

1 **Wildfire alters the structure and seasonal dynamics of nocturnal pollen-transport**
2 **networks**

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4 *Running head: Wildfire affects nocturnal pollination*

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28 Abstract

- 29 1. Wildfires drive global biodiversity patterns and affect plant-pollinator interactions,
30 and are expected to become more frequent and severe under climate change. Post-fire
31 plant communities often have increased floral abundance and diversity, but the effects
32 of wildfires on the ecological process of pollination are poorly understood. Nocturnal
33 moths are globally important pollinators, but no previous study has examined the
34 effects of wildfire on nocturnal pollination interactions.
- 35 2. We investigated the effects of wildfire on nocturnal pollen transport networks. We
36 analysed the abundance and species richness of moths and flowers, and the structure
37 of these networks, at three burned and three unburned sites in Portugal for two years,
38 starting eight months after a large fire.
- 39 3. Nocturnal pollen-transport networks had lower complexity and robustness following
40 the fire than at nearby unburned sites. Overall, 70% of individual moths carried
41 pollen, and moths were found to be transporting pollen from 83% of the flower
42 species present. Burned sites had significantly more abundant flowers, but less
43 abundant and species-rich moths. Individual moths transported more pollen in
44 summer at burned sites, but less in winter; however, total pollen-transport by the moth
45 assemblage at burned sites was just 20% of that at unburned sites. Interaction turnover
46 between burned and unburned networks was high.
- 47 4. Negative effects of fire upon moths will likely permeate to other taxa through loss of
48 mutualisms. Therefore, if wildfires become more frequent under climate change,
49 community resilience may be eroded. Understanding the responses of ecological
50 networks to wildfire can inform management that promotes resilience and facilitates
51 whole-ecosystem conservation.

52 **Resumo Português (Second language abstract: Portuguese)**

- 53 1. Os fogos florestais induzem padrões mundiais de biodiversidade, afectando as
54 interações planta-polinizador, e é expectável que se tornem mais frequentes e severos
55 num cenário de alterações climáticas. As comunidades vegetais do pós-fogo
56 apresentam frequentemente maior abundância e diversidade florística. No entanto, os
57 efeitos dos fogos florestais sobre o processo ecológico da polinização são pouco
58 conhecidos. Os lepidópteros nocturnos são polinizadores importantes a nível mundial,
59 mas apesar disso nenhum estudo escrutinou, até à data, os efeitos dos fogos florestais
60 sobre as interações produzidas entre as plantas e os polinizadores nocturnos.
- 61 2. Investigámos os efeitos dos fogos florestais nas redes de transporte de pólen por
62 polinizadores nocturnos. Analisámos a abundância e riqueza específica de traças e
63 plantas em flor, e a estrutura destas redes, em três áreas ardidas e três não ardidas em
64 Portugal, durante dois anos, com início oito meses após um grande fogo.
- 65 3. As redes nocturnas de transporte de pólen apresentaram menor complexidade e
66 robustez após o fogo quando comparadas com áreas próximas não ardidas.
- 67 Globalmente, 70% das traças transportavam pólen do qual 83% pertencia a plantas em
68 flor presentes no local. Nas áreas ardidas a floração foi significativamente mais
69 abundante, mas a abundância e a riqueza específica das traças foram menores. Nas
70 áreas ardidas, cada traça individualmente transportou mais pólen no Verão, mas
71 menos no Inverno; no entanto, o total de pólen transportado pelo conjunto das traças
72 foi de apenas 20% do das áreas não ardidas. O *turnover* das interações entre áreas
73 ardidas e não ardidas foi elevado.
- 74 4. Os efeitos negativos dos fogos sobre as traças irão provavelmente fazer-se sentir
75 noutros taxa em consequência da perda de mutualismos. Portanto, se os fogos
76 florestais se tornarem mais frequentes por causa das alterações climáticas, a

77 resiliência das comunidades pode ser afectada. Compreender as respostas das redes
78 ecológicas aos fogos florestais pode contribuir para uma gestão que promova a
79 resiliência e facilite a conservação do ecossistema como um todo.

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82 **Keywords**

83 Disturbance, ecological networks, fire, flowering plants, Lepidoptera, Mediterranean, moths,
84 pollination

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89 **Introduction**

90 Wildfire drives biodiversity patterns globally through heterogeneous disturbance regimes
91 (Kelly & Brotons, 2017). It is especially important within Mediterranean ecosystems (Faivre,
92 Roche, Boer, McCaw, & Grierson, 2011), where wildfires have become more frequent and
93 severe since the 1970s because agricultural abandonment has caused fuel accumulation
94 (Moreira, Rego, & Ferreira, 2001; Pausas & Fernández-Muñoz, 2011). Climate change is
95 expected to drive further increases in frequency and severity of fires (Flannigan et al., 2013).

96 Fires can shape plant-pollinator communities (Brown, York, Christie, & McCarthy, 2017;
97 Ponisio et al., 2016), leading to reduced abundance of pollinators and flowers (Potts, Dafni,
98 & Ne'eman, 2001) and reductions in plant reproductive success (Ne'eman, Dafni, & Potts,
99 2000), or increased floral resources through a flush of secondary succession (Capitanio &
100 Carcaillet, 2008; Potts et al., 2003). By altering community composition, fire may have
101 secondary effects on plant-pollinator networks (Welti & Joern, 2017), but no study has
102 investigated the direct effects of fire on plant-pollinator network properties (Brown, York,
103 Christie, & McCarthy, 2017). Ecological network metrics are increasingly used as tools for
104 biodiversity monitoring and assessment of environmental change (Derocles et al., 2018),
105 because they can describe important changes in the structure and function of whole
106 ecosystems that might not be detected by measuring species abundance and diversity.

107 Moths are potentially pollinators of global importance (Macgregor et al., 2019; Macgregor,
108 Pocock, Fox, & Evans, 2015), and may be especially important in the Mediterranean (Banza,
109 Belo, & Evans, 2015). They are in decline (Conrad, Warren, Fox, Parsons, & Woiwod,
110 2006), with probable drivers of those declines including habitat fragmentation, climate
111 change (Fox et al., 2014), and artificial light at night (Macgregor, Evans, Fox, & Pocock,
112 2017; van Langevelde et al., 2018). Wildfire may also affect moths; of the few studies of the

113 effects of wildfire upon Lepidoptera, most find negative impacts (Kral, Limb, Harmon, &
114 Hovick, 2017). Fire can lead to mortality of larvae through host plant destruction (Fowles,
115 Bailey, & Hale, 2004), subterranean pupae (Schmid, Thomas, & Rogers, 1981), and even
116 adults (Gerson & Kelsey, 1997). However, the effects of fire on moths and their pollen-
117 transport interactions at community-level have not been studied.

