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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

# Fires can benefit plants by disrupting antagonistic interactions

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**Abstract** Fire has a key role in the ecology and evolution of many ecosystems, yet its effects on plant–insect interactions are poorly understood. Because interacting species are likely to respond to fire differently, disruptions of the interactions are expected. We hypothesized that plants that regenerate after fire can benefit through the disruption of their antagonistic interactions. We expected stronger effects on interactions with specialist predators than with generalists. We studied two interactions between two Mediterranean plants (*Ulex parviflorus, Asphodelus ramosus*) and their specialist seed predators after large wildfires. In *A. ramosus* we also studied the generalist herbivores. We sampled the interactions in burned and adjacent unburned areas during 2 years by estimating seed predation, number of herbivores and fruit set. To assess the effect of the distance to unburned vegetation we sampled plots at two distance classes from the fire perimeter. Even 3 years after the fires, *Ulex* plants experienced lower seed damage by specialists in burned sites. The presence of herbivores on *Asphodelus* decreased in burned locations, and the variability in their presence was significantly related to fruit set. Generalist herbivores were unaffected. We show that plants can benefit from fire through the disruption of their antagonistic interactions with specialist seed predators for at least a few years. In environments with a long fire history, this effect might be one additional mechanism underlying the success of fire-adapted plants.

## Introduction

Fire is one of the most common disturbances worldwide and can play an important role in the ecology and evolution of many ecosystems (Pausas and Keeley 2009). In environments with a long fire history, such as tropical savannas and Mediterranean ecosystems, fire structures communities and landscapes (Verdú and Pausas 2007; Keeley et al. 2011; Dantas et al. 2013). The effects of fire on plants are relatively well-known (Bond and Van Wilgen 1996; Keeley et al. 2012) and information on the effects of fire on animal populations is also increasing steadily (Swengel 2001; Izhaki 2012; New 2014). Studies on the role of fire in plant–animal interactions have been largely focused on mammal herbivory (e.g., Fuhlendorf et al. 2009; Wan et al. 2014) and, to a lesser extent, on seed predation (e.g., Bond 1984; Andersen 1988; Broncano et al. 2008). However, less is known about how fires disrupt plant–insect interactions and the implications for the plants (Vickery 2002; Knight and Holt 2005; Dafni et al. 2012).

Both antagonistic (e.g., herbivory) and mutualistic (e.g., pollination) interactions between plants and insects are crucial components of natural ecosystems and can determine ecological and evolutionary processes (Herrera and Pellmyr 2002). In ecosystems where wildfires are historically

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recurrent, many plant species are capable of quickly recovering via resprouting or recruitment from a fire-resistant seedbank (Pausas et al. 2004) and reproduce shortly after the fire. In contrast, fires can directly cause drastic declines in many insect populations, whose recovery then depends on the fire regime and intrinsic characteristics like movement capacity (Swengel 2001; Moretti et al. 2006). Because the different interacting species are likely to respond to fire in varying ways, disruptions of the plant–insect interactions are expected. The dynamics of these disruptions and the postfire recovery of the interactions could, therefore, have strong consequences for plant populations and constitute important selective pressures for species living in fire-prone environments.

The effects for plants may be different depending on whether fire disrupts mutualistic interactions, potentially decreasing reproductive success, or antagonistic interactions such as herbivory and seed predation. Fires can for example increase seed predation and herbivory when generalist insects are involved (Andersen 1988; Radho-Toly et al. 2001; Lopes and Vasconcelos 2011). However, there is also evidence of a postfire decrease in insect herbivory in different ecosystems (Whelan and Main 1979; Auld and O'Connell 1989; Vickery 2002; Knight and Holt 2005). In the latter cases, plants could benefit through a release from negative interactions that limit their performance (Hendrix 1988). The reduction of negative effects can be stronger if the interactions involve seed predators, and this can be particularly beneficial for plants in which the success of their first life stages depends on fire.

