions (Chittka and Schürkens, 2001; Traveset and Richardson, 2006). On a broader temporal scale, most ecosystems have experienced some level of natural disturbance to which many organisms are adapted (Elmqvist *et al.*, 2003). Assessing the effects of natural disturbances (e.g. wildfires) on pollination interactions may contribute to understand their resilience, which is important in the current context of increasing anthropogenic perturbations.

Wildfires are common natural disturbances that have shaped communities for millennia (Pausas and Keeley, 2009), resulting in the evolution of numerous adaptive traits and strategies that allow plants and animals from fire-prone regions to succeed

under different fire regimes (Schütz *et al.*, 1999; Keeley *et al.*, 2011; He *et al.*, 2012; Castellanos *et al.*, 2015; Pausas and Parr, 2018). Despite this long fire history in many terrestrial ecosystems, the way in which pollination interactions cope with fire has only recently received attention (Dafni *et al.*, 2012; Brown *et al.*, 2017), and most research on this topic has been focused on pollination by bees (Ne'eman *et al.*, 2000; Potts *et al.*, 2001; Moretti *et al.*, 2006; Lazarina *et al.*, 2016). Assessing the effects of fires on plant pollination is especially relevant given the current anthropogenic-driven disruptions of the natural fire regimes in different regions.

Fires affect plant and pollinator communities as well as their interactions (Potts *et al.*, 2003; Lazarina *et al.*, 2016; Ponisio *et al.*, 2016). The time since the last fire (post-fire age) shapes the pollinator community because it alters vegetation structure, floral rewards and the pollinator's access to bare ground and nesting places (Pauw, 2007; Moretti *et al.*, 2009). During the first year after a fire, if the vegetation recovery is rapid, an increase in nesting sites and floral resources provided by fire-stimulated plants, via resprouting or germination from the seed bank, can attract many pollinators into the burnt area. However, if post-fire recovery is slow, low availability of water and food

resources (DeBano and Conrad, 1978) can delay pollinator recolonization. This can be accentuated if pollinators are highly sensitive to fires (i.e. they do not survive, escape or move to unburnt refugia). In such cases, recently burnt areas would continue to have low pollinator richness and abundance, resulting in low levels of plant reproduction (Ne'eman and Dafni, 1999; Ne'eman et al., 2000). Post-fire age can also interact with ecological and functional traits of pollinators, such as niche specialization, body size or life cycle, leading to differences in ability to recolonize after fire (Bradstock et al., 2002; Moretti et al., 2006). In addition, other factors characterizing the fire regime such as fire intensity and frequency may affect the post-fire succession and ultimately pollinator responses.

For plant species with generalized pollination systems (i.e. a diverse set of floral visitors that are effective pollinators) the negative impact of fires can potentially be buffered if pollinators respond differently to fire (Bond, 1994; Potts et al., 2001; Pauw, 2007), as shown by studies on different disturbances (Ashworth et al., 2004; Aguirre and Dirzo, 2008; Hallett et al., 2017). This is consistent with theoretical predictions of the advantages of generalized pollination (Waser et al., 1996), and could be explained, for example, if the different pollinators belong to a variety of functional groups that are differentially affected by disturbance (referred to as 'response diversity'; Ives et al., 1999; Walker et al., 1999; Bartomeus et al., 2013). However, fires can have stronger effects on plants with specialized interactions as we have previously shown for seed predation (García et al., 2016). For plants that rely on one or a few species of pollinators for reproduction, the loss of their interacting partners after fires will trigger a decrease in plant reproductive success, at least until the interaction is recovered. That is, for these plant species, the vulnerability to fire may be related to the resilience (i.e. the capacity of a system to maintain its function and identity after a change) of their mutualistic interactions. A variety of responses by pollinators with different nesting preferences or by plants and pollinators varying in their dispersal abilities may provide resilience to pollination systems under disturbance.

We hypothesize that plant species with specialized pollination systems will be negatively affected by fires due to impacts on their few pollinators that in turn affect the plant's reproduction. To test our hypothesis we used the pollination system of the dwarf palm *Chamaerops humilis* (Arecaceae). Current knowledge indicates that this dioecious palm is exclusively pollinated by the nursery weevil *Derelomus chamaeropsis* (Curculionidae; Anstett, 1999; Dufay and Anstett, 2004). The weevil feeds and develops inside persistent old palm inflorescences, which are burnt during fires and thus a strong decrease in pollinator abundance in burnt areas is expected. In addition to *D. chamaeropsis*, small sap beetles (Nitidulidae) are also visitors of the palm's inflorescences (Anstett, 1999; our per. obs.). Because sap beetles are important pollinators of other palm species (Henderson, 1986; Anderson et al., 1988; Aguirre and Dirzo, 2008; Barfod et al., 2011), we also predict that *Meligethinus pallidulus* (Nitidulidae) could contribute to the pollination of *C. humilis*. In addition, the strength of the interactions can vary along the distance inside the burnt area while recolonization takes place, as has been shown for herbivory and seed predation in large wildfires (Knight and Holt, 2005; García et al., 2016). This may lead to stronger post-fire effects on pollinator abundance and fruit set levels with increased distance inside the burnt area.

In summary, we study the resilience of *C. humilis* pollination to wildfires by comparing the abundance of pollinators on the palm's inflorescences, and their consequences for fruit set, in burnt and in unburnt (paired) sites with different post-fire ages. We also test whether the effects of fire on the two beetle pollinators and on palm fruit set are stronger with increasing distance from the fire's edge.

MATERIAL AND METHODS

Study system

The Mediterranean dwarf palm *Chamaerops humilis* is a small dioecious palm native to the coastal shrublands of the western Mediterranean Basin. The plant resprouts quickly after fires and produces flowers the following spring (Paula et al., 2009). With or without fire, flowering occurs in early spring, with male anthesis starting 1 or 2 weeks before female anthesis (Anstett, 1999). Although *C. humilis* can occasionally show polygamous individuals, we did not observe functional hermaphroditic flowers in the studied populations. New yellow-greenish inflorescences emerge from the palm trunks while old brown inflorescences remain for years. Male and female individuals have branched inflorescences enclosed by two bracts (prophyll) that gradually open during flowering. Female flowers have three free carpels and develop into a polydrupe with 1–3 drupes. Each drupe was considered as a fruit as it acts as the dispersal unit containing the seeds.

