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Citation for final published version:

Banza, Paula, Evans, Darren M., Medeiros Mirra, Renata, MacGregor, Callum J. and Belo, Anabela D. F. 2021. Short-term positive effects of wild fire on diurnal insects and pollen transport in a Mediterranean ecosystem. *Ecological Entomology* 46 (6) , pp. 1353-1363. 10.1111/een.13082 filefile

Publishers page: <https://doi.org/10.1111/een.13082>  
<<https://doi.org/10.1111/een.13082>>

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1        **Short-term positive effects of wildfire on diurnal insects and**  
2        **pollen transport in a Mediterranean ecosystem**

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21  
22        Running title: **Wildfire and pollen transport on diurnal insects**

23 **Abstract**

24 1. Climate change is a key driver of increased wildfire activity globally. Whilst the  
25 recovery of plant communities after fire is generally understood, the impacts on  
26 ecological processes, such as pollen transport by insects, have received little  
27 attention.

28 2. We investigated the effects of wildfire on diurnal insects and pollen transport over  
29 two years following a large fire in Southern Portugal. By comparing samples  
30 collected at burned and adjacent unburned sites, we examined wildfire effects on  
31 a) abundance and species richness of insects across seasons, b) pollen being  
32 transported; c) three of the most abundant species: *Oxythyrea funesta*,  
33 *Heliethaurus ruficolis* (both Coleoptera) and *Apis mellifera* (Hymenoptera).

34 3. Wildfire and season had significant, interacting effects on the abundance of  
35 insects but not species richness. Abundance and species richness increased  
36 over time at both burned and unburned sites, most notably each spring.

37 4. Pollen loads, and species richness, found on individual insects were significantly  
38 higher in burned sites in the first spring only, but generally increased with time  
39 after the wildfire.

40 5. The abundance of *O. funesta* was similar between burned and unburned sites in  
41 the spring, but in the winter was significantly higher in burned sites; there were  
42 no significant differences in summer and autumn. *H. ruficolis* abundance was  
43 higher in burned sites. *A. mellifera* abundance was unaffected.

44 6. Overall, across almost all the community metrics, our results suggest that wildfire  
45 affects pollen transport by diurnal insects, at least in the short term, but with time  
46 these become similar to unburned habitats.

47 Key words: pollination, plant-insect interactions, Mediterranean, mutualisms, ecosystem  
48 services

## 49 **Introduction**

50 Wildfires are a natural feature of ecosystem disturbance and their importance is  
51 recognized for vegetation dynamics (Moreno & Oechel 1994; Lloret et al. 1999; Paula &  
52 Pausas 2008, Velle et al. 2012). Most studies on post-fire regeneration in Mediterranean  
53 ecosystems have focused on plants (Guo 2001; Mitchell et al. 2009; Schaffhauser et al.  
54 2012; Marzano et al. 2012; Francos et al. 2019). These studies have shown that plants  
55 have numerous strategies to survive, regenerate and colonize after the fire (Lloret et al.  
56 1999), which include fire-stimulated germination, or resprouting from stumps,  
57 lignotubers, or burls (James 1984).

58 Whilst the recovery of plant communities from fire is generally understood, the  
59 importance of fire recovery on animals and plant-animal mutualisms such as pollination,  
60 only recently received more attention (Brown et al. 2017; Garcia et al. 2018; Carbone  
61 2019; Lazarina 2019; LaManna et al. 2020; Nicholson & Egan 2020). The pollination of  
62 flowering plants by animals is a crucial ecosystem service of great value to humanity  
63 because without it most flowering plants would not reproduce sexually and humans  
64 would lose food and other plant origin products (Buchmann & Nabhan 1996; Klein et al.  
65 2007; Ollerton et al. 2010; Breeze et al. 2011; Potts et al. 2016). The number of flower-  
66 visiting species worldwide may total nearly 300,000 (Nabhan & Buchmann 1997). The  
67 importance of pollination to wild plants and as an ecosystem service, as well as a range  
68 of other ecological processes provided by pollinating insects, highlights that pollination  
69 systems should be a high priority for conservation (Kearns 1998; Vanbergen 2013).

70 Carbone et al. (2019) concluded that pollinators tended to be promoted after a wildfire  
71 event, increasing after fire and during early post-fire succession stages; however, fire  
72 frequency increase has the opposite effect, decreasing pollinators, especially  
73 lepidopterans. Recent research concurs that fires induces changes at the community  
74 level and influences the dynamics of pollination service. Fire characteristics such as size,

75 frequency, intensity and patchiness, as well as the life history traits of organisms are  
76 crucial in determining the responses of those organisms to fire (Brown et al. 2017;  
77 Carbone et al. 2019; Pausas 2019). The magnitude of insect decline could be related to  
78 the degree of exposure to flames as well as to the mobility of insects (Swengel & Swengel  
79 2007). Eggs and larvae are considered the most vulnerable to fire due to the lack of  
80 mobility to escape or avoid fire (Anderson et al. 1989; Huesbschman & Bragg 2000), but  
81 inactivity may be beneficial if food resources are low immediately following the fire.  
82 Different feeding guild locations affect insect responses to fire because they are exposed  
83 in different ways to flame and heat. Above ground individuals are potentially more at risk  
84 of higher mortality because there are fewer areas of refuge (Kral et al. 2017). Brown et  
85 al. (2017) refer that nest location and floral resource utilization, primarily mediate  
86 pollinator survival after fire; by nesting above ground, univoltine pollinators may be  
87 particularly vulnerable under expected fire regime changes.