The consequences of a fire-driven disruption of antagonistic interactions on plant populations will depend, among other factors, on two important interrelated aspects. First, postfire changes in the existing habitat can have a greater impact on species that are tightly dependent on specific habitat characteristics like specialists, compared to generalists (Ewers and Didham 2006). For instance, herbivory and seed predation are often exerted by highly specialized phytophagous insects which interact only with one or a few host plants (Ehrlich and Murphy 1988; Jaenike 1990). Consequently, the alteration of their host plants may lead to changes in their abundance and distribution (Larsson et al. 2000). The recolonization of burnt areas by generalist animals might, therefore, be faster than by specialists, because the specialist's mobility into the interior of the burnt may be restricted to the presence and the regeneration of their only host. Second, the distance to unburned vegetation might also have an impact on the speed of recolonization and, therefore, on the duration of the disruption, which can result in spatial variation in the interaction from the edge towards the interior of the burned area. The contrast between specialists and generalists may be even stronger in large fires where species have to migrate long distances to reach the center of the burned area. A stronger disruption of specialized interactions compared to generalist ones would thus be expected, and this effect could be exacerbated as one moves from the edge to the center of the fire. While some previous studies show that fire may modify the plant–insect interaction, less is known about the implications for the plant's reproductive performance (e.g., Whelan and Main 1979; Auld and O'Connell 1989; Vickery 2002), and particularly on how these implications differ depending on the level of specialization of the insect.

Our hypothesis is that plants that quickly regenerate after fire may additionally benefit from it because fire disrupts antagonistic interactions, and that this effect will be exacerbated with the distance to the unburned vegetation. To test it, we studied two interactions between plants and their specialist seed predators after recent wildfires in Mediterranean shrublands of eastern Spain: (1) the Mediterranean gorse *Ulex parviflorus* and its seed predator, the weevil *Exapion fasciolatum*; and (2) the branched asphodel *Asphodelus ramosus* and the specialist mirid bug *Horistus orientalis,* together with other generalist insects. In the two systems the life cycles of the specialist insects depend entirely on their host plants. We expected that fires would have strong negative effects on the local populations of both specialist predators, and would in turn benefit the host plants by reducing seed predation.

## Materials and methods

### Plant–insect interaction I: *Ulex parviflorus–Exapion fasciolatum*

The Mediterranean gorse, *Ulex parviflorus* Pourr. (Fabaceae) is a spiny perennial shrub from the western Mediterranean Basin. It can live up to 25 years (Baeza and Vallejo 2006) and, as observed in this study, individuals can reach their mature stage as soon as 2 years after fire. One or two (occasionally more) seeds develop inside small pods and are dispersed explosively at the beginning of the summer. A preliminary analysis suggested that the variance in the number of seeds per pod is not related to contrasted fire regimes (mean number of seeds/pod = 1.29 and 1.34 in populations growing under high or low fire frequency, respectively, $N = 3206$ pods examined). *U. parviflorus* is common in fire-prone Mediterranean shrublands where it recruits massively after fire, when high soil temperatures break seed dormancy and induce germination (postfire obligate seeder; Paula et al. 2009; Moreira et al. 2010; Moreira and Pausas 2012).

*Ulex parviflorus* seeds are attacked by the weevil *E. fasciolatum* Wagner (Brentidae: Apioninae). Information on this species is scarce, but *Exapion* species are specialist predators of the Genisteae tribe (Fabaceae;

**Table 1** Fire location name, year of fire occurrence and sampling years for each study system: (a) *U. parviflorus* and the specialist weevil *E. fasciolatum* and (b) *A. ramosus* and the specialist bug *H. orientalis* and its generalist herbivores

| System | Fire location | Year | Sampling years |
|---|---|---|---|
| *U. parviflorus–E. fasciolatum* | Cortes | 2012 | 2014 and 2015 |
| | Andilla | 2012 | 2014 and 2015 |
| *A. ramosus*-herbivores | Cortes | 2012 | 2014 and 2015 |
| | Segorbe | 2014 | 2014 and 2015 |

Alonso-Zarazaga 1990), including *Ulex* (Barat et al. 2007; Tarayre et al. 2007). In the closely related *Exapion ulicis*–*Ulex europaeus* interaction, weevil predation can damage up to 90 % of the gorse pods and may explain phenological shifts in the plant to reduce predation impacts (Barat et al. 2007; Tarayre et al. 2007). The weevil's life cycle depends entirely on the host plant. In early spring, females lay their eggs inside the gorse ovaries or small green pods, where larvae and pupa develop while feeding on the seeds. Adults emerge with ripe pod dehiscence. *U. parviflorus* pods can also contain a parasitoid wasp (*Eurytoma* sp.) feeding on the larvae and pupae of *E. fasciolatum*.