Chamaerops humilis has a specialized nursery pollination system involving the weevil *Derelomus chamaeropsis* (Curculionidae; Anstett, 1999). During the winter, weevil larvae develop from eggs laid the previous spring inside the rachis of persistent old inflorescences (Dufay and Anstett, 2004; Jácome-Flores et al., 2018). Adult *D. chamaeropsis* (mean body length 2.9 ± 0.4 mm, excluding the rostrum, $n = 6$) emerge in early spring and are attracted to flowering plants by a chemical signal emitted by leaves during the flowering season (Dufay et al., 2003). Female and male leaves produce a similar odour preventing the weevil from avoiding female palms, although the insect shows a preference for male individuals, where it feeds on pollen (Dufay et al., 2003, 2004; Jácome-Flores et al., 2018).

Our field observations suggest that there is another common visitor on *C. humilis* inflorescences, the sap beetle *M. pallidulus* (Nitidulidae, mean length 1.7 ± 0.2 mm, $n = 6$) although its role on the palm's pollination is unknown. Occasionally honey-bees visit male inflorescences but we have never seen them on female flowers and thus do not consider them as potential pollinators. Ants are erratic and infrequent visitors and also unlikely to pollinate this dioecious plant. There have been suggestions that wind could also play a role in pollination of *C. humilis* (Herrera, 1989; Jácome-Flores et al., 2016). Although most previous evidence does not support this possibility (Anstett, 1999; Dufay and Anstett, 2004), we experimentally test it here (see Results).

Study areas

The study was carried out during 2016 and 2017 in four burnt sites in eastern Spain after wildfires (see Table 1 and Fig. 1 for details). Two sites (Dénia and Tivissa) were studied in both 2016 and 2017, and two other sites (Xàbia and Carcaixent)

were studied in 2017 only. This design involved replicated sampling of sites during 1, 2 and 3 years post-fire (Table 1). All sites are located in coastal Mediterranean shrublands dominated by *Cistus monspeliensis* and *Ci. albidus* (Cistaceae) and Fabaceae species such as *Calicotome spinosa* and *Ulex parviflorus*. All fires were typical Mediterranean crown fires (Keeley et al., 2012), that is, of high intensity and fully affecting most plants (little unburnt islands, see Fig. 1).

Pollinator exclusion experiment: the role of the different pollinators

To investigate the role of *M. pallidulus* in *C. humilis* pollination and rule out the possible contribution of wind, we conducted a pollinator exclusion experiment during the flowering peak of *C. humilis* in 2017. We selected 12 female *C. humilis* plants from natural unburnt populations in Dénia. We chose four undehisced inflorescences per plant (in one or two stems) and assigned one inflorescence to each of four pollination treatments in which the inflorescences were either enclosed in mesh bags of different pore diameters or left as an unbagged open control. All bags were tied to the stems and the aperture sealed with silicone. We also added silicone to the base of

inflorescences in the control treatment to control for possible effects of the experimental manipulation. The four treatments were: (1) pollination exclusion using a paper bag to exclude both wind and insect pollination; (2) potential wind pollination by enclosing the inflorescence in a bag with pore diameter 0.15 mm; (3) potential wind and small-insect (i.e. *M. pallidulus*) pollination, by enclosing the inflorescence in a bag with pore diameter 1.10 mm; and (4) unbagged control, in which wind, *M. pallidulus* and *D. chamaeropsis* were able to pollinate.

We used the palm's fruit set as an estimate of female reproductive success by counting the flowers and fruits for each inflorescence in late June. We bagged the inflorescences and collected the fruits on the same day for all plants across treatments. We estimated fruit-set as the number of drupes produced in relation to the total potential drupes (i.e. the total number of flowers in the inflorescence multiplied by three carpels). For this, we collected all sampled inflorescences and counted all drupes produced and the scars left by aborted flowers on the inflorescence rachis. The number of flower scars is a good estimator of the potential fruit production (Pearson correlation between number of flowers in fully open inflorescences and flower scars in the same inflorescences was 0.95, $P < 0.001$, $n = 262$, tested in plants from burnt and unburnt areas during the sampling of the palm's fruit set, see below).

TABLE 1. Information on the study sites.

Site	Province	Latitude	Longitude	Fire date	Sampling year	Fire ages	Burnt area (ha)
Dénia	Alacant	38.808054	0.160267	Sept. 2014	2016, 2017	2, 3	445
Tivissa	Tarragona	40.979691	0.693141	June 2014	2016, 2017	2, 3	890
Xàbia	Alacant	38.731141	0.169339	Sept. 2016	2017	1	800
Carcaixent	València	39.105267	-0.400584	June 2016	2017	1	2000