88 Ecosystem changes affect the distribution, abundance, and effectiveness of pollinators  
89 (MA 2005; Biesmeijer et al. 2006; Vanbergen 2013; Potts et al. 2016). Successful post-  
90 fire regeneration depends upon the reinstatement of pollination services and it can be a  
91 useful tool for examining the recovery of ecosystem functioning post-fire, by comparing  
92 disturbed communities with reference communities (Forup et al. 2008). Previously, we  
93 investigated the effects of fire on nocturnal pollen-transport networks following a large  
94 wildfire that occurred in Southern Portugal in 2012, and found they had lower complexity  
95 and robustness compared to unburned areas (Banza et al. 2019). Burned sites had  
96 significantly more abundant flowers, but less abundant and species rich moths, and total  
97 pollen transport by moths was just 20% of that at unburned sites. However, it is unclear  
98 whether these patterns are consistent for diurnal pollinating insects, and for the quantity  
99 and diversity of pollen they transport.

100 In this study, we examine the impacts of wildfire on diurnal insects and pollen transport  
101 following the same wildfire mentioned above. We aim to answer the following questions:

102 1) Is there an effect of burning on the abundance, and species richness of diurnal insects  
103 and how does this vary across seasons? 2) Does burning affect the amount and diversity  
104 of pollen being transported by diurnal insects and how does this vary across seasons?  
105 3) How does burning affect the three more abundant species? In burned areas we expect  
106 potentially more flower-visiting insects due to the flush of flowers after the fire. We also  
107 expect seasonal effects on insect abundance, with higher numbers in the spring and  
108 autumn compared with summer and winter, consistent with Mediterranean trends.  
109 However, we do not anticipate differences in community composition and species  
110 richness as a result of burning, as these are more likely to be driven by seasonal  
111 variation. We expect higher pollen loads being carried by diurnal insects in burned areas  
112 due to the flush of flowers after the fire (with some plants potentially contributing with  
113 more pollen, and others less) and more pollen transported in the spring and autumn.

114

## 115 **Materials and Methods**

### 116 *Field site*

117 The study was conducted in an area of semi-natural cork oak-wood heathland of high  
118 conservation value dominated by *Cistus ladanifer* L. (gum cistus), *Lavandula stoechas*  
119 L. subsp. *stoechas* (lavender), *Arbutus unedo* L. (strawberry tree), *Erica arborea*  
120 (heather), and *Quercus suber* L. (cork oak) with some patches of *Pinus* spp. (pines). The  
121 area is used mainly for honey production and hunting with very few cattle and low  
122 woodland management.

123 The sites (Table S1, Supporting Information) were selected in an area burned in July  
124 2012 and in unburned adjacent areas located in Eastern Algarve (Serra-do-Caldeirão),  
125 Portugal (full details are in Banza et al. 2019). The dominant composition and  
126 physiognomy of the vegetation mentioned above was similar in burned and unburned  
127 areas before the wildfire. There were no fire events in the area between 1990-2012  
128 (ICNF 2019). The study began in April 2013 and continued until May 2015. Within the

129 area we selected three 40 x 40 m<sup>2</sup> post-fire plots and three unburned plots as a reference  
130 for potential ecological status before any fire damage. All plots had similar altitude, slope  
131 and exposure and they were at least 300 meters apart from each other. Each plot was  
132 visited approximately once every two months to sample insects and flowering plants in  
133 flower. During each visit, temperature, wind speed and weather conditions were also  
134 recorded.

135

#### 136 *Floral resource surveys*

137 To quantify floral resources for insect pollinators, two parallel 10 m transect lines were  
138 established, 10 m apart, at the centre of each plot. A 1 x 1 m<sup>2</sup> quadrat was placed every  
139 two meters along each transect line (n = 10). In each quadrat, percentage cover and  
140 height of all plant species currently in flower were recorded. Specimens of all plants in  
141 flower were collected and identified using the Iberian Flora (Castroviejo 1986-2014) and  
142 collections in the University of Évora Herbarium (HUEV). A pollen reference collection  
143 was also prepared to assist with subsequent pollen analysis, by sampling pollen from all  
144 flowering plants in flower present at the sites and fixing it on a microscope slide using  
145 fuchsin jelly (Beattie 1972). The reference collection contained pollen of 86 plant species  
146 from 34 families, including all species recorded on transects (Table S2, Supporting  
147 Information).