### Plant–insect interaction II: *Asphodelus ramosus–Horistus orientalis*

*Asphodelus ramosus* L. (=*A. aestivus* Brot., Liliaceae) is a Mediterranean geophyte widely distributed along the Mediterranean basin (Lifante 1996). It has a short rhizome surrounded by tubers and a basal rosette of leaves that produces a branched flowering scape. Thanks to the resprouting capacity from the rhizome, this species is favored by heavy grazing and recurrent fires (Pantis and Margaris 1988); in fact, it flowers massively in burned areas.

*Horistus orientalis* Gmelin (=*Capsodes lineolatus* Br., Hemiptera: Miridae) is a phytophagous bug that feeds on *A. ramosus*. Members of the mirid family exhibit a high degree of host-plant specificity (Cassis and Schuh 2012) and in our study region this species has never been confirmed feeding on other plants (Luis Vivas pers. comm). Mirids often develop synchronously with the plant, from the deposition of the eggs within the scape tissues, until adult emergence after the nymph stage (Wheeler 2001; Cassis and Schuh 2012). Published information about *H. orientalis* is very limited, but our observations suggest that its entire life cycle occurs on the plant, as in the closely related bug *Capsodes infuscatus*. The eggs are deposited inside the inflorescence stalk in the spring and adults disperse the next spring (Ayal and Izhaki 1993; Izhaki et al. 1996). Both nymphs and adults feed on leaves and especially on flowers and fruits. In the case of *C. infuscatus*, the

damage produced on *A. ramosus* can reach 100 % of fruit loss (Ayal and Izhaki 1993). *A. ramosus* is also attacked by generalist herbivores; we mainly observed two phytophagous beetles from the subfamily Cetoniinae, *Tropinota squalida* Scop. and *Oxythyrea funesta* Poda, and the bug *Carpocoris fuscipinus* Boh. (Pentatomidae), among others.

### Study sites and sampling

Each interaction was studied during two consecutive years in two burned locations from different wildfires in Eastern Spain (Valencia; see Table 1). The region shows a typical Mediterranean climate with frequent fires (Pausas 2004; Pausas and Paula 2012). To study the effect of fire on the interactions we sampled plots inside each burned location plus unburned adjacent (control) plots where no fires have been registered for at least 20 years. Unburned plots were carefully chosen to be representative of the pre-fire conditions (e.g, same plant species composition, dominant species and soil characteristics), and when possible, close to the to fire perimeter. The same control and burned plots were sampled during the 2 years of the study when possible. To assess the effect of the distance to unburned vegetation on the interactions, plots were assigned to three different categories according to their distance to the fire's perimeter: (a) control plots in the adjacent unburned areas ("Unburned"), (b) plots located inside the burned area and up to 500 m (mean 268) from the fire perimeter ("Edge") and (c) plots at more than 500 m (mean 1199, maximum 2400) from the fire perimeter ("Center"). Plots at burned areas were carefully selected to avoid the proximity of unburned patches. Distances were estimated using geographic information tools and digital maps provided by the regional government of Valencia.