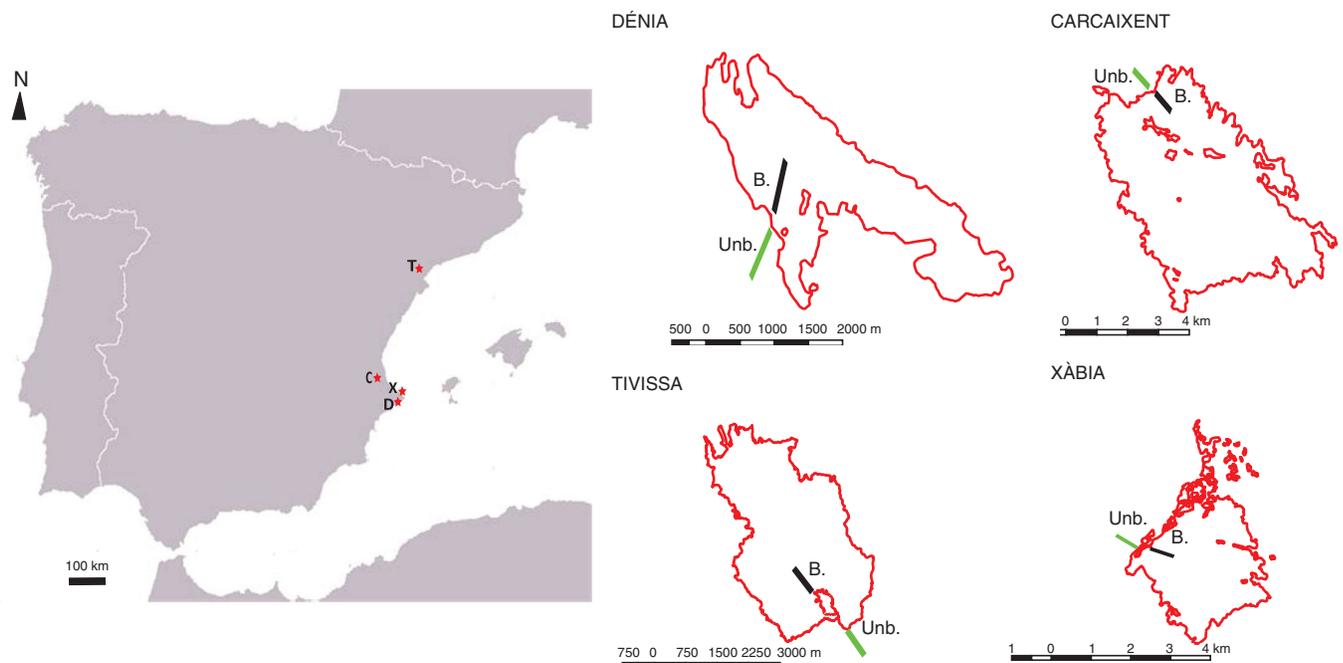


FIG. 1. Location of the study sites in eastern Spain (left), and the burnt (B., in black) and adjacent unburnt (Unb., in green) areas sampled at each site (right). Red polygons denote the fire perimeter at each site. C = Carcaixent, D = Dénia, T = Tivissa, X = Xàbia.

To test the effectiveness of the bags used for excluding the flow of airborne pollen (treatments 1 and 2), we performed an additional experiment using the common anemophilous grass *Hyparrhenia hirta*. This species has hermaphroditic and staminate flowers with pollen grains of similar size (diameter $28.20 \pm 1.82 \mu\text{m}$, $n = 10$) to *C. humilis* pollen (diameter $20.45 \pm 1.53 \mu\text{m}$, $n = 10$). We bagged non-flowering shoots of ten *H. hirta* plants using one bag of both mesh size per plant. These shoots were surrounded by other flowering individuals of *H. hirta*, but were not directly touching any other flowers. Each bag contained two adhesive strips (1 cm^2) to retain wind-dispersed pollen grains that entered the bag. After 1 week we dyed the adhesive strips with fuchsine jelly (Beattie, 1972). We counted any pollen grains observed with the ImageJ software (Rasband, 2007). The results suggested that bags of the wind pollination treatment did not reduce the amount of wind-dispersed pollen [mean number of grains per adhesive strip: 186 ± 98 in 1.10 mm pore bags vs. 204 ± 115 in 0.15 mm pore bags, generalized linear model (GLM) with Poisson error distribution: estimate = 0.040 ± 0.033 , z -value = 1.209, $P = 0.22$, $n = 10$ bags of each pore size], and thus the bags used were appropriate for the experiment.

Insect pollen loads

To test for differences in the numbers of pollen grains carried by *M. pallidulus* and *D. chamaeropsis*, we haphazardly captured one individual of each species from each of 20 flowering *C. humilis* plants (ten per sex) at each study site in 2017. We individually kept the insects in Eppendorf tubes at -20°C until a sample of the pollen loads was collected from the whole body surface of each individual using fuchsine jelly cubes. We melted the cubes on microscope slides and then identified the pollen loads from insects collected on female palms by comparing with a reference pollen library constructed by collecting anthers of *C. humilis* and 12 co-flowering plant species from the study sites. We dyed the pollen grains of each plant species with fuchsine jelly and identified them under a microscope (Leica DMR). To measure pollen size (of *C. humilis* and the co-flowering plant species) for the reference pollen library and count the number of *C. humilis* grains carried by the insects we used the ImageJ software (Rasband, 2007) with a specific script developed for the counting analysis.

Postfire changes in pollinators and fruit set

To study post-fire changes in pollinators and fruit set at each site, we tagged palms within the perimeter of the burnt area and in adjacent unburnt (control) areas with conditions (soil type, topography and plant species composition) similar to those within the burnt area prior to the fire. Burnt and adjacent unburnt areas were embedded in the same vegetation matrix type (shrublands). We performed all sampling in mid-April at the peak of anthesis of male plants, and the beginning of female flowering. In each burnt and unburnt area, we sampled 98–197 *C. humilis* plants of both sexes separated from each other by at least 5 m. To test the effects of the distance from the edge on pollinator abundance and palm fruit set, plants were sampled

along transects (of approx. 30–700 m) from the fire's edge to the interior (Fig. 1). We sampled and georeferenced a total of 744 plants in 2016 and 796 in 2017 ($n = 1540$ plants). At burnt areas, transects allowed us to investigate the effect of distance from the edge of the fire on the abundance of the two beetles and on the palm's fruit set; this distance was computed from the geographical coordinates with Quantum GIS v. 2.8 (Quantum GIS Team, 2013) software.