#### 148 *Diurnal insect surveys*

149 One transect of 15 m was conducted at each plot and all insects observed visiting plants  
150 in flower were captured using a hand net or directly into killing tubes with a drop of ethyl  
151 acetate for later identification and pollen analysis. Each insect caught was transferred to  
152 a killing tube as quickly as possible to reduce stress and decrease the chance of any  
153 pollen loss. Sampling occurred between 10 am and 4 pm and the timing of plot visits was  
154 randomised during the sampling period to avoid any effect of daytime on potential  
155 pollinator activity. All samples collected were frozen at the end of each day to reduce

156 decomposition. Insects were later identified using a binocular microscope and a selection  
157 of field guides (Delachaux 1990; Chinery 1979; Maravalhas 2000). Any insects that could  
158 not be identified were morphotyped.

159

#### 160 *Pollen analysis*

161 All frozen insects were placed in a re-hydration box for 12 hours before processing them.  
162 The head, proboscis and legs of caught insects were swabbed using a small cube of  
163 Fuchsin-glycerin jelly (Beattie 1972) and a microscope slide was prepared and examined  
164 at 400x magnification (microscope: Leitz HM-Lux 3). Pollen was identified to the lowest  
165 possible taxonomic level using the pollen reference collection mentioned above. For  
166 each slide we counted the number of pollen grains (“total pollen load”) up to 200 grains  
167 above which an estimate of the total was made; total number of pollen morphotypes was  
168 also registered.

169

#### 170 *Statistical methods - overview*

171 Analyses were conducted in R version 3.6.3 (R Core Team 2018) with a diverse selection  
172 of packages, of which the most important was lme4 (Bates et al. 2015; for constructing  
173 the majority of generalized linear mixed-effects models). A full list of packages used, with  
174 their references, is given in Table S3 (Supporting Information).

175 We grouped our data according to sampling period and treatment (i.e. burned and  
176 unburned). Seasons were defined as follows: October-December (“autumn”), January-  
177 March (“winter”), April-June (“spring”), and July-September (“summer”). These reflected  
178 four clearly separable phases in the annual cycle of floral and insect abundance. As  
179 sampling took place between April 2013 and May 2015, this resulted in a total of 9  
180 seasons being sampled. For clarity, “season” henceforth refers to a four-level variable  
181 (autumn, winter, spring and summer) and “sampling period” refers to a nine-level  
182 continuous variable (spring of year 1, etc) that describes the number of seasons since



183 the study commenced. Species richness was extrapolated using the Chao2 estimator  
184 (Chao 1987) to calculate the estimated values.

185

### 186 *Statistical testing*

187 We used general and generalised linear mixed-effects models to test the effects of fire,  
188 sampling period and the interaction between the two variables on abundance and  
189 estimated species richness of diurnal insect samples (Poisson family and log link  
190 function) and on pollen count and pollen species richness (Gaussian family with log 10  
191 transformation). If the interaction between fire and sampling period was not significant,  
192 the model was retested with the main effects only in additive form and a new model  
193 containing fire and season would then be fitted to test for the interaction between fire and  
194 season. We separately retested the effects of fire on insect abundance for three species  
195 of insects that dominated the sample: *Apis mellifera* (Linnaeus, 1758) (Order  
196 Hymenoptera, Family Apidae), *Heliotaurus ruficollis* (Fabricius, 1781) (Order  
197 Coleoptera, Family Tenebrionidae) and *Oxythyrea funesta* Poda, 1761 (Order  
198 Coleoptera, Family Cetoniidae). These three species collectively represented 43.7% of  
199 all individual insects sampled (13.8% *Apis mellifera*, 14.3% *Heliotaurus ruficollis* and  
200 15.6% *Oxythyrea funesta*). To investigate effects on pollen transport, we first checked  
201 the proportion of insects found to be carrying pollen; using individual, pollen-carrying  
202 insects as replicates, we then tested for effects of fire and sampling period (or season)  
203 on the pollen transport metrics.

204 To account for spatial autocorrelation, we included site as a random effect in models for  
205 all analyses where we had multiple replicates per sampling period in each treatment;  
206 additionally, we included year as a random effect in the models containing season and  
207 not sampling period. Significance of fixed effects was tested using Likelihood Ratio Tests  
208 (LRT); as a consequence, where interaction terms were found to be significant and  
209 retained, we present  $\chi^2$  and P-values for the interaction term only (not independently for

210 its constituent variables, since LRT tests for improvement in model fit from inclusion of  
211 the term of interest, and two interacting variables are treated as a single term).  
212 Additionally, we tested for differences in community composition of insects at family level,  
213 comparing communities sampled in burned and unburned sites using Bray-Curtis  
214 dissimilarities tested by permutational multivariate analysis of variance, using the *adonis*  
215 function of *Vegan* (Oksanen et al. 2016).