Seed predation on *U. parviflorus* was measured in 48 plots in two locations where large wildfires (of more than 20,000 ha each) had occurred in the summer of 2012: Cortes de Pallás (hereafter, Cortes) and Andilla, both in the province of Valencia (Table 1). Before the fires, all plots were Mediterranean shrublands dominated by *Rosmarinus officinalis*, *U. parviflorus*, several *Cistus* species and *Quercus coccifera*. Field work was carried out between late March and June in 2014 and 2015 and corresponded to the first two postfire flowering years for the newly recruited individuals of *U. parviflorus*. The sampling included 34–35 burned plots and 13–14 plots in the adjacent unburned areas (see Table S1 in Supplementary Material for details on plots at each fire location). At each plot, 400 mature pods were collected from 10 haphazardly chosen *U. parviflorus* plants (40 pods per plant), separated from each other by at least 5 m. The 400 pods from Andilla's burned plots in 2014 were collected from 20 plants (20 per plant) because fruit production per plant was lower in that location. We

chose a fixed number of pods per plant to estimate the levels of seed predation as opposed to attempting to quantify whole-plant production, a difficult task given the massive and extended flowering period of *U. parviflorus*. Overall the total number of pods sampled was 18,370 in 2014 and 19,265 in 2015.

The content of each pod was observed at the laboratory under a stereo-microscope. The presence of the weevil at larva, pupa or adult stage was recorded in each pod. When a parasitoid wasp was observed inside the pod, it was also counted as predated, i.e., we assumed that wasps had emerged from a weevil larva (Barat et al. 2007). We used the proportion of predated pods as a measure of the effect of the seed predator on the fitness of the plant. This method directly estimates weevil predation within each pod and allows to differentiate their effect from other predispersal predators as mentioned above (Barat et al. 2007).

The study on *A. ramosus* was conducted in Cortes and in a second smaller wildfire that occurred in February 2014 in Segorbe (province of Castellón; Table 1). Sampling was performed during spring when *A. ramosus* was already in bloom, and included a total of 15 plots in 2014 (9 burned and 6 unburned plots) and 14 in 2015 (8 burned and 6 unburned plots, for details see Table S2 in Supplementary Material). At each plot, the presence and activity of the specialist bug *H. orientalis* and the most abundant herbivores (Cetoniinae and Pentatomidae) were recorded on 50 haphazardly chosen *Asphodelus* plants separated from each other by at least 5 m; censuses were conducted between 10:00 and 16:00 hours. Other generalist herbivores were observed only rarely and were thus not included in the analyses. The number of branches, floral buds and flowers were also recorded for each plant. At the end of the flowering season (May–June) we collected ripening fruits from all plants and counted healthy seeds in the laboratory in all plots within the burned areas. The proportion of fruits in relation to the number of flowers produced (fruit set) was considered an indicator of reproductive success and was analyzed with respect to the presence of the seed predators on the plant (see below). We used fruit set as a proxy for reproductive success because it corrects for variation in plant size as opposed to using the absolute number of fruits or seeds produced per plant. Although fruit set is not a direct measure of the plant damage, it may reflect the total effects of the different feeding habits of the insects including green parts of the plant and also fruits. In fact there is evidence of a strong negative relationship between plant fruit set and the bug's abundance in the closely related *Asphodelus aestivus–Capsodes infuscatus* interaction (Ayal and Izhaki 1993; Izhaki et al. 1996). Fires could also affect other factors linked to plant fruit set such as resource availability and pollination. We expect a limited effect of pollination, because this species has a generalized pollination system (Lifante 1996; Lázaro et al. 2016) and flying pollinators tend to recover quickly after fires (Potts et al. 2003).The increase in resources often associated with post-fire environments could also have positive effects on fruit production. However, we did not find a difference either in the number of flowers nor in the absolute seed production between burned and unburned sites (see "Results"), suggesting a limited relevance of the potential changes in resources.

## Statistical analysis

To examine whether seed predation on *U. parviflorus* at the plant level differed between burned and unburned plots, we used a generalized linear mixed model (GLMM), with a binomial error distribution. For each year of sampling, the GLMM included the burned vs unburned treatment as a fixed factor and plot nested within locality as random factor. The same approach was used to test whether seed predation varied between Edge and Center zones (i.e., within the burned area).