118 Here, we examined the response of nocturnal moth-plant interaction networks to a large fire
119 in southern Portugal. By assessing the abundance and diversity of moths, flowers, and their
120 networks of pollen-transport interactions year-round at three burned and three unburned large
121 sites for two years following the fire, we tested four hypotheses about the effects of wildfire
122 on nocturnal pollen-transport systems: (i) that burned sites would have more flowers than
123 unburned sites, because some species would respond to fire by flowering; (ii) that burned
124 sites would have fewer moths than unburned sites, because of damage to larval host plants;
125 (iii) that pollen-transport networks at burned sites would be less interaction-rich (because
126 under hypothesis ii, the abundance and species richness of moths would be lower) and have
127 lower complexity than at unburned sites; and (iv) that pollen-transport networks at burned
128 sites would have lower robustness (a measure of the tolerance of networks to species
129 extinctions (Memmott, Waser, & Price, 2004)) than at unburned sites, because generalist
130 species play important roles in maintaining network stability (Tylianakis, Laliberté, Nielsen,
131 & Bascompte, 2010), but the loss of larval host plants might drive random local extinctions
132 of generalist flower-visiting moths.

133 **Materials and methods**

134 *Study system*

135 The study followed a large fire in July 2012, affecting approximately 225 km² in the Serra do
136 Caldeirão region near Faro, Portugal (see Fig. S1 in Supporting Information). This is a

137 mountainous shrubland ecosystem (maximum altitude 575 m) containing semi-natural cork
138 oak woodland with high conservation value.

139 Fieldwork took place from April 2013 to May 2015. We established three 40 x 40 m study
140 sites each in the burned area and a nearby unburned area (Fig. S1). All sites had intermediate
141 densities of oak trees and shrubs at a similar successional stage. The sets of burned sites and
142 of unburned sites each contained a similar range of aspects and altitudes, and all were situated
143 on slopes of > 10% gradient (Table S1). Sites within the same treatment were separated by >
144 300 m, and sites in different treatments by > 500 m. Throughout the study, sites were
145 sampled approximately every two months by moth sampling and floral transects. Each site
146 was sampled on 13-15 occasions in total.

147 *Moth sampling*

148 Moths were sampled using Heath-style light traps (Heath, 1965) baited with 6 W actinic
149 tubes (Philips TL6W/05, Philips, Amsterdam, Netherlands) powered by 12 V batteries. Traps
150 were situated at the centre of the site and operated between sunset and sunrise; exact set-up
151 and collection times varied throughout the year (Fig. S2). Captured moths were retained in
152 individual tubes for subsequent pollen analysis. Moths were identified to the lowest possible
153 taxonomic level, using a local reference collection and several UK field guides (Manley,
154 2008; Sterling & Parsons, 2012; Waring & Townsend, 2009).

155 *Floral transects*

156 Two parallel 10 m transects were established, 10 m apart, at the centre of each plot. A 1 x 1
157 m quadrat was placed every two metres along each transect line (n = 10). For each quadrat,
158 percentage cover of all plant species currently in flower (henceforth referred to as flowers)
159 was recorded. Specimens of all flowers were collected and identified using the Iberian Flora

160 (Castroviejo, 1986-2014), Flora-On: Flora de Portugal Interactiva (<http://flora-on.pt>), and
161 collections in the University of Évora herbarium (HUEV); nomenclature and family-level
162 taxonomy were subsequently corrected to follow the Plant List (<http://www.theplantlist.org>).
163 A pollen reference collection was prepared to assist with pollen analysis, by sampling pollen
164 from each species of flower present at the sites and fixing it on microscope slides. The
165 reference collection contained pollen of 86 plant species from 34 families, including all
166 species recorded on transects.

167 *Pollen identification*

168 All sampled moths were examined for pollen. After relaxation for 12 hours, the head,
169 proboscis and legs of each moth was swabbed with a small cube of fuchsin jelly (Beattie,
170 1972), and a microscope slide prepared with the swab and examined at 400x magnification.
171 Pollen was identified to the lowest possible taxonomic level using the pollen reference
172 collection described above. Whilst pollen-transport by moths does not prove the existence of
173 successful pollination of any plant (King, Ballantyne, & Willmer, 2013), it is a commonly-
174 used proxy in pollination networks (Banza, Belo, & Evans, 2015), being less time-consuming
175 to collect data on than alternative measures such as single-visit deposition.

176 *Analytical methods*

177 Analyses were conducted in R version 3.4.4 (R Core Team, 2018), using a range of packages
178 (Table S2).

179 Seasons were defined as follows: October-December (“autumn”), January-March (“winter”),
180 April-June (“spring”), and July-September (“summer”). These represented clearly-separated
181 phases in annual cycles of floral and moth abundance, with flushes in spring and autumn.
182 Over the study period, we sampled for 9 seasons. Therefore, “season” henceforth refers to a

183 four-level categorical variable (spring, summer, etc.), and “sampling period” refers to a nine-
184 level continuous variable (spring of year 1, etc.) describing the number of seasons since the
185 study commenced. For network analysis, we pooled interactions across sites and samples into
186 distinct networks for each treatment (burned or unburned) and sampling period, to construct a
187 total of 9 pairs of networks.

188 *Sampling completeness*

189 Detecting 90% of species and/or interactions comprising a network has previously been
190 proposed as a balance between obtaining a representative sample of the network, and the
191 diminishing returns of increasing sampling effort (Chao, Colwell, Lin, & Gotelli, 2009). For
192 each of our networks we estimated sampling completeness of species and interactions.