216

## 217 **Results**

### 218 *Overview*

219 A total of 28 different families of flowering plants in flower were recorded in the study  
220 area (see Banza et al. 2019 for the analyses of survey results). The most representative  
221 plant families are shown in Figure 1 (and Table S5, Supporting Information). Floral  
222 resources were more abundant and species-rich in spring across all plots, and at burned  
223 sites in winter. We observed different effects of burning on spring-time floral resources  
224 provided by annual and perennial plants: annual flowers were more abundant and  
225 species-rich at burned sites than unburned sites, whereas perennial flowers were less  
226 abundant (but equally species-rich) at burned sites.

227 A total of 572 insects were caught and identified into 138 morphotypes (Table S4,  
228 Supporting Information). Our total sample contained at least 138 taxa of at least 44  
229 families mainly from the Orders Coleoptera, Lepidoptera, Hymenoptera and Diptera. The  
230 assembly composition of insects is shown in Figure 2 (and Table S4, Supporting  
231 Information); all morphotypes were included in subsequent analyses, regardless of the  
232 level of identification. The most abundant species found across all sampling periods were  
233 *Apis mellifera* with a total of 79 individuals, *Heliethaurus ruficolis* with a total of 82  
234 individuals and *Oxythyrea funesta* with a total of 89 individuals.

235 Almost every caught insect was found to be carrying pollen with a total of 151,422 pollen  
236 grains. Overall, insects carried pollen from 57 plant species, representing 81.5% of the  
237 70 plant species identified on floral surveys. In the spring, pollen loads on insects were  
238 greatly dominated by *Tuberaria guttata* (L.) Fourr, followed by *Coleostephus myconis*  
239 (L.) Rchb. f. and *Lavandula stoechas* L.; in the summer, the most common pollen species  
240 carried by insects was *Ulex argenteus* Welw. ex Webb; in the winter, these were  
241 *Lithodora prostrata* (Loisel.) Griseb., *Ulex argenteus*; and *Ulex eriocladus* C.Vicioso; and  
242 in the autumn pollen loads were dominated by *U. eriocladus*, followed by *C. myconis*.  
243 (Fig. 2 and Table S5; Supporting Information).

#### 244 *Impacts of burning on insect abundance, species richness, and community composition*

245 Fire and sampling period had significant, interacting effects on the abundance of insects  
246 ( $\chi^2 / \text{LRT} = 23.645$ , d.f.= 8,  $p=0.0026$ , Figure 3, Table S4), but not on estimated species  
247 richness (LRT;  $\chi^2 = 4.663$ , d.f.= 8,  $p= 0.7929$ ). Once the interaction was removed,  
248 estimated species richness was not significantly affected by fire alone ( $\chi^2 / \text{LRT} = 0.010$ ,  
249 d.f. = 1,  $p = 0.9221$ ) but there were significant differences among sampling periods ( $\chi^2 /$   
250  $\text{LRT} = 71.439$ , d.f. = 8,  $p < 0.0001$  - Figure 4, Table S4). The interaction between fire  
251 and season was also not significant in explaining estimated species richness ( $\chi^2 / \text{LRT}$   
252  $= 0.75336$ , d.f.= 3,  $p= 0.8606$ ).

253 Insects were significantly more abundant in burned sites than unburned sites in the first  
254 spring and winter but there were no significant differences in abundance between burned  
255 and unburned sites in the summer and autumn or in the subsequent spring and winter  
256 seasons. Generally, both the abundance and species-richness of insects peaked in the  
257 spring; insect abundance was also significantly higher in the winter compared to summer  
258 or autumn, but species richness was not (Figures 3 & 4). There was no significant effect  
259 of burning on the insects' community composition at family level (*Anosim Stat*  $R=0.667$ ,  
260  $p=0.1$ , Fig 1.), although some seasonal variation was detected, driven by phenological

261 differences between taxa. In particular, Nymphalidae and Lycaenidae (Lepidoptera)  
262 formed a large part of the community in summer, whereas the winter community was  
263 dominated by Cetoniidae (Coleoptera).

264

#### 265 *Pollen transport*

266 Burning and sampling period had significant interacting effects on the two pollen  
267 transport metrics that we tested (Table S7, Supporting Information): the total pollen load  
268 (Figure 5) and number of pollen morphotypes (Figure 6) per pollen-carrying individual  
269 insect. Specifically, the total pollen load and number of pollen morphotypes transported  
270 by individual insects was significantly greater in burned sites in the first spring but no  
271 other significant differences or general patterns were found between burned and  
272 unburned sites in the remaining sampling periods. Overall, pollen loads and number of  
273 pollen morphotypes tended to be greater in spring compared to the other seasons; there  
274 is a general tendency for both variables to increase across the whole sampling period  
275 (Figures 5 & 6).