For each male plant, we counted the number of inflorescences and, in one inflorescence at anthesis, the abundance of *D. chamaeropsis* and the presence (2016) or number (2017) of *M. pallidulus* individuals during 3-min censuses. When part of the male inflorescence was not completely outside the prophyll, we carefully opened the prophyll to count all beetles. The insects are easily detected at the base of inflorescences, moving around the bracts that enclose them. We conducted the pollinator censuses between 0930 and 1600 h on sunny days with similar weather conditions across all sites. To assess whether the maturity of *C. humilis* inflorescences differed between burnt and control areas in a way that could affect other analyses, we classified the phenological stage of each sampled male inflorescence as either: (1) beginning of anthesis (many closed anthers and small amounts of pollen); (2) anthesis (yellow flowers producing pollen); and (3) end of anthesis (flowers turning brown with small amounts of pollen present). For female plants we counted the total number of inflorescences and tagged one of them (at anthesis) to estimate fruit set later in the season (see below). The number of *D. chamaeropsis* and *M. pallidulus* on female inflorescences was also recorded over 3 min. We then classified the phenological stage of the female inflorescence as closed (including partially open inflorescences) or open (inflorescences with only their lowest part inside the prophyll). We estimated fruit-set in late June, when fruits were developing, in all tagged inflorescences and by using the same methodology as described in the pollinator exclusion experiment.

Statistical analysis

We investigated the effects of the three pollination exclusion treatments and control treatment on palm fruit set (the proportion of drupes in relation to potential drupes) as a response variable using a GLM with a quasi-binomial error distribution to control for overdispersion and the logit link function in the *stats* package in R (R Core Team, 2017). Pollination treatment was included as a predictor variable and the number of experimental stems per plant (one or two) as a covariate. We then tested for differences in pollination treatments by post-hoc pairwise comparisons adjusted by Bonferroni's correction for multiple tests with the *multcomp* package in R (Hothorn et al., 2008). To explore potential differences in the pollen loads carried by *D. chamaeropsis* and *M. pallidulus* we fitted a GLM with number of pollen grains (with Poisson error distribution) as the response variable and insect species, plant sex and their interaction as predictors.

To test the effect of fire on *D. chamaeropsis* abundance on *C. humilis* we used a GLM with a negative binomial distribution and a log link function. We included as predictor variables fire treatment (unburnt vs. burnt), number of inflorescences per plant, plant sex, site, and the interaction between fire treatment and site. To analyse the effect of distance from the edge

of the fire on *D. chamaeropsis* abundance, we ran a similar GLM in which the distance of each plant from the fire edge was included as a predictor variable. Only plants inside the burnt areas ($n = 354$ in 2016 and $n = 401$ in 2017) were included in the distance model, and interactions that did not contribute significantly were removed from the final model. To test whether the effect of distance to the edge varied when considering the post-fire age categories, an additional GLM grouping the sites by post-fire age (1 year vs. 3 years post-fire) was also fitted.

We ran equivalent models for *M. pallidulus* abundance on the plant in 2017. To test for differences in the presence of *M. pallidulus* beetles on *C. humilis* plants in 2016, when only presence data were available, we used GLMs with a binomial error distribution (presence vs. absence) and a logit link function. For *M. pallidulus* presence, the fire and distance from the edge models included both the same predictor variables and sample sizes as the abundance models.

Before analysing fruit set data, we checked for differences in the proportions of the developmental stages of inflorescences in our samples from the burnt and unburnt areas. No differences were detected in male ($\chi^2 = 1.83$, d.f. = 2, $P = 0.40$, $n = 808$ plants) or female inflorescences ($\chi^2 = 0.41$, d.f. = 1, $P = 0.55$, $n = 732$ plants).

To test whether fire affected *C. humilis* fruit set, we used a generalized linear mixed model (GLMM) with a binomial error distribution and a logit link function. To account for overdispersion we included an observation-level random effect (Harrison, 2015) by running a GLMM with individual plant as a random factor using the *lme4* package in R (Bates et al., 2015). We included as fixed factors fire treatment (unburnt vs. burnt), site and their interaction. We added the number of female inflorescences as a covariate in the model after checking its independence from the predictors. To test whether these models were congruent with the three post-fire age categories, we ran additional GLMMs of the effects of fire on fruit set where sites were grouped by post-fire age (1, 2 and 3 years post-fire, with plant and site as random factors).

To investigate the response of *C. humilis* fruit set to the distance from the fire's edge we ran a GLMM with female plants from burnt areas. We included the distance of each plant from the fire's edge and site as fixed effects, new produced inflorescences as a covariate and plant as a random factor.

Because of the differences in the number of studied sites (two in 2016 and four in 2017), we fitted fire (unburnt vs. burnt) and distance models separated for each sampling year. Prior to model fitting, the two continuous predictors, distance inside the burnt areas and number of inflorescences, were mean-centred. To test for differences of fire treatment (burnt vs. unburnt) among the study sites (in all models with a significant interaction term), we conducted post-hoc pairwise comparisons for multiple test as described above (Bonferroni-adjusted). All analyses and graphical treatments were performed in R software version 3.4.2 (R Core Team, 2017).

RESULTS

Pollination exclusion experiment

The pollinator exclusion experiment confirmed that *C. humilis* is exclusively insect-pollinated, i.e. wind is not involved on

its pollination (see also Jácome-Flores, 2015). Inflorescences from the open controls produced a 12.15 % higher fruit set (28.30 ± 7.61 % mean fruit set, $n = 12$ plants) than any bagged treatment (Fig. 2, $P < 0.01$ in all comparisons, see Supplementary Data Table S1 for details). In addition, *C. humilis* inflorescences from the wind and small-insect pollination treatment showed a higher fruit set (16.15 ± 10.41 % mean fruit set, $n = 12$ plants) than those in the wind pollination (1.19 ± 2.32 % mean fruit set, $P < 0.001$, $n = 12$ plants, Fig. 2) and pollination exclusion treatments (0.87 ± 0.75 % mean fruit set, $P < 0.001$, $n = 12$ plants, Fig. 2). No significant differences were observed between inflorescences with wind pollination only and complete pollination exclusion bags ($P = 0.95$, $n = 12$ plants, Fig. 2, Table S1). The number of sampled stems (one or two) did not affect the palm fruit set (estimate = 0.155 ± 0.224 , t -value = 0.691 $P = 0.49$, $n = 12$ plants).