193 Sampling completeness of moth and flower species was calculated for each network as $(100$
194 \times observed richness) \div (estimated richness), where the estimated species richness was
195 calculated using the Chao2 estimator (Chao, 1987). Sampling completeness of interactions
196 was calculated following Macgregor, Evans, & Pocock (2017), using SCW2 and the Chao2
197 estimator. Interaction sampling completeness was estimated for each observed moth species
198 as $(100 \times$ observed interactions) \div (estimated interactions), where the estimated interaction
199 richness was calculated using Chao2, and the mean of all species’ interaction sampling
200 completeness was taken, weighted by each species’ estimated interaction richness.

201 *Pollen-transport networks*

202 We constructed 9 pairs of bipartite pollen-transport networks using the pooled data from each
203 sampling period and treatment, and calculated weighted descriptive metrics for analysis. We
204 created quantitative, interaction frequency-weighted pollen-transport networks, weighting
205 each interaction by the number of individual moths of a species carrying pollen of a plant
206 species, because interaction frequency predicts the relative strength of pollination interactions

207 well (Vázquez, Morris, & Jordano, 2005). Specifically, to test the effects of burning on
208 network complexity and consumer-resource asymmetry, we analysed: linkage density (a
209 measure of network complexity), generality of plants and of moths (measures of consumer-
210 resource asymmetry; sometimes termed ‘vulnerability’ and ‘generality’ respectively), and
211 niche overlap (a measure of the degree to which species share interaction partners).
212 Additionally, we compared the ‘robustness’ (tolerance to species extinctions (Burgos et al.,
213 2007)) of burned and unburned networks by simulating the random loss of moth species
214 (taking the mean robustness across 1000 bootstrapped simulations). For comparison, we
215 repeated these analyses with quantitative, pollen load-weighted pollen-transport networks,
216 weighting interactions by the total number of pollen grains of a plant species carried by all
217 individual moths of a species.

218 *Statistical testing*

219 We used generalised linear models (GLMs) and generalised linear mixed-effects models
220 (GLMMs) to test the effects of burning, season, sampling period and their two-way
221 interactions. We tested for effects on abundance and estimated species richness (using
222 Chao2) of moths and flowers between samples, separately retesting the effects of fire on
223 floral abundance and richness of annual and biennial plants only (henceforth ‘annuals’) and
224 all other plant species (perennials, bulbs, shrubs and trees; henceforth ‘perennials’).
225 Additionally, we tested for differences in community composition of moths and flowers at
226 family-level, and moths, flowers and interactions at species-level, between burned and
227 unburned sites, using Bray-Curtis dissimilarities tested by permutational multivariate analysis
228 of variance.

229 To investigate effects on pollen-transport, we first tested for effects on the proportion of
230 moths carrying pollen. Using individual, pollen-carrying moths as replicates, we tested for

231 effects on pollen count and species richness. We then pooled the pollen loads of all moths
232 within each sample, and tested for effects at sample-level on the total quantity and species
233 richness of pollen being transported by the entire moth assemblage. We examined the relative
234 abundance of species recorded on floral transects and in winter, when a single plant species
235 (*Ulex argenteus* Webb) dominated the assemblage, we separately retested the effects of
236 burning on floral abundance, proportion of moths carrying pollen, and pollen count at
237 individual- and sample-levels, both for *U. argenteus* alone and for all other plant species
238 combined.

239 Finally, we tested for effects on the five network metrics described above. We used treatment
240 and season in all models as fixed effects; an interaction term between the two was initially
241 included, but if found to be non-significant, was removed and the model retested with the two
242 variables included separately. For analyses with multiple replicates per sampling period (i.e.
243 when replicates were individual moths (n = 3406), pollen-carrying moths (n = 2934), samples
244 of moths (n = 73), or quadrats on floral transects (n = 1260), but not when replicates were
245 networks (n = 18)), we also included sampling period as a fixed effect, and tested its two-way
246 interactions with both treatment and season as above. To account for spatio-temporal
247 autocorrelation, we included site as a random effect in all analyses with multiple replicated
248 per sampling period, but no random effects were included when networks were replicates.
249 For dependent variables, we selected between Poisson and log-transformed Gaussian error
250 distributions on a case-by-case basis (selecting the best-fitting model by visual inspection of
251 model residual plots). The exceptions to these were the proportion of moths carrying pollen,
252 for which we used a binomial error distribution, and the five network metrics, for which we
253 used untransformed Gaussian error distributions. Significance of fixed effects was tested in
254 GLMs using F-tests and GLMMs using Likelihood Ratio Tests; consequently, where

255 interaction terms were significant and retained, we present χ^2 and P -values for the interaction
256 term only (not independently for its constituent variables).

257 Moths might have cross-contaminated each other with pollen whilst in moth-traps, so we
258 repeated all relevant main analyses using only the individual-level pollen-transport
259 interactions where ≥ 5 pollen grains of a plant species were sampled from a single moth. This
260 approach has been used previously in similar studies (Banza, Belo, & Evans, 2015; Devoto,
261 Bailey, & Memmott, 2011) to provide a conservative estimate of true flower-visitor
262 interactions, and is likely to be sufficient to exclude all such contamination (Del Socorro &
263 Gregg, 2001), but might also lead to exclusion of some functional pollination interactions.

264 To test the effect of burning on species' degree (number of links formed per species), we also
265 aggregated data from all sampling periods to form a single network for each treatment ($n = 1$
266 pair) and for each combination of treatment and season ($n = 4$ pairs). We tested the effect of
267 burning on the frequency distribution of degree of each network for both moths and plants
268 overall and in each season, using one-tailed Kolmogorov-Smirnov tests, with the null
269 hypothesis that degree distribution was not higher for unburned sites than burned sites.

270 *Interaction turnover*

271 We examined the causes of spatial interaction turnover between burned and unburned
272 networks within pairs. Interaction turnover can be driven by change in species presence (of
273 plants, moths, or both), or change in interactions despite universal presence of both partners
274 (interaction rewiring). All scenarios are plausible outcomes of burning, so we calculated the
275 β -diversity of the pair of networks for each of the 9 sampling periods attributable to,
276 respectively, change in moth and/or plant species presence, and network rewiring, following
277 Kemp, Evans, Augustyn, & Ellis (2017). This was the number of interactions present in one
278 network but absent from the other for each reason, as a fraction of the total number of unique

279 interactions across both networks. We also calculated the total Jaccard β -diversity of each
280 pair of networks, which is the total number of interactions present in only one network
281 divided by the total number of unique interactions, and was therefore equal to the sum of the
282 β -diversity attributable to each cause of turnover. We inspected these results for seasonal
283 trends in the causes of interaction turnover between burned and unburned networks.