276 Overall, across almost all the community metrics, the significant interaction between  
277 burning and sampling period (Tables S6-S7, Supporting Information) indicates that over  
278 this period of 1-3 years post-fire there was generally a return to the state comparable to  
279 the unburned area (Figures 5 & 6).

280

#### 281 *Apis mellifera*

282 This species was not recorded in any of the two summer sampling periods but was  
283 present in all other sampling periods. There was no significant interaction between  
284 burning and sampling period ( $\chi^2 / \text{LRT} = 1.205$ , d.f.= 3,  $p=0.7517$ ) or between burning  
285 and season ( $\chi^2 / \text{LRT} = 0.9676$ , d.f.= 2,  $p= 0.6164$ ) in the abundance of *Apis mellifera*.  
286 There was also no individual effect of burning ( $\chi^2 / \text{LRT} = 3.4344$ , d.f.= 1,  $p=0.1161$ ) but

287 there was a positive marginally significant effect of sampling period ( $\chi^2 / \text{LRT} = 12.607$ ,  
288 d.f.= 6,  $p=0.0497$ ) driven by a greater abundance of *Apis mellifera* in the second spring  
289 (a mean of  $5.23 \pm 1.37$  SE) compared to the other sampling periods (highest mean =  
290  $3.02 \pm 0.71$  SE for the third spring).

291

#### 292 *Heliothaurus ruficolis*

293 This species was only found in the spring hence the interaction and effects of burning  
294 and year were tested, instead of sampling period or season. There was no significant  
295 interaction between burning and year in the abundance of *Heliothaurus ruficolis* ( $\chi^2 /$   
296  $\text{LRT} = 1.2573$ , d.f.= 1,  $p= 0.2622$ ) but there was a marginally non-significant effect of  
297 burning ( $\chi^2 / \text{LRT} = 3.5781$ , d.f.= 1,  $p= 0.0585$ ) and a significant effect of year ( $\chi^2 / \text{LRT}$   
298  $= 10.1212$ , d.f.= 2,  $p= 0.0063$ ). Although the interaction between burning and year is not  
299 significant, abundance of *Heliothaurus ruficolis* is slightly greater in burned areas (mean  
300  $6.13 \pm 0.94\text{SE}$ ) compared to unburned areas (mean  $3.65 \pm 0.78$  SE) and it is greater in  
301 the first sampling year (mean  $9.81 \pm 2.32$  SE), compared to the second (mean  $3.64 \pm$   
302  $0.73\text{SE}$ ) or the third (mean  $5.25 \pm 0.94$  SE).

303

#### 304 *Oxythyrea funesta*

305 This species was only found in the spring and the winter. The interaction between  
306 treatment and sampling period was not tested because there was not enough data  
307 across all categories but there was a marginally non-significant effect of sampling period  
308 alone ( $\chi^2 / \text{LRT} = 9.2555$ , d.f.= 4,  $p= 0.055021$ ), seemingly driven by the lower  
309 abundance of *O. funesta* in the third spring (mean  $0.61 \pm 0.80$  SE), compared to the first  
310 and second springs (mean  $1.76 \pm 0.80$  SE and  $1.59 \pm 0.49$  SE, respectively). There was  
311 also a significant interaction between burning and season in the abundance of *Oxythyrea*

312 *funesta* ( $\chi^2$  / LRT = 4.5873, d.f.= 1, p= 0.03221). The abundance of *Oxythyrea funesta*  
313 was similar between burned and unburned areas in the spring (mean  $1.40 \pm 0.529$  SE  
314 and mean  $1.00 \pm 0.577$  SE, respectively) but in the winter, there was significantly greater  
315 abundance in burned areas (mean  $17.75 \pm 2.107$  SE) compared to unburned areas  
316 (mean  $2.00 \pm 0.7071$  SE).

317

## 318 **Discussion**

319 Wildfire had significant, interacting effects on the abundance of diurnal flower-visiting  
320 insects but not species richness, with some seasonal effects, but no significant effect on  
321 community composition at the family level. Individual insect pollen loads and species  
322 richness were significantly higher during the first spring post-fire, but not subsequently.  
323 However, there was a general tendency for both pollen load and species richness to  
324 increase during the study, irrespective of fire.

