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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 m² 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 m² 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 χ^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, *Heliothaurus 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 (χ^2 / 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 ± 1.37 SE) compared to the other sampling periods (highest mean =
290 3.02 ± 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 (χ^2 / 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 ± 0.78 SE) and it is greater in
301 the first sampling year (mean 9.81 ± 2.32 SE), compared to the second (mean $3.64 \pm$
302 0.73SE) or the third (mean 5.25 ± 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 ± 0.80 SE), compared to the first
310 and second springs (mean 1.76 ± 0.80 SE and 1.59 ± 0.49 SE, respectively). There was
311 also a significant interaction between burning and season in the abundance of *Oxythyrea*

312 *funesta* (χ^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 ± 0.529 SE
314 and mean 1.00 ± 0.577 SE, respectively) but in the winter, there was significantly greater
315 abundance in burned areas (mean 17.75 ± 2.107 SE) compared to unburned areas
316 (mean 2.00 ± 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 *Heliethaurus 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 (1st 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

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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. rufficolis* 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.

525

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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.