284 **Results**

285 *Overview*

286 A total of 3406 moths of 327 morphotypes, representing at least 311 species in 31 families
287 (Table S3), were caught in light-traps. Of these, 2394 individuals (70.3%), of 297
288 morphotypes (90.8%) representing at least 282 species of 31 families, carried pollen of 66
289 morphotypes. Of 70 plant species (representing 28 families; Table S4) identified on floral
290 transects, at least 58 (82.9%) were also identified as pollen carried by moths. Applying a
291 conservative threshold to remove potential cross-contamination of pollen within light-traps,
292 the number of moths carrying at least 5 pollen grains of a given plant species was only 950
293 (27.9%) of 186 morphotypes (56.9%). 52 pollen morphotypes were found in quantities of at
294 least 5 pollen grains on an individual moth.

295 *Abundance, richness and composition*

296 We found that burning and season had significant, interacting effects on the abundance of
297 both moths (Table S5; $\chi^2 = 36.24$, $P < 0.001$) and of flowers ($\chi^2 = 34.81$, $P < 0.001$). There
298 was no interaction between the effects of burning and season on estimated species richness of
299 either moths or flowers, but estimated species richness of moths was significantly affected by
300 both burning ($\chi^2 = 9.39$, $P = 0.002$) and season ($\chi^2 = 41.71$, $P < 0.001$), whilst estimated
301 species richness of flowers was significantly affected by season ($\chi^2 = 17.96$, $P < 0.001$) but

302 not by burning ($\chi^2 = 1.88, P = 0.170$). Specifically, moths were more abundant and species-
303 rich in unburned sites, and peaked in abundance in summer (Fig. 1). Flowers peaked in
304 abundance and richness in spring, but were less abundant in unburned sites in winter (Fig. 1):
305 a pattern driven primarily by annual flowers, whereas perennial flowers had reduced
306 abundance at burned sites (Fig. S3). Both burning and season significantly altered community
307 composition at family level of both moths and flowers (Table S6), whilst at species level,
308 community composition of moths, flowers and interactions was significantly altered by
309 burning but not by season (Fig. S4).

310 *Pollen-transport*

311 Burning and season had significant, interacting effects on four pollen-transport metrics (Table
312 S7): the proportion of moths carrying pollen ($\chi^2 = 33.21, P < 0.001$), the total pollen load (χ^2
313 = 8.84, $P = 0.032$) and number of pollen types ($\chi^2 = 11.17, P = 0.011$) per individual pollen-
314 carrying moth, and the number of pollen types per sample of moths ($\chi^2 = 9.65, P = 0.022$).
315 The total pollen count per sample of moths was also affected by both burning ($\chi^2 = 11.82, P <$
316 0.001) and season ($\chi^2 = 44.28, P < 0.001$), but without interaction. Specifically, moths were
317 most likely to carry pollen in spring, when over 95% of moths carried pollen at burned and
318 unburned sites alike (Fig. 2). However, individual moths were more likely to carry pollen,
319 and had larger and more species-rich pollen loads, in burned sites than unburned sites during
320 summer, and *vice versa* during winter (Fig. 2). In winter, moths were less likely to carry
321 pollen of the dominant flower species, *Ulex argenteus*, at burned sites, but equally likely to
322 carry pollen from other species; the abundance of *U. argenteus* was significantly reduced at
323 burned sites whereas other flowers were more abundant (Fig. S5). The total quantity and
324 species richness of pollen transported by the moth assemblage was lower at burned sites than
325 unburned sites in all seasons, except that species richness did not differ between treatments in

326 autumn (Fig. 2). Repeating these analyses with only interactions consisting of ≥ 5 pollen
327 grains did not qualitatively change our findings (Table S7), except that there was no
328 significant effect of burning on the species richness of individual moths' pollen loads.

329 *Network analysis*

330 We found that linkage density of pollen-transport networks was significantly affected by both
331 burning ($\chi^2 = 4.77$, $P = 0.049$) and season ($\chi^2 = 6.83$, $P = 0.006$), without interaction. Linkage
332 density was lower in burned networks across all seasons, and lower in autumn and winter
333 than spring and summer (Fig. 3). Likewise, network robustness was significantly affected by
334 both burning ($\chi^2 = 5.04$, $P = 0.044$) and season ($\chi^2 = 4.69$, $P = 0.022$), being lower in burned
335 networks and in winter (Fig. 3). Generality (mean links per species) both of moths and of
336 plants was significantly affected by season (plants: $\chi^2 = 7.10$, $P = 0.005$; moths: $\chi^2 = 13.13$, P
337 < 0.001) but not by burning (plants: $\chi^2 = 4.10$, $P = 0.066$; moths: $\chi^2 = 0.97$, $P = 0.344$).
338 Generality of plants was highest in summer, and of moths in spring (Fig. 3). Niche overlap
339 was not affected by either variable (burning: $\chi^2 = 0.87$, $P = 0.370$; season: $\chi^2 = 2.44$, $P =$
340 0.813). Results were qualitatively similar when we weighted pollen-transport networks by
341 pollen load, except linkage density was not significantly affected by burning (Table S8).
342 Likewise, repeating analyses with only interactions consisting of ≥ 5 pollen grains, we found
343 the same directional trends as described above (Table S9), but reductions in linkage density
344 and robustness at burned sites were no longer significant. This is most likely because these
345 networks contained many fewer interactions, increasing the error margins around metrics.

346 The frequency distribution of degree (no. links per species) was significantly lower at burned
347 sites than unburned sites for both moths and plants (Fig. S6), indicating that species formed
348 fewer interactions at burned sites. Testing seasons separately, degree distribution was

349 significantly lower in burned networks for moths in winter only, and for plants in winter and
350 spring.

351 *Longevity of effects of fire*

352 Overall, across almost all community and network metrics, we found no significant
353 interaction between burning and sampling period, once season was taken into account (Tables
354 S5-S10). This indicates that temporal trends over the duration of our study did not differ
355 between burned and unburned sites.