325 Wildfires generally increase plants and pollinators abundance resulting in a  
326 homogenization of species composition of both pollinators and flowering plants  
327 (LaManna et al. 2020). However, mix-severity wildfires promote regional and local  
328 species richness as well as abundance of both pollinators and flowering plants (LaManna  
329 et al. 2020). The impact of moderate fires in communities creates openings in the  
330 vegetation creating a mosaic pattern in terms of environmental heterogeneity and  
331 resources and promotes the diversity of many pollinator guilds at local landscapes  
332 (Brown et al. 2017; Lazarina 2019). So, wildfires have mixed impacts in communities  
333 (Nicholson & Egan 2019); they can negatively affect plants and pollinators, e.g. by  
334 disturbing seed germination patterns (Pausas & Keeley 2014) and mortality rates  
335 (Ne'eman et al. 2000; Thom et al. 2015).; but they can have positive effects by creating  
336 early successional habitats with more resources such as light and soil nutrients for plants  
337 (Potts et al. 2001; Swanson et al. 2011; Van Nuland et al. 2013). In generalist plants

338 pollinator replacement can ensure plant reproduction success, depending on the level of  
339 specialization of interactions, promoting resilience to fire disturbance (García et al. 2018).  
340 Within burned plots of the study area, there was evidence of secondary succession with  
341 a flush of flowering plants, like in other studies of Mediterranean plant community post-  
342 fire recovery (Capitanio & Carcaillet 2008) and accompanying diurnal pollinators (Potts  
343 et al. 2003; Van Nuland et al. 2013). Our floral resource surveys (Banza et al. 2019)  
344 showed an overall increase in winter floral abundance at burned plots, whilst in spring,  
345 annual flowers were more abundant, and perennial flowers less abundant at the burned  
346 sites. This is likely due to the fact that some plants may be stimulated by fire (Herranz et  
347 al. 1998) or because of higher light levels associated with reduced shrub cover at burned  
348 sites. The correspondence between positive responses to burning in winter and spring  
349 for both floral resources and insects may be explained by the secondary succession flush  
350 of flowering plants after the fire, creating more opportunities for insects to feed. Insects  
351 depend on plants for feeding, particularly at larval stages but as adults the flowers are a  
352 very important source of food, either for nectar or pollen or both. Insects were more  
353 abundant in the burned plots in the first spring and winter, in accordance with a higher  
354 availability of food.

355 The community composition of insects at the family level was not affected by burning but  
356 there were some seasonal effects. Abundance and species richness peaked in the spring  
357 and insects were more abundant at burned sites in the first spring and winter. Again, this  
358 was likely response to plant turnover in the spring and in the winter. However, there were  
359 no significant differences in abundance between burned and unburned plots in the  
360 summer, autumn or in the subsequent spring and winter seasons. As bushes and other  
361 perennial flowering plants recovered in the burned areas, the number of annual flowers  
362 stabilized and that likely affected the abundance of insects.

363 Examining pollen transport gives a good indication as to how important ecological  
364 processes recover after a fire. Our results showed that burning had a positive effect only

365 in the first spring, insects carried more pollen and from more pollen types in burned sites  
366 than in unburned sites. However, no other significant differences or general patterns  
367 were found between burned and unburned sites in the remaining sampling period. This  
368 can be explained again by the fact that there were more flowers in the spring than the  
369 other seasons, and hence more possibilities for insects to carry pollen from them.  
370 Summer is usually very hot with less flowers, so pollen transport was relatively lower  
371 than in spring. Many plants flower after the first autumn rains, creating what is known  
372 locally as the “second spring”, and flowering continues into winter because temperatures  
373 are mild (e.g. February and March had a mean temperature of above around 20°C or  
374 more; Table S8, Supporting Information).

375 However, there was a general tendency for both pollen load and species richness to  
376 increase during the study. This pattern was observed across both burned and unburned  
377 sites, and may have been driven by factors other than the fire. It is also possible that the  
378 fire may have caused regional-scale disturbance to pollination systems (affecting all  
379 sites, not just the burned sites) which then recovered over time. Such effects cannot be  
380 identified with the space-for-time experimental design that we used, and would require  
381 baseline data to have been collected at burned sites before a fire occurred.

382 Separate analyses of dominant diurnal flower-visiting species caught showed no  
383 significant interaction between burning and sampling period or between burning and  
384 season in their abundance. *Apis mellifera* was not recorded in the Summer months,  
385 perhaps due to the higher temperatures (average temperature in Summer 2013 –  
386 32.4°C; Summer 2014 – 31.9°C), which makes insect mobility more difficult, or the  
387 scarcity of flowers, reducing the availability of pollen and nectar resources. This species  
388 collects pollen from a wide range of taxa (Schmalzel 1980), and is able to adapt to  
389 different vegetation characteristics. The most abundant bee species tend to be generalist  
390 flower visitors, what gives them numerous advantages because of the general higher  
391 availability of pollen and nectar resources in burned areas (Potts et al. 2003). According



392 to Lazarina (2019), bees and wasps are central-foragers commuting between floral  
393 resources and nest-sites to provision for their offspring; therefore, bee flight might be  
394 constrained by the species-specific foraging range (maybe related with their body size,  
395 smaller bees utilize resources at a smaller spatial scale). However, we found a difference  
396 in the pollen they collected from burned areas compared to unburned areas, except in  
397 the Autumn, when the pollen was collected mainly from *Ulex eriocladus* in both cases.  
398 In the Spring pollen collected from burned areas was mostly from plants of the  
399 Asteraceae family and *Lavandula stoechas* and in unburned areas was collected mostly  
400 from two types of plant: *Lavandula stoechas* and *Tuberaria guttata*; the diversity of pollen  
401 types was higher in the burned areas compared to unburned areas. In the Winter, pollen  
402 collected from burned areas was dominated by *Ulex eriocladus* but in unburned areas  
403 the pollen collected was mainly from *Lavandula stoechas* and *Cistus salviifolius* L.  
404 (Figure b, Supporting Information).