Insect pollen loads

Both *D. chamaeropsis* and *M. pallidulus* carried pollen from *C. humilis* male plants to female plants (Fig. 3). Only a very small proportion of the pollen transported to female inflorescences was not from *C. humilis* (0.86 % of that on *D. chamaeropsis* and 1.54 % of that on *M. pallidulus*). Insects collected at male inflorescences were carrying more grains than insects from female inflorescences (for *D. chamaeropsis*: 4180 ± 2041.4 vs. 826 ± 207.6 mean grains per individual; for *M. pallidulus*: 803 ± 202.1 vs. 387 ± 91.2 , estimate = 0.729 ± 0.007 , z -value = 103.1 , $P < 0.001$, $n = 80$ individuals per insect species, Fig S1). *Derelomus chamaeropsis* carried more pollen grains than *M. pallidulus* on both

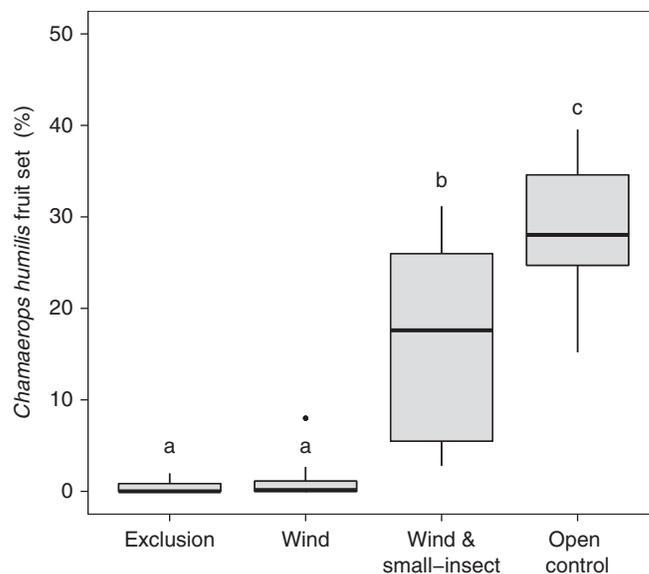


FIG. 2. *Chamaerops humilis* fruit set (proportion of developed drupes in relation to the potential drupes) of inflorescences with different pollinator exclusion treatments (pollination exclusion, wind pollination, wind and small-insect pollination, and open control). Different letters indicate statistically significant differences among treatments (for statistical values see Supplementary Data Table S1). In all figures boxplots show the median, quartiles and range of each response variable. Outliers are represented by filled circles.

male and female inflorescences (estimate = 0.760 ± 0.007 , z -value = 106.2, $P < 0.001$, $n = 80$, Fig. S1).

Post-fire changes in pollinators and fruit set

Burnt areas showed a marked reduction in *D. chamaeropsis* abundance compared with unburnt areas, and the weevil was almost absent in the first and second year after fire (88 % and 74 % average reduction, respectively; Fig. 4). Weevil numbers were significantly lower inside the burnt areas in the two most recently burnt sites (Xàbia and Carcaixent), and in Tivissa 2 and 3 years after the fire (Fig. 4, Table 2; see Tables S2 and S3). Male plants had more weevils than female plants, both outside and inside the burnt areas (mean number of weevils per male inflorescence = 4.70 ± 5.93 at controls vs. 1.85 ± 3.12 at burnt areas, and 0.95 ± 1.67 at controls vs. 0.58 ± 1.34 weevils per female inflorescence at burnt areas; $n = 808$ males and $n = 732$ females; Table 2). Plants from burnt sites in 2017 showed a negative relationship between weevil abundance and distance from the fire's edge ($P < 0.001$, Table 2 and Table S3 for full details). However, the posterior model grouping of the sites by post-fire age (1 year vs. 3 years) revealed that this effect occurred only in palms from recently burnt sites (interaction between distance and 1-year post-fire age, estimate = -0.009 ± 0.002 , t -value = -4.25 , $P < 0.001$, $n = 401$ plants at Xàbia and Carcaixent sites, Fig. 5).

Burnt and control areas showed similar numbers of *C. humilis* plants with *M. pallidulus* beetles (46.7 % in burnt and 51.4 % in unburnt areas). For 2017 (the year with quantitative data for both insect species), the number of *M. pallidulus* individuals per inflorescence was also similar after the fires (unburnt vs. burnt: $P = 0.33$, $n = 796$ plants, Table S3 and Fig. S2). That is, neither fire nor distance effects were detected on the sap beetle's abundance on *C. humilis* plants in 2017, nor on its presence in 2016 (Table 2, see Tables S2 and S3 for statistics).

Despite lower *D. chamaeropsis* abundance, fruit set decreased only in the recently burnt Xàbia and, to a less extent, in Tivissa 2 years after the fire (Fig. 6, Table 2, see Table S4 for details). We did not detect significant differences in fruit set 3 years after the fires, or any effect of distance from the fire's edge (Fig. 6, Table 2, see Tables S2 and S3 for statistics). The GLMMs on the

effects of fire on fruit set in which sites were grouped by post-fire age also showed that fruit set was only negatively affected 1 year post-fire (unburnt vs. burnt: estimate = 0.72 ± 0.175 , z -value = 4.16, $P < 0.001$, $n = 196$ plants).

DISCUSSION

Our study highlights the importance of pollinator replacement as a way of providing resilience to disturbance in plant–pollinator interactions, even in a plant with a limited number of pollinators. Although we recorded a marked decline in numbers of the weevil pollinator after fires, *C. humilis* fruit set was barely affected. A temporary replacement by the sap beetle *M. pallidulus*, an effective pollinator that has not been previously recognized as such (Herrera, 1989; Anstett, 1999; Dufay and Anstett, 2004), explains the fast recovery. The abundance of this beetle was unaffected by the fires and provided resilience to the pollination process. As a result, fires did not alter the palm's reproduction in most study sites and fruit set showed a complete recovery in only 3 years.