356 *Interaction turnover*

357 In all sampling periods there was high spatial turnover of interactions between burned and
358 unburned networks, indicating that few interactions were present in both (Fig. 4). From
359 spring to autumn, the principal cause of this turnover was change in the moth species present
360 in the network; however, in winter, there was comparatively high turnover attributable to
361 change in both moths and flowers, indicating that winter-time interactions at burned and
362 unburned sites involved very different assemblages of both flowers and moths.

363 *Sampling completeness*

364 On average, the sampling of our 18 networks was substantially less complete than the ideal
365 threshold of 90% (Fig. S7), especially for moths (mean sampling completeness 48.3%), with
366 plants (75.0%) and interactions (73.5%) being slightly better-sampled. Nevertheless,
367 sampling completeness did not differ significantly between burned and unburned networks
368 for moths ($t = 1.93$, d.f. = 13.17, $P = 0.076$), plants ($t = 1.48$, d.f. = 15.29, $P = 0.158$) or
369 interactions ($t = 0.52$, d.f. = 14.20, $P = 0.613$), suggesting that any conclusions drawn from
370 our comparisons between burned and unburned sites are robust.

371 **Discussion**

372 We show the disruptive effects of wildfire on moth communities and nocturnal pollen-
373 transport networks, contrasting with positive effects of fire reported in some diurnal plant-
374 pollinator systems (Capitanio & Carcaillet, 2008; Potts et al., 2003). It may therefore be
375 important to merge diurnal and nocturnal networks to gain an unbiased understanding of the
376 effects of environmental change on pollination systems. After burning, nocturnal pollen-
377 transport networks were less robust to perturbation and comprised a substantially-changed set
378 of interactions. Moths provided abundant pollen-transport, with 70% of individuals carrying
379 pollen, but the total effect of burning on pollen-transport was negative in all seasons, in spite
380 of increased floral abundance after burning, because moths were less abundant and speciose
381 at burned sites. These negative impacts could permeate to other taxa, but building resilience
382 into ecosystems, especially those under managed burning, might be facilitated by
383 understanding relationships between fire history and plant-pollinator network properties
384 (Brown, York, Christie, & McCarthy, 2017).

385 *Fire as a driver of environmental change*

386 Previous studies of the effects of fire on Mediterranean plant communities (Capitanio &
387 Carcaillet, 2008) and diurnal pollinators (Potts et al., 2003; Van Nuland et al., 2013) reported
388 a flush of secondary succession, consistent with the increase in winter floral abundance at our
389 burned sites. In fire-prone systems, some native plants may be stimulated to germinate by fire
390 (Herranz, Ferrandis, & Martínez-Sánchez, 1998) or assisted by increased light levels
391 associated with reduced shrub cover at burned sites.

392 The negative effects of wildfire on moth populations over a period of 1-3 years after burning,
393 with no detectable return to pre-fire states, can be interpreted in the light of demonstrated
394 negative impacts of wildfire on moths (Fowles, Bailey, & Hale, 2004; Gerson & Kelsey,

395 1997; Schmid, Thomas, & Rogers, 1981). Whilst most abundant bee species are generalist
396 flower-visitors and could capitalise on increased general availability of pollen and nectar
397 resources in burned areas (Potts et al., 2003), many Lepidoptera are specialists as larvae
398 (Bernays & Chapman, 1994), and may be unable to breed in burned areas if host plants are
399 destroyed by fire. We found that the moth community changed significantly at burned sites,
400 indicating that the severity of the effects of fire may vary between different moths. Further
401 research might reveal whether this variation is linked to life-history or functional traits in
402 moths, or more directly to changes in the availability of each species' larval host plants.
403 Whether ecological succession would, over a longer timescale, cause the burned sites to
404 converge on the state of the unburned sites, or whether they would instead reach an
405 alternative stable state, remains to be seen.

406 However, the long-term role of wildfires in driving moth population declines remains
407 unclear. Wildfires are mostly of low importance in countries where moth declines have been
408 most convincingly shown, e.g. in the UK (Conrad, Warren, Fox, Parsons, & Woiwod, 2006),
409 but play a substantial role in shaping ecosystems in other regions (Flannigan et al., 2013;
410 Kelly & Brotons, 2017). Evaluating trends in moth populations in such regions at a large
411 spatio-temporal scale would therefore be valuable. Potential interactions between wildfire
412 and other drivers of environmental change also warrant further attention. Climate change and
413 agricultural abandonment may be especially important since both drivers are of known
414 importance to Lepidoptera (Parmesan, Ryrholm, Stefanescu, & Hill, 1999; Uchida &
415 Ushimaru, 2014) and play a role in increasing fire frequency (Flannigan et al., 2013; Price &
416 Rind, 1994; Pausas & Fernández-Muñoz, 2011), which might reduce the long-term ability of
417 communities to recover (Oliver et al., 2015).

418 Finally, it should be noted that our results pertain to the effects of a single wildfire, due to the
419 logistical challenges that would be posed by sampling after multiple fires. All burned sites
420 were burned at the same time, by the same fire, and burned and unburned sites were spatially
421 more clustered within treatments than between treatments. Therefore, further study of the
422 effects of other wildfires, covering a wider range of conditions than was feasible in this study
423 (e.g. fires on different continents, in different ecosystems and habitat types, of different sizes
424 and intensities, with burning occurring at different times of year, in association with different
425 weather conditions, and so forth), might unveil even greater complexity in the responses of
426 moth and plant communities.

427 *Moths as pollinators*

428 Our findings add to the evidence that moths are previously undervalued providers of pollen-
429 transport (Macgregor et al., 2019; Macgregor, Pocock, Fox, & Evans, 2015); perhaps
430 especially in Mediterranean systems (Banza, Belo, & Evans, 2015), where we detected the
431 highest proportion of moths carrying pollen in any study to date. The pollen of some 83% of
432 locally-flowering plants was carried by moths. An important future research question is the
433 functional importance of moths as pollinators of the plant species whose pollen they
434 transport.