405 The abundance of *Heliothaurus ruficollis* was slightly higher in burned areas compared  
406 to unburned areas. It is a phytophagous beetle species that feeds from pollen, mainly on  
407 plants whose pollen structures are more accessible, such as those in the Asteraceae  
408 family (Figure c, Supporting Information). After the fire the number of these plants  
409 increased (1<sup>st</sup> Spring), what might explain the slightly higher abundance of these species  
410 in the burned areas.

411 Regarding *Oxythyrea funesta*, the abundance was similar between burned and unburned  
412 areas in the spring but in winter there was significantly higher abundance in burned areas  
413 compared to unburned areas. *O. funesta* is a phytophagous beetle species that feeds on  
414 pollen, but also raid floral organs, damaging especially colour flowers buds and flowers.  
415 Again, the differences in the winter between burned and unburned areas might be  
416 explained by the type of flowers present in those areas. In burned areas most of the  
417 pollen found in those insects was from *Cistus* spp. and *Ulex argenteus* and in unburned  
418 areas was from *Cistus salviifolius* (Figure d, Supporting Information).

419 The increase in abundance of *Heliothaurus ruficollis* and *Oxythyrea funesta* could also  
420 be attributed to the fact that the local populations survived the fire as eggs or larvae  
421 protected in the soil but also to the reduction of their predators as a result of the fire  
422 (Pausas et al. 2018). Also, beetles in general, are noncentral places foragers that appear  
423 to respond to wildfires on larger spatial scales; they tend to move more freely and depend  
424 on multiple resources (Lazarina 2019).

425 Recently, we demonstrated the impacts of the same wildfire on nocturnal pollen-carrying  
426 moths, ultimately showing that pollen-transport networks in burned areas became less  
427 robust to perturbation and comprised a substantially changed set of interactions. In spite  
428 of increased floral abundance after burning, the total effect of burning on pollen transport  
429 was negative in all seasons, because moths were less abundant and species rich at  
430 burned sites (Banza et al. 2019). Those results are in line with the conclusions of  
431 Carbone et al. (2019) about the negative response of Lepidoptera to wildfires likely due  
432 to the higher larval susceptibility to direct fire effects. Furthermore, there was no evidence  
433 of a return to pre fire state. This result contrasts with the present study of diurnal pollen-  
434 carrying insects, which shows some positive effects of fire in the diurnal plant-pollinator  
435 systems and some evidence of a return to a state comparable to the unburned area.  
436 Both studies complement each other and show the importance of studying the entire  
437 plant-insect community in order to understand better how it recovers from the  
438 disturbance caused by fire.

439 Our work highlights a number of directions for future research on post-fire pollination  
440 function. Firstly, pollen transport does not necessarily translate to successful pollination  
441 in all cases (King et al. 2013), that is, the effects of the changes in pollinator abundance  
442 and pollen transport that we observed do not necessarily reflect the actual reproductive  
443 success and productivity of plants in burned and unburned areas. Secondly, recent  
444 studies have combined diurnal and nocturnal pollinators (e.g. Knop et al. 2017; Walton

445 et al. 2020), whereas we analysed data on diurnal pollinators (this study) and nocturnal  
446 pollinators (Banza et al. 2019) separately, due to different sampling methodologies.

447 Future work merging diurnal and nocturnal pollination could be valuable to understand  
448 overall impacts of wildfire on pollination systems, since the individual effects on the  
449 different pollinator guilds were very different. Such studies might be facilitated by using  
450 standardized methods across diurnal and nocturnal surveys, by conducting nocturnal  
451 transects instead of light-trapping (e.g. Macgregor et al. 2017). Finally, our findings are  
452 likely to be mainly a reflection of changing foraging habits of adult insects responding to  
453 the variation in the availability of floral resources. Understanding the impacts of fires on  
454 insect population may require study of the immediate impacts on all stages of the insect  
455 life-cycle.

456

## 457 **Conclusions**

458 We found evidence that wildfire affects pollen transport by diurnal insects soon after the  
459 event, with positive effects on both pollen load and insect diversity in the short term.  
460 There was a general tendency for both pollen load and insect species richness to  
461 increase during the study. However, there was no significant effect of burning on the  
462 insect community composition at family level. Our study demonstrated that even a small  
463 sample of diurnal flower-visiting insects can carry a large amount of pollen and that  
464 overall pollen-transport can be disturbed by wildfire. However, more research is needed  
465 to better understand the functional consequences of wildfire on insects. To achieve this,  
466 incorporating diurnal and nocturnal insects (together with information on their traits) into  
467 more complete ecological network analyses would provide numerous opportunities to  
468 understand and manage the resilience of fire-prone ecosystems.