In unburnt conditions, visits by the sap beetle *M. pallidulus* produced a mean 16.15 % fruit set compared to 28.30 % in the controls also visited by *D. chamaeropsis*. Differences between these two treatments are probably explained by the higher amount of pollen carried by *D. chamaeropsis*. This is consistent with the known importance of the weevil as a pollinator (Anstett, 1999; Dufay and Anstett, 2004), although further research is needed to evaluate the possible differences in pollination efficiency between the two species. In contrast to the unburnt areas, our study suggests that at the most recently burnt sites (where the weevil was virtually absent), *C. humilis* pollination relies on the sap beetle (which was not affected by fire), and this replacement may last until the weevil recolonizes the burnt sites. In addition, pollen loads of both insects consisted mainly of *C. humilis*, suggesting a marked specialization (at least while the plant is flowering) which may avoid potentially negative effects of heterospecific pollen deposition (Thomson et al., 1982; Ashman and Arceo-Gómez, 2013).

Fires had contrasting effects on the presence and abundance of the two beetle species, with a stronger negative effect on *D. chamaeropsis* than on *M. pallidulus*. This striking weevil decline is consistent with earlier evidence on the negative effects of wildfires on other weevil species from temperate zones (Moretti et al., 2004). The life cycle of *D. chamaeropsis* is completely dependent on old dry *C. humilis* inflorescences, within which female individuals lay their eggs and the weevil develops (Anstett, 1999; Dufay and Anstett, 2004). Most old inflorescences burn in wildfires, and we did not detect any *D. chamaeropsis* larvae in a preliminary sampling of the palm immediately after fire (unpubl. data). Experimental tests on a similar interaction between butterflies and cycads have shown that fire temperatures can kill all pupae growing inside fronds of the host plants (Thom et al., 2015). In all such cases, the burnt area must be recolonized from surrounding populations, which can result in spatial gradients in insect abundance and in turn in their interactions inside the burnt area (Knight and Holt, 2005). Consistently, we observed a significant decline in weevil abundance on *C. humilis* plants with increasing distance to the edge of the burnt area in the first post-fire year, followed

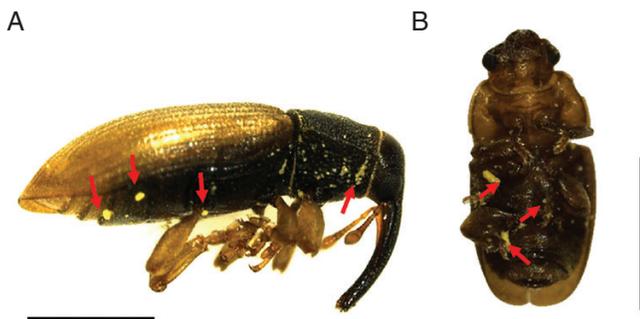


FIG. 3. Pollen loads carried by the main flower visitors of *Chamaerops humilis*: (A) the weevil *Derelomus chamaeropsis* (Curculionidae) and (B) the sap beetle *Meligethinus pallidulus* (Nitidulidae). Red arrows indicate pollen grains. Scale bars = 1 mm.

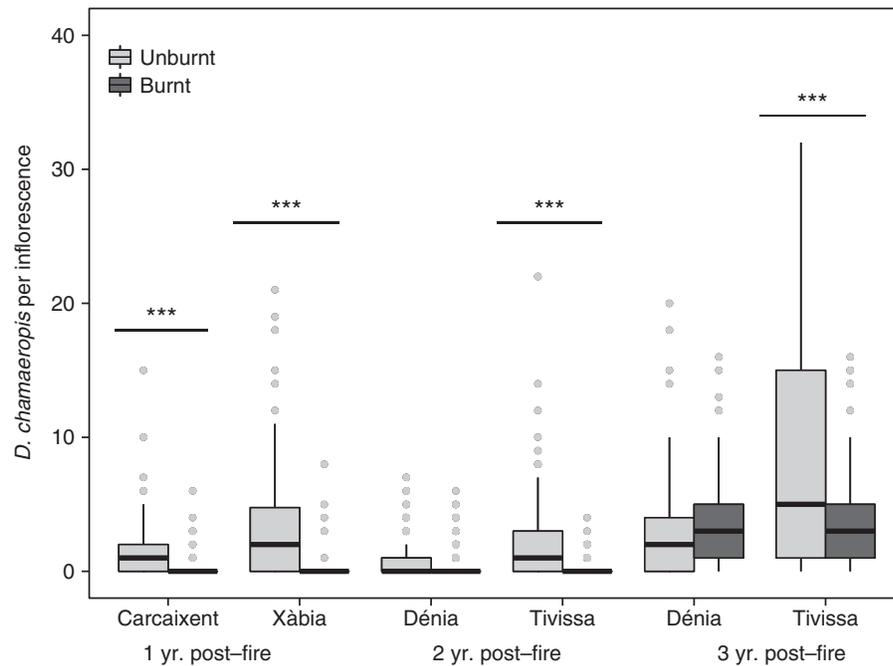


FIG. 4. Number of *Derelomus chamaeropsis* individuals per inflorescence in each study site in unburnt and burnt areas for three post-fire ages. Asterisks indicate a significant decrease of *Derelomus* individuals at the burnt area at that study site. *** $P < 0.001$.