435 Pollen-transport by individual moths was increased at burned sites in summer, but reduced in
436 winter, despite the increase in floral abundance and richness. In winter, moths mainly
437 transported pollen of *Ulex argenteus* at unburned sites, but rarely did so at burned sites (Fig.
438 S5). Potentially, more moths may have visited *U. argenteus* at unburned sites in search of
439 nectar (Stokes, Bullock, & Watkinson, 2003) because there were fewer alternative floral
440 resources (Fig. 1). Moths were less abundant at burned sites in summer but floral abundance
441 was unchanged, potentially increasing the likelihood of pollen removal by making each moth

442 more likely to be among the first visitors to any given flower (Young & Stanton, 1990).
443 Variation in diurnal visitation rates between burned and unburned sites could also have
444 influenced pollen availability in all seasons. Finally, changes in community composition at
445 burned sites could have made certain species with important roles in pollen-transport
446 relatively more or less abundant.

447 When the pollen loads of all moths in a sample were aggregated, the overall effect of burning
448 was a consistent reduction in nocturnal pollen-transport across all seasons. This reflected
449 previous studies of other pollinator taxa, where flower-visitation was reduced after fire
450 (Ne'eman, Dafni, & Potts, 2000), even for plant species that respond to fire by flowering
451 (Geerts, Malherbe, & Pauw, 2011).

452 *Networks*

453 Ecological network approaches have considerable potential to help understand the effects of
454 fire on the risk of cascading extinctions due to loss of mutualisms (Brown, York, Christie, &
455 McCarthy, 2017). We find significant structural differences between networks at burned and
456 unburned sites. Reduced robustness at burned sites indicates that wildfire leads to nocturnal
457 pollen-transport systems that are less tolerant of further perturbation, and at greater risk of
458 cascading extinctions. There was high interaction turnover between networks at burned and
459 unburned sites, driven by change in moth species presence (in all seasons) and plant species
460 presence (in winter). The interactions comprising networks can vary spatio-temporally with
461 little associated change in network structure (Kemp, Evans, Augustyn, & Ellis, 2017; Olesen,
462 Bascompte, Elberling, & Jordano, 2008); turnover is often demonstrated within seasons or
463 over consecutive years. By gathering year-round data, we showed that the direction and
464 significance of the effects of wildfire changed seasonally. Future ecological network studies
465 could therefore run across seasons to avoid over-simplified conclusions.

466 *Conclusions*

467 Improving the understanding of the functional importance of nocturnal pollinators, especially
468 in Mediterranean systems where very large proportions of moths carry pollen, is important.
469 The effects of drivers of environmental change on nocturnal plant-pollinator networks have
470 generally not been investigated (but see Knop et al., 2017). Given that our results contrasted
471 with the positive effects of wildfire reported in some diurnal plant-pollinator systems, it is
472 unsafe to assume that the effects of drivers of change on nocturnal pollination networks will
473 be the same as their known effects on diurnal systems.

474 The negative impacts of wildfire on moth abundance and pollen-transport were likely driven
475 by direct mortality of immature life stages and reduction in availability of larval resources.
476 However, future mechanistic studies are required to understand the relative importance of
477 these mechanisms at population- and community-level, and the impacts on co-evolutionary
478 dynamics. Further study, over time as the burned ecosystem regenerates and across multiple
479 fires at the same sites, could establish the influence of repeated pulse perturbations on
480 ecosystem recovery, improving our understanding of the resilience of fire-prone systems and
481 the potential importance of increasingly frequent fires under climate change. A deeper
482 understanding of the responses of ecological networks to wildfire may facilitate whole-
483 ecosystem conservation (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010) and restoration
484 (Raimundo, Guimarães, & Evans, 2018), allowing resilience to be built into fire-prone
485 ecosystems (Evans, Kitson, Lunt, Straw, & Pocock, 2016).

486 **Acknowledgements**

487 We thank our field assistant Todd Jenkins, and several volunteers at A Rocha Portugal who
488 provided additional assistance in the field, in the lab, and with insect identification. We are
489 grateful to Penny Wolf for providing funding for the field study. C.J.M. was funded by the

490 Natural Environment Research Council and Butterfly Conservation (Industrial CASE
491 studentship, grant ID: NE/K007394/2). We thank Jason Tylianakis and Roy Sanderson for
492 their helpful comments on an early draft of this manuscript.

493 **Author contributions**

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

498 **Data accessibility**

499 Data will be made available from the Dryad Digital Repository upon acceptance.

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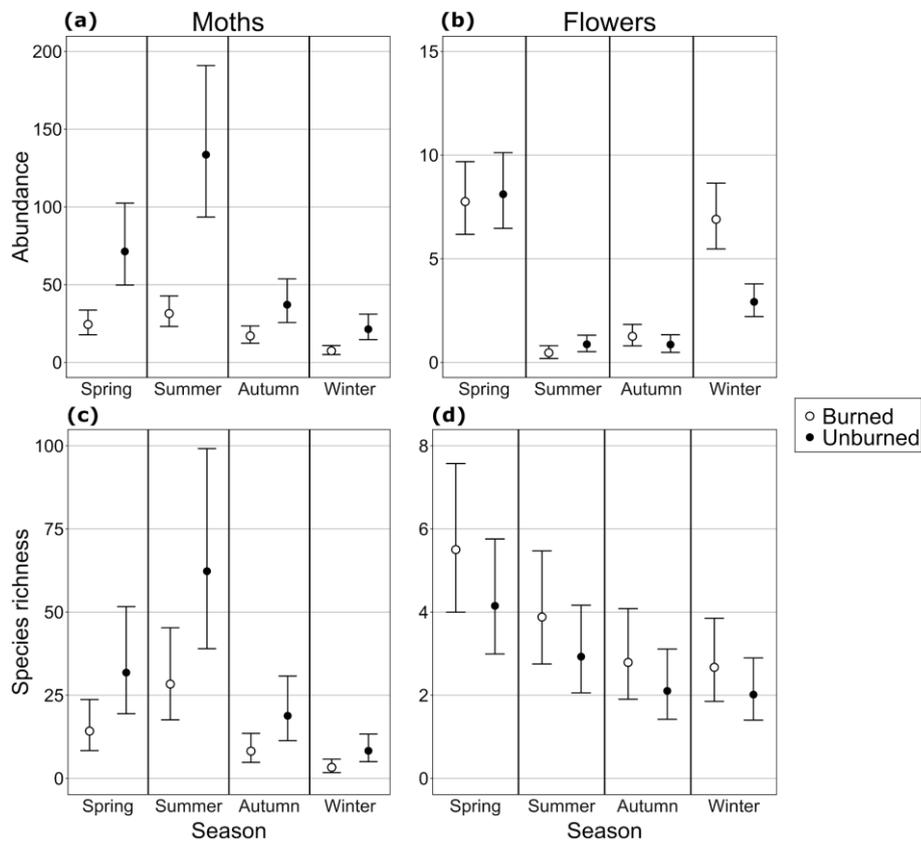
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656 **Figures**