469

470 **Data Availability Statement**

471 Data available on request from the authors.

472

473

474 **Acknowledgements**

475 We thank several volunteers at A Rocha Portugal who provided assistance in the field,  
476 in the laboratory, and with insect identification. This work was partially funded by National  
477 Funds through Fundação para a Ciência e Tecnologia (FCT, Portugal) - Foundation for  
478 Science and Technology under the Project UID/AGR/00115/2019 and with support from  
479 the Natural Environment Research Council (NERC, UK) - Industrial CASE studentship  
480 awarded to C.J.M. (Project Reference: NE/ K007394/1).

481

482 **Author contributions**

483 This study was instigated by P.B., A.D.F.B. and D.M.E. Field and laboratory work was  
484 conducted by P.B. The statistical analysis was conducted by R.M. and C.J.M., in  
485 consultation with P.B. and D.M.E.; and PB prepared the first draft of the manuscript. All  
486 authors contributed substantially to revising the manuscript.

487

488 **Conflict of interest Statement**

489 The authors have no conflicts of interest to declare. All co-authors have seen and agree  
490 with the contents of the manuscript and there is no financial interest to report. We certify  
491 that the submission is original work and is not under review at any other publication.

492

493 **Short Supporting Material Legends**

494 **Table S1** Locations of the six study sites.

495

496 **Table S2** Summary of the plant families identified on floristic surveys.

497

498 **Table S3** R packages used during analysis

499

500 **Table S4** Summary of captured insects.

501

502 **Table S5** – Number of pollen grains found on insects.

503

504 **Table S6** R software outputs showing summary of analyses of the effects of burning and  
505 season over consecutive sampling periods on the abundance (A) and species richness  
506 (B) of insects.

507

508 **Table S7** R software outputs showing summary of analyses of the effects of burning and  
509 season over consecutive sampling periods on pollen transport (A. pollen load and B.  
510 pollen type).

511

512 **Table S8** – Mean temperatures taken between 12 – 16 pm on each day of fieldwork.

513

514 **Figure a.** Assemblage composition by species of insects caught in burned and unburned  
515 areas of Serra-do-Caldeirão, Portugal, and across seasons.

516

517 **Figure b.** Assemblage composition by families of pollen carried by *Apis mellifera* caught  
518 in burned and unburned plots of Serra-do-Caldeirão, Portugal, and across seasons.

519

520 **Figure c.** Assemblage composition by families of pollen carried by *H. rufficollis* caught in  
521 burned and unburned plots of Serra-do-Caldeirão, Portugal, and across seasons.

522

523 **Figure d.** Assemblage composition by families of pollen carried by *O. funesta* caught in  
524 burned and unburned plots of Serra-do-Caldeirão, Portugal, and across seasons.

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697

698

699 **Figure Legends**

700 **Figure 1.** Assemblage composition by families of pollen carried by insects caught in  
701 burned and unburned plots of Serra-do-Caldeirão, Portugal, and across seasons.  
702 Families never comprising >7% of individuals in any combination of season and  
703 treatment are grouped as “Other”, and all other families are shown independently.

704 **Figure 2.** Assemblage composition by family of insects caught in burned and unburned  
705 areas of Serra-do-Caldeirão, Portugal, and across seasons. Families never comprising  
706 >10% of individuals in any combination of season and treatment are grouped as “Others”,  
707 and all other families are shown independently.

708 **Figure 3.** The effects of fire and seasons on the abundance of insects at burned plots  
709 (closed circles) and unburned plots (open circles) in Serra-do-Caldeirão, Portugal.  
710 Circles represent the model-predicted abundance. Error bars show 95% confidence  
711 intervals.

712 **Figure 4.** The effects of fire and seasons on the species richness of insects at burned  
713 plots (closed circles) and unburned plots (open circles) in Serra-do-Caldeirão, Portugal.  
714 Circles represent the model-predicted abundance. Error bars show 95% confidence  
715 intervals.

716 **Figure 5.** The effects of fire and seasons on the pollen load (total number of pollen  
717 grains) of insects per individual pollen-carrying insect at burned sites (closed circles) and  
718 unburned sites (open circles) in Serra-do-Caldeirão, Portugal. Error bars show 95%  
719 confidence intervals of the model-predicted pollen loads.

720 **Figure 6.** The effects of fire and seasons on the pollen species richness per individual  
721 pollen-carrying insect at burned sites (closed circles) and unburned sites (open circles)  
722 in Serra-do-Caldeirão, Portugal. Error bars show 95% confidence intervals of the model-  
723 predicted pollen loads.