To test whether the number of specialist *H. orientalis* individuals differed between *A. ramosus* plants from burned and control plots, we used a similar GLMM model structure as above, in this case with a Poisson error distribution. We also used the same model structure to test for differences in the number of generalist herbivores (Pentatomidae plus Cetoniinae), in the total herbivores (*H. orientalis* and generalists together) and in the number of flowers and seeds produced per plant. We then tested for distance effects in the number of the three insect groups (specialist, generalist and total) by fitting a GLMM to the distance class variable (Edge vs Center). To evaluate to what extent the variability observed in herbivores in the burned zone correlates with the variability in plant fitness, we fitted the fruit set against the number of *Horistus* bugs using a GLMM with a binomial error distribution. For this, we used the number of *Horistus* bugs in relation to the number of flowers of each plant, and tested it with the nested design mentioned above to account for plot variability. We used a similar model with the number of total herbivores (also corrected by the number of flowers). For both studied interactions we also fitted a GLMM that included the combined data of both sampling years and the year as a random factor. Overdispersion was tested and corrected when necessary. All models were run with 'lme4' package in R (Bates et al. 2015).

## Results

*Ulex* plants from burned plots showed a much lower proportion of predated pods by their specialist seed predator (<5 %) than the adjacent unburned plots (>15 %; Table 2;

**Table 2** Results from generalized linear mixed models of the effects of fire on seed predation and herbivory in two Mediterranean plants (*U. parviflorus* and *A. ramosus*)

| | Test | 2014 | | | 2015 | | | 2014 and 2015 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | N | Estimate | P | N | Estimate | P | N | Estimate | P |
| *Ulex parviflorus* | | | | | | | | | | |
| Predated pods | U vs B | 578 | −1.46 | *** | 469 | −1.73 | *** | 1047 | −1.60 | *** |
| | E vs C | 480 | −0.56 | ** | 334 | – | ns | 814 | −0.45 | * |
| Specialist weevil | U vs B | 578 | −1.38 | *** | 469 | −1.42 | *** | 1047 | −1.40 | *** |
| | E vs C | 480 | −0.47 | ** | 334 | – | ns | 814 | −0.45 | ** |
| *Asphodelus ramosus* | | | | | | | | | | |
| Specialist bug | U vs B | 729 | −1.90 | *** | 686 | −1.60 | ** | 1415 | −1.77 | *** |
| | E vs C | 433 | – | ns | 400 | – | ns | 833 | – | ns |
| Generalist herbivores | U vs B | 729 | – | ns | 686 | – | ns | 1415 | – | ns |
| | E vs C | 433 | – | ns | 400 | – | ns | 833 | – | ns |
| Total herbivores | U vs B | 729 | −0.38 | * | 686 | −1.19 | ** | 1415 | −0.61 | ** |
| | E vs C | 433 | – | ns | 400 | – | ns | 833 | – | ns |

For each response variable and year of study, we first compared plants from unburned vs burned (U vs B) plots, and then for the burned plots, we compared edge vs center plots (E vs C). For *U. parviflorus*, the models test for differences in the incidence of seed predation by the weevil *E. fasciolatum* and the number of *E. fasciolatum* weevils. For *A. ramosus*, response variables were the number of *H. orientalis* (specialist bug), the number of generalist herbivores, and the total number of herbivores. The table shows the sample sizes (*N*) and, for each significant model, the estimated parameter for the fixed effects (Estimate) and the associated significance (*P*, *ns* not significant; * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001). Estimate refers to the coefficient of burned (in relation to unburned) and of the center (in relation to the edge)