657 **Figure 1: The effects of fire and season on the abundance and estimated species richness**
658 **of moths and flowers at burned sites (open circles) and unburned sites (closed circles).**

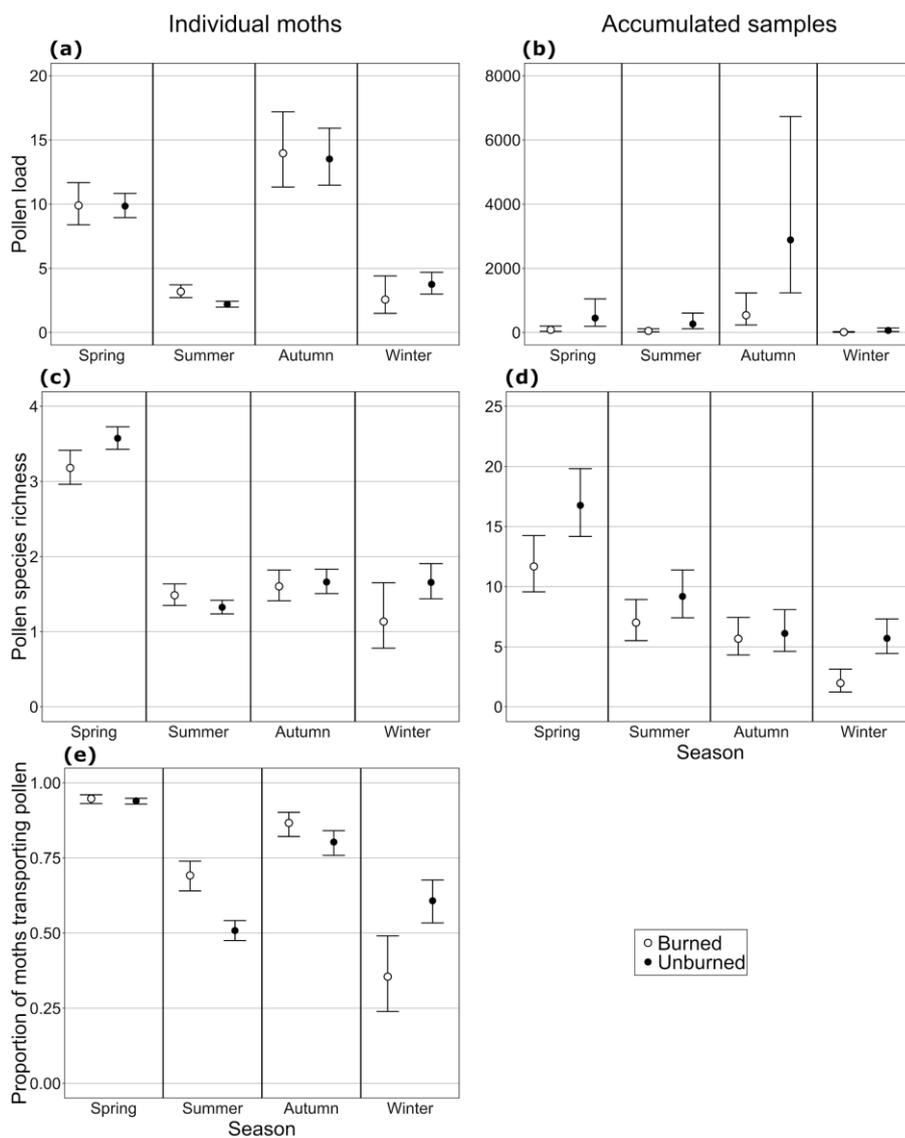
659 For moths, circles represent the model-predicted abundance and species richness per trap; for
660 plants in flower, circles represent the model-predicted percentage cover and species richness
661 per transect. Error bars show 95% confidence intervals. Species richness was estimated using
662 the Chao2 incidence-based estimator. Analyses of moth abundance and species richness were
663 based on moth-trap samples (n = 73); analyses of floral abundance and species richness were
664 based on 1 x 1 m quadrats (n = 1260).



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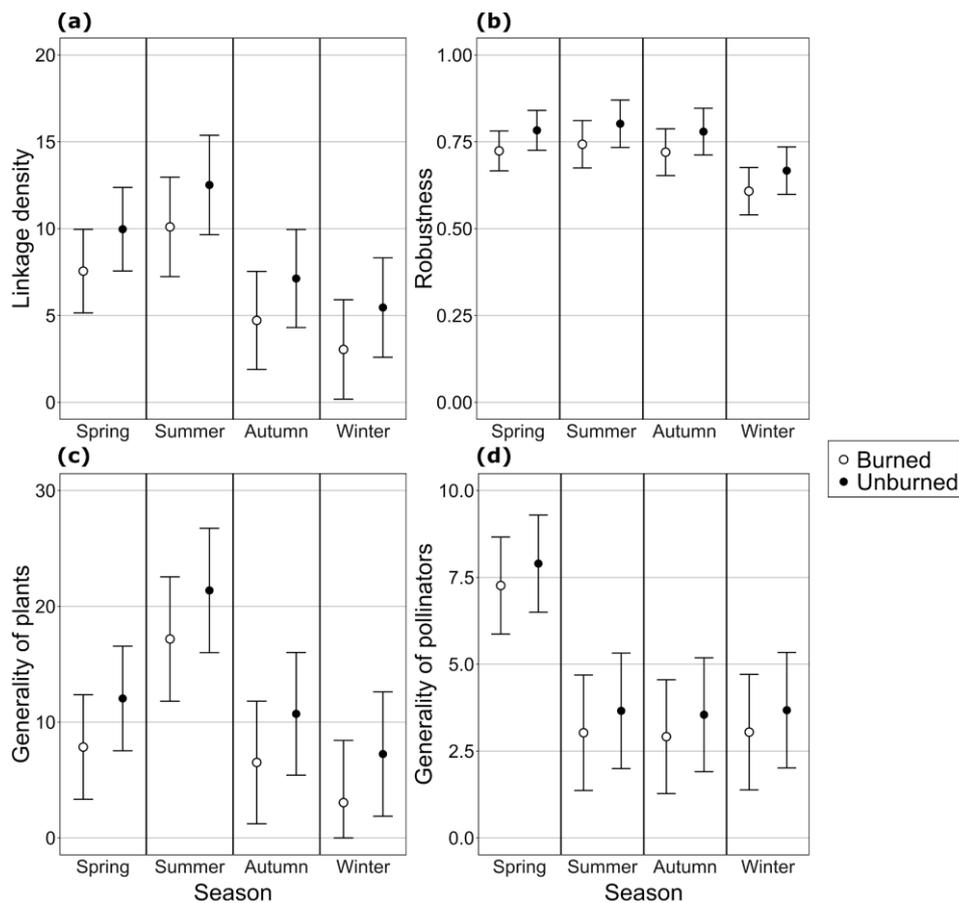
666