TABLE 2. Effects of fire (unburnt vs. burnt areas) and distance (to the fire edge) on the number of *Derelomus chamaeropsis* weevils, *Meligethinus pallidulus* beetles and *Chamaerops humilis* fruit set; for each response variable, the table shows the results of the GLMs and GLMMs on the effects of fire or distance inside the fire

Sampling year	Response	Model	Predictor variables					
			U. vs. B.	Distance	Inflorescences	Site	Plant sex	U. × Site vs. B. × Site.
2016	<i>D. chamaeropsis</i>	Fire	**	—	***	** [T]	***	***
		Distance	—	n.s.	*	** [T]	***	—
2016	<i>M. pallidulus</i>	Fire	n.s.	—	n.s.	***[T]	***	n.s.
		Distance	—	n.s.	n.s.	**[T]	***	—
2016	Fruit set	Fire	n.s.	—	n.s.	n.s.	—	**[T]
		Distance	—	n.s.	n.s.	n.s.	—	—
2017	<i>D. chamaeropsis</i>	Fire	n.s.	—	*	***[X], **[C]	***	***[T], ***[X], ***[C]
		Distance	—	***	n.s.	***[X], ***[C]	***	—
2017	<i>M. pallidulus</i>	Fire	n.s.	—	**	n.s.	***	n.s.
		Distance	—	n.s.	*	n.s.	***	—
2017	Fruit set	Fire	n.s.	—	n.s.	***[T], ***[X]	—	***[X]
		Distance	—	n.s.	n.s.	***[T], ***[X], *[C]	—	—

Full models for fire effects included the two-way interaction ('×') between fire treatment (U. vs. B. = unburnt vs. burnt) and study site. All models included the number of inflorescences, site and plant sex (only for models on *D. chamaeropsis* and *M. pallidulus* abundances) as predictor variables. Names in square brackets represent the study site with statistically significant effects (T = Tivissa, X = Xàbia, C = Carcaixent). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = non-significant. For detailed statistics see Supplementary Data, Tables S2 (year 2016) and S3 (year 2017) and Table S4 for post-hoc pairwise comparisons of the interaction between fire treatment and study site.

over the years by an increase in the number of weevils in the depleted parts of the burnt area.

Meligethinus pallidulus also appears to be specialized on *C. humilis* pollen at least during the plant's flowering season. Little is known about the biology of this sap beetle, but its life cycle is likely to depend on *C. humilis* (Ponel and Lemaire, 2012; Audisio et al., 2014). We have not detected any *M. pallidulus* larvae inside the palm's inflorescence: an examination of complete old inflorescences from 180 male plants at three sites only

revealed the presence of *D. chamaeropsis* and some Lepidoptera (data not shown). There are three possible explanations for the rapid post-fire recovery of *M. pallidulus*. First, *M. pallidulus* larvae may develop inside the palm's stem. Adults are often seen inside the stems (Fig. S3) where they could survive fires thanks to the protection by the fibrous bark-like structure (e.g. Brennan et al., 2011). The second possible explanation is that the higher densities of *M. pallidulus* on the plant, compared to the weevil in the unburnt sites, may allow faster recolonization.

This is consistent with a previous study where high numbers of sap beetles contributed to ensure a tropical palm set fruit even in highly fragmented zones (Aguirre and Dirzo, 2008). Finally, larger dispersal distances by the sap beetle might also be a mechanism explaining its fast recolonization from the surrounding areas (Saint-Germain et al., 2004). Further studies are needed to determine whether either of these routes to post-fire recovery is driving the sap beetle's response. Regardless, the fast recovery of *M. pallidulus* appears to maintain *C. humilis* pollination after fires. This, together with quick resprouting by the palm (Paula et al., 2009), and its ability to flower in the

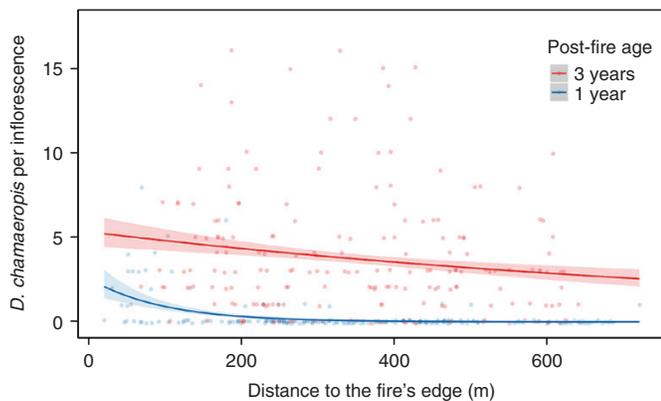


FIG. 5. The relationship between *Derelomus chamaeropsis* weevils on *Chamaerops humilis* with the distance to the fire edge at two different post-fire ages in 2017 ($n = 401$ plants). The negative effect of distance to the edge on the number of weevils per plant was significant only at 1 year post-fire (Xàbia and Carcaixent sites, blue solid line). Dark shading indicates 95 % confident intervals.

spring following a fire contribute to the high success of the palm in fire-prone environments. In addition, the quick availability of fruits at burnt sites may have broader implications for ecosystem resilience, such as maintaining frugivorous vertebrates and accelerating the post-fire recolonization of plants in fire-prone landscapes. Fruit dispersers such as badgers, foxes and deer can also transport seeds of other species (Herrera, 1989; Fedriani and Delibes, 2011; Castañeda et al., 2017) from the surrounding areas, which ultimately may promote the arrival of seeds in freshly burnt sites.

However, fire did decrease palm fruit set in two sites. This reduction in the Xàbia site during the first post-fire year could be related to the marked significant reduction in weevil abundance together with the low numbers of the sap beetles (although not significant) at the burnt area (Table 2, Fig. S2). In Tivissa 2 years after the fire, weevil abundance was very low; *M. pallidulus* was present but we lack information on its abundance and thus we cannot fully explain the reduction of fruit set in this case. Abiotic factors not measured here, such as soil nutrient and water availability, could also alter the plant reproductive success after fire (Carbone and Aguilar, 2017) and explain some of this variation. While fire may reduce *C. humilis* fruit set in some instances, this is not a general outcome, and only 3 years after the fires effects on fruit set were no longer detectable.