**Fig. 1** Predation rate of *U. parviflorus* pods in unburned plots (*grey box*) and burned plots (*white boxes*, "Edge" and "Center") for 2 years of sampling. *N* = 13 and 14 "Unburned" plots, and *N* = 15 and 14 "Edge" plots in 2014 and 2015 respectively. *N* = 20 for "Center" plots on both years
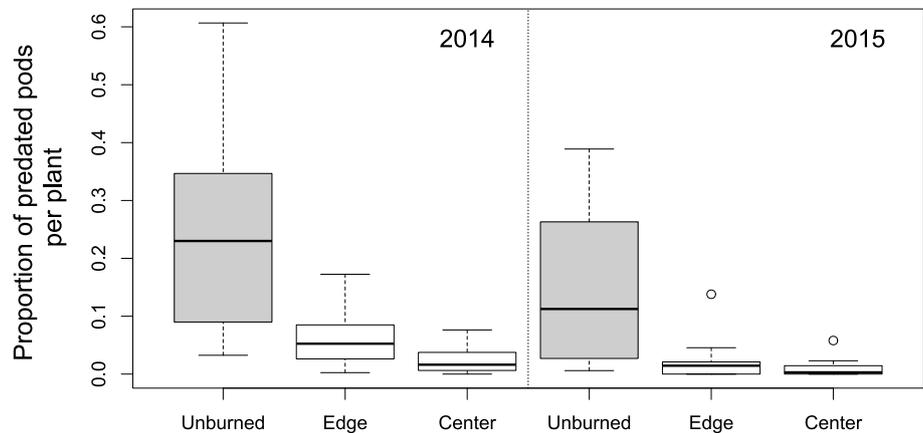


Fig. 1 and Table S1 in Supplementary Material). The number of *Exapion* weevils was also lower in burned plots and, unexpectedly, decreased on the second sampling year (Tables 2, S1). The predation of *Ulex* pods and the number of weevils decreased from the Edge to the Center of the burnt; this decrease was significant for 2014 and for the overall period, but not for 2015 (Table 2; Fig. 1 and Table S1 in Supplementary Material).
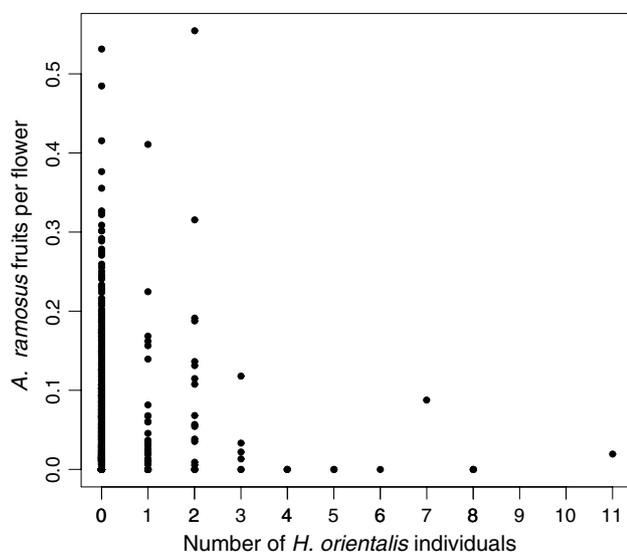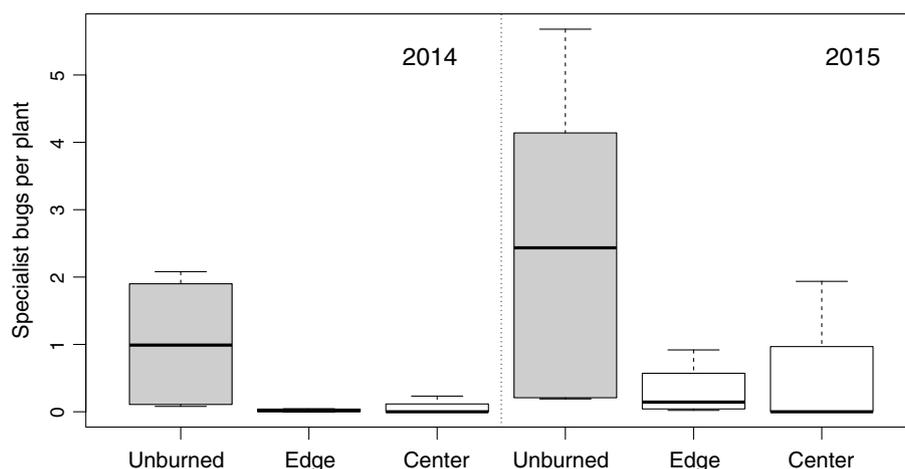
The number of specialist *H. orientalis* bugs as well the total number of herbivores on *Asphodelus* plants were significantly lower in burned than in the unburned plots on both years of sampling (Table 2; Fig. 2 and Fig. S1 in Supplementary Material). However, the number of generalist herbivores did not differ neither between the