667 **Figure 2: The effects of fire and season on the pollen loads of moths.** Circles represent the
 668 model-predicted pollen load (a) and species richness (c) of pollen of individual moths, the
 669 cumulative pollen load (b) and richness (d) of all moths in a sample, and (e) the model-
 670 predicted proportion of moths found to be carrying pollen (open = burned sites, closed =
 671 unburned sites). Error bars show 95% confidence intervals. Analyses of the pollen loads of
 672 individual moths were based on pollen-carrying moths ($n = 2394$), analyses of accumulated
 673 samples of pollen were based on moth-trap samples ($n = 73$), and analysis of the proportion
 674 of moths carrying pollen was based on all individual moths ($n = 3406$).



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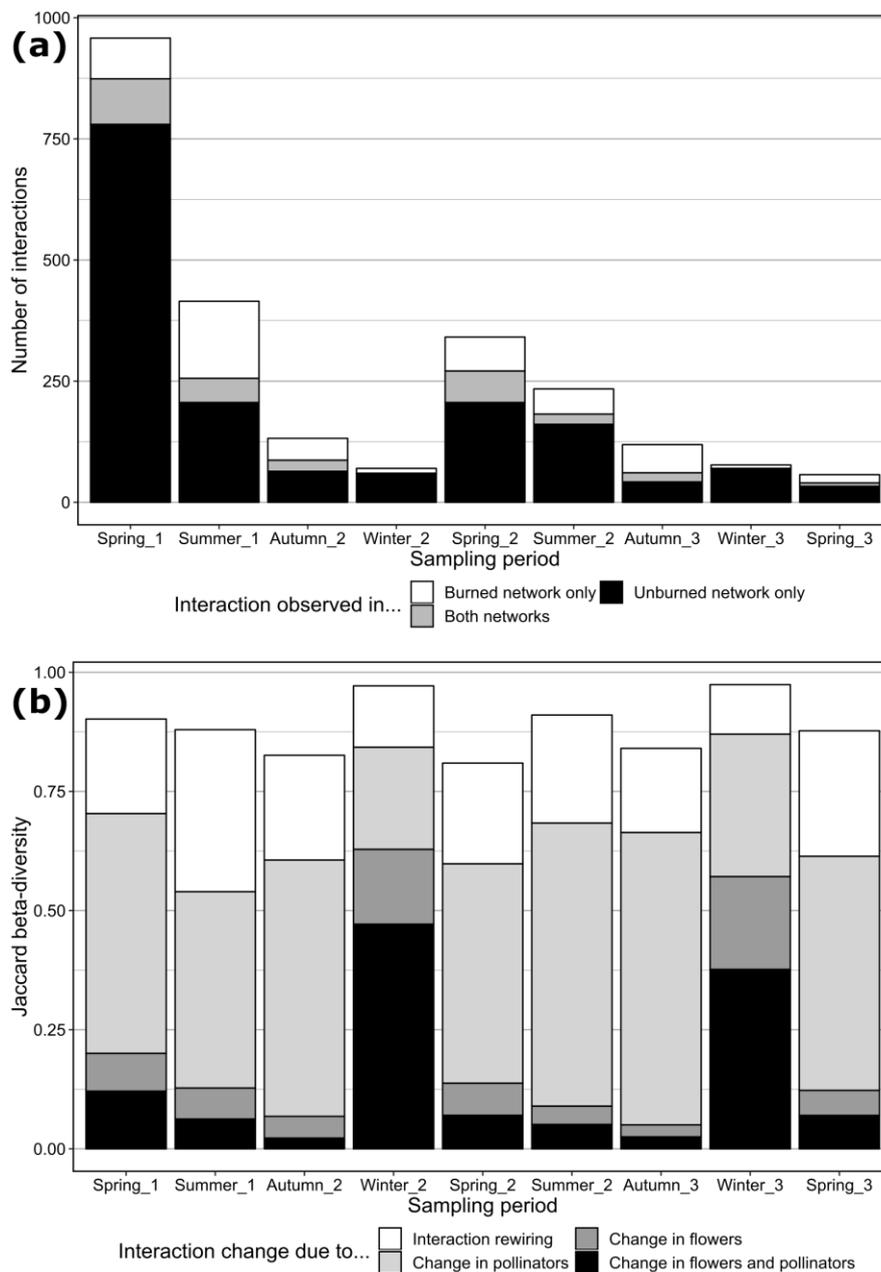
676 **Figure 3: The effects of fire and season on a selection of network metrics** (linkage
677 density, robustness, generality of plants and generality of moths) calculated for quantitative,
678 interaction frequency-weighted, pollen-transport networks. Points represent the model-
679 predicted network metrics and error bars show 95% confidence intervals. Analyses were
680 based on one burned network and one unburned network for each sampling period in the
681 study ($n = 18$).



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684 **Figure 4: The quantity and causes of spatial interaction turnover between burned and**
 685 **unburned networks.** In (a), bars show the total number of unique interactions observed in
 686 each sampling period, and coloured sections show the proportion of those interactions
 687 observed in the burned or unburned network only or in both networks. In (b), bars show the
 688 total Jaccard β -diversity value for spatial turnover of interactions in each sampling period,
 689 and coloured sections show the proportion of interaction turnover caused by change in
 690 flowers, moths or both, or by interaction turnover (Table S10).



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