The frequent asymmetric nature of plant–pollinator interactions (specialist species interact with generalist ones) provides resilience to disturbance (Ashworth et al., 2004; Vázquez and Aizen, 2004). This has led to the prediction that disturbances will have strong consequences on symmetric pollination interactions because of the reciprocal dependence between the mutualistic partners. However, empirical studies assessing

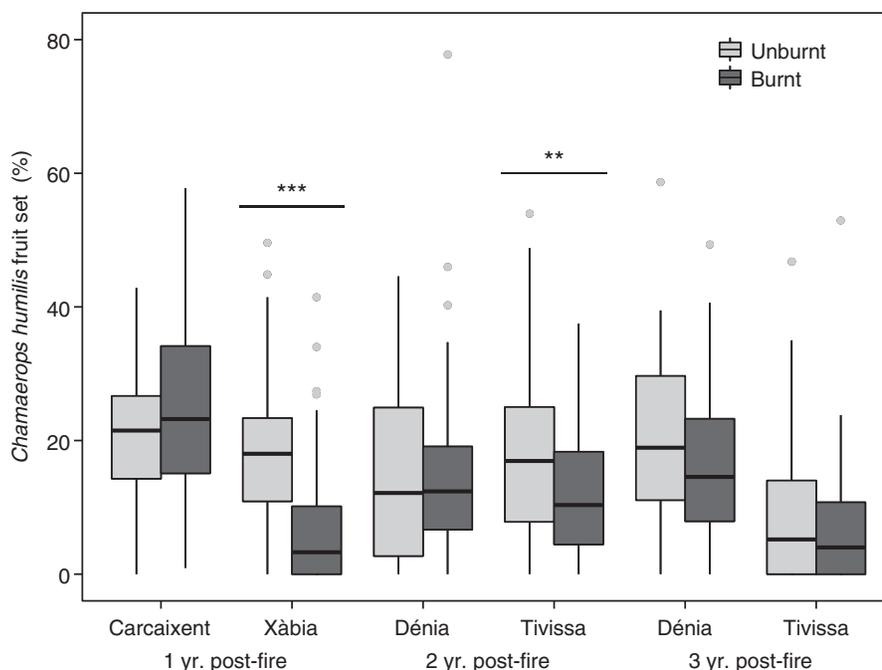


FIG. 6. *Chamaerops humilis* fruit set (percentage of developed drupes in relation to total number of flowers produced, i.e. potential drupes) at each study site in burnt and unburnt areas during the two years of the study and the three post-fire ages. Asterisks indicate a significant decrease of *C. humilis* fruit set at the burnt area of that study site. $**P < 0.01$ and $***P < 0.001$.

the reproductive costs of disturbance for plants engaged in obligatory pollination systems are still scarce (Bronstein and Hossaert-McKey, 1995; Lemke and Porembski, 2013; Suchan *et al.*, 2015). Some of these studies have shown that these highly specialized interactions can be also resilient if the species involved have traits that confer a rapid ability to respond (Bronstein and Hossaert-McKey, 1995) or if the plant has additional (but overlooked) non-nursery pollinators at disturbed areas as we show here (Suchan *et al.*, 2015).

This resilience could be more frequent in specialized interactions from disturbance-prone environments, such as fire-prone ecosystems, as plants and animals in these areas have evolved persistent traits under recurrent disturbances (Schütz *et al.*, 1999; Keeley *et al.*, 2011; He *et al.*, 2012; Castellanos *et al.*, 2015; Pausas and Parr, 2018). Yet only a few studies have assessed the effects of fire on specialized pollination interactions. For instance, the higher seed set levels at early post-fire ages in fire-stimulated flowering orchids depended on specialist oil-collecting bees for reproduction (Pauw, 2007). In contrast, old fires were positively related to pollinator visitation in a specialist Australian orchid (Brown *et al.*, 2016; Brown and York, 2017a). These studies, together with our results, support the view that different species reach a reproductive optimum at different post-fire succession stages (Moretti *et al.*, 2006, 2009; Lazarina *et al.*, 2016). It is also noteworthy that other fire characteristics such as fire frequency or the diversity of fire histories at the landscape level ('pyrodiversity') can also alter the outcome of plant–pollinator interactions at different spatial scales (Brown *et al.*, 2016; Ponisio *et al.*, 2016; Brown and York 2017b; Carbone and Aguilar, 2017). The success of highly specialized pollination systems in floras from different fire-prone regions (Gottsberger, 1986; Johnson and Steiner, 2003; Johnson, 2010) calls for further research on the idea that resilience is common in such environments.

CONCLUSIONS

The resilience of plant communities to face disturbances may rely, at least in part, on the ability of reorganizing their mutualistic interactions, which can offset the indirect negative effects on plant reproduction. Previous studies suggested that a high diversity of interacting species may ensure a generalist plant species' success under fluctuating environmental conditions (Albrecht *et al.*, 2012; Bartomeus *et al.*, 2013). Such high diversity may allow for pollinator replacement and thus the resilience of the reproduction after disturbance (Potts *et al.*, 2001). Here we provide field evidence of an unexpected pollinator replacement after fire in a specialized pollination system. To what extent post-fire pollination replacement is common in other specialized systems remains to be studied. Overall, the current fire regime changes in many ecosystems call for further research on the effects of fire on the dynamics of plant–animal interaction assemblages and ultimately on the implications for plant reproduction. Only with this research we can really evaluate the impact of future fire regimes on biodiversity.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: Post-hoc

pairwise comparisons of regression coefficients among pollinator exclusion treatments. Table S2: Detailed statistical results of the GLMs and GLMMs of the effects of fire and distance from the fire's edge on the number of *Derelomus chamaeropsis*, presence of *Meligethinus pallidulus* and *Chamaerops humilis* fruit set in 2016. Table S3: Detailed statistical results of the GLMs and GLMMs of the effects of fire and distance from the fire's edge on the number of *Derelomus chamaeropsis* and *Meligethinus pallidulus* and on *Chamaerops humilis* fruit set in 2017. Table S4: Post-hoc pairwise comparisons of regression coefficients of the interaction between fire treatment and study site from the models of fire effects. Figure S1: Number of *Chamaerops humilis* pollen grains carried per individual by the two pollinator species. Figure S2: Number of *Meligethinus pallidulus* individuals per inflorescence at each study site. Figure S3: *Meligethinus pallidulus* inside and outside the prophyll of a male inflorescence of *Chamaerops humilis* from one of the burnt areas.

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