two environments nor between the Edge and the Center (Table 2; Fig. 2). Neither the number of flowers nor seeds produced per plant showed significant differences between unburned and burned plots (*N* = 1414, *P* = 0.09 and *P* = 0.54, respectively). *Asphodelus* fruit set showed a significant negative relationship with the abundance of *Horistus* and also with the abundance of total herbivores when data from the 2 years were combined (see Fig. 3).

## Discussion

Previous studies on the responses of insect herbivory to fire have shown an increment in herbivory related to a post-fire

**Fig. 2** Number of specialist bugs *H. orientalis* on *A. ramosus* plants from unburned (*grey box*) and burned plots (*white boxes* in categories "Edge" and "Center") in 2 years. The number of individuals was estimated in 50 *A. ramosus* plants per plot (*N* = 6 unburned and *N* = 4 "Center" plots in the two studied years. *N* = 5 and 4 "Edge" plots in 2014 and 2015)



**Fig. 3** *Asphodelus ramosus* fruit set (proportion of fruits in relation to flowers) in relation to the number of the specialist bug *H. orientalis* in plants from burned plots. The relation is significant either considering *Horistus* only (*N* = 833, Estimate = −16.47, *P* = 0.018) or total herbivores (*N* = 833, Estimate = −12.57, *P* = 0.018) in a GLMM considering random effects and correcting for plant size

increase in herbivore abundance (Andersen 1988; Radho-Toly et al. 2001; Lopes and Vasconcelos 2011). Typically these studies have focused on generalized interactions where the insects do not depend on the recovery of a specific plant to recolonize the burned areas. Our study, however, shows that fires can instead benefit plants by decreasing their herbivory pressure particularly from specialist seed predator insects (Auld and O'Connell 1989; Vickery 2002). Even 3 years after the fire, *U. parviflorus* plants experienced lower seed damage in burned plots than in control unburned sites (Table 2; Fig. 1). For *A. ramosus*, we found that the variability in fruit set in burned areas is significantly related to the presence of the specialist bug. That is, the disruption

of the specialized interaction can affect plant fitness. In plant species with a quick recovery after fires, this disruption also coincides with an increase of resources and reduced competition after fire. Thus, the evidence suggests that the disruption of antagonistic interactions between plants and insects following a fire might be one mechanism contributing to plant success in fire-prone ecosystems.

Many insect populations decline immediately after a fire; furthermore, fire temporarily decreases the presence of the host plant required for insect development. Both the drop in insect populations and the reduction in food resources may have a stronger impact on specialist than on generalist insects (Swengel 1996, 1998, 2001). Generalist herbivores have access to a wider range of recovering plants, thus showing a faster re-colonization than the specialists. Consistently, in this study the presence of two specialist predators was much lower in plants from burned plots while generalist herbivores recorded on *A. ramosus* remained unaffected.

After 3 years of the wildfires we did not find a consistent effect of the distance from the perimeter of the fire on seed predation, herbivory pressures or plant fitness (Table 2). Several previous studies had shown a reduction of herbivory with the distance to unburned vegetation. For example, *Banksia* and *Eucalyptus* seedlings experienced a lower damage by generalist grasshoppers in large burned areas compared with small ones (Whelan and Main 1979). In a sandhill ecosystem, plants from the center of a burnt suffered half of the impact of insect herbivory compared to plants from the fire's edge (Knight and Holt 2005). The limited distance effect in the present study may be explained by the low postfire predation levels on *U. parviflorus* and the low number of *H. orientalis* individuals recorded in most burned plots. In fact, we did detect a significant decrease in *Ulex* predation towards the center of the burned zone in 2014 (Table 2), when the predation by the weevil was five times higher than in 2015. The causes

behind the decreased densities in specialist predators are unknown, and seem to be unrelated to climate conditions, which did not show major differences between the two sampling years. Despite there is little knowledge on the population dynamics of the studied specialist insects, our results suggest that fires may have a great negative effect on their populations and it may last for several years while recolonization takes place.

The disruption of the interaction by fire is likely to have long-term benefits for the plant. *U. parviflorus* benefits from fire because the heat reached during a fire breaks seed dormancy and greatly stimulates germination from the soil seedbank (Paula et al. 2009; Moreira et al. 2010; Moreira and Pausas 2012), and thus the postfire population size is greater than in prefire populations. *Asphodelus* can also take advantage of the fire because the canopy gap opened allows this species to flower profusely, otherwise the high density of the shrubland limits sexual reproduction (Pantis and Margaris 1988; Pantis and Mardiris 1992). Here we show that fires can generate an additional benefit to the plant by creating a window of opportunity for reproduction under a lower predation pressure from their specialist herbivores. Although this release is likely temporary, it may have long-term effects because it ensures the quick refill of the seedbank after fire, and thus the ability to massively recruit even under short fire intervals. For *Asphodelus*, it increases fruit set and promotes sexual reproduction under suitable postfire recruitment conditions. To what extent these beneficial effects can be generalized to other fire-adapted plant species reminds to be studied; previous research on this regard is limited to single populations or to prescribed fire regimes (Auld and O'Connell 1989; Vickery 2002).

Additionally to predispersal predation, fires can affect postdispersal seed predation which may also have implications on plant fitness (Andersen 1988; Ordóñez and Retana 2004; Zwolak et al. 2010; Keeley et al. 2012). For example, seed predation on *Pinus* species from the Mediterranean increased after fires coinciding with a high presence of ants and rodents (Ordóñez and Retana 2004; Broncano et al. 2008). These changes on secondary seed predation are related with the dispersal season and the time since fire (Ordóñez and Retana 2004). Our two studied plants disperse seeds from spring (*U. parviflorus*) to summer (*A. ramosus*), when ants can be especially abundant after fires (Ordóñez and Retana 2004). Although ants are known as the main seed predators in burned zones (Rey et al. 2002; Broncano et al. 2008), there is evidence that *U. parviflorus*, which has elaiosomes, can show higher germination rates after ant-dispersal (López-Vila and García-Fayos 2005). We are not aware of any information on seed predation by ants in *A. ramosus*. In any case, further studies depicting the relative role of ants as predators and dispersers (Auld

and Denham 1999) on the two studied plants at burned areas would contribute to better understanding their success in burning ecosystems.

Despite the accepted key role of fire in many ecosystems, the responses of plant–insect interactions to fire are not well known (Dafni et al. 2012). This gap in the knowledge is even more remarkable for fire-prone ecosystems such as the Mediterranean ones, where there is evidence of fire-adaptive traits in many different species (Keeley et al. 2011). Our study, for which we monitored two plant–insect interactions across several years at different locations, indicates that when fire has disrupted specialized antagonistic interactions between insects and plants capable of quickly regenerating after fire, these plants can benefit from this for several years. This "cleaning" effect by fire might be one of the factors promoting the success of fire-adapted plants. It remains to be determined how wide-spread these effects are across different ecological settings. However, we feel that the fact that we observed beneficial effects for two plant species—interacting with different insects after multiple fires at two different locations in two consecutive years—suggests that it may be a general phenomenon. However, fires will not always benefit plants as they can also disrupt mutualisms (Dafni et al. 2012) and change the dispersal-predation balance of generalized interactions (Andersen 1988; Radho-Toly et al. 2001; Ordóñez and Retana 2004; Broncano et al. 2008; Lopes and Vasconcelos 2011). The current crisis of biotic interactions and the expected increase in fire size and frequency associated with anthropogenic activities, make understanding the effects of fire on plant–insect interactions an urgent need.

**Author contribution statement** JGP conceived the idea, JGP and MCC designed the study. MCC and YG collected the data at field. YG performed the statistical analyses and wrote the first version of the manuscript. All authors contributed to the final version of the manuscript.

**Compliance with ethical standards**

**Conflict of interest** We declare no conflict of interest.

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