

Fire influences the structure of plant–bee networks

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Abstract

1. Fire represents a frequent disturbance in many ecosystems, which can affect plant–pollinator assemblages and hence the services they provide. Furthermore, fire events could affect the architecture of plant–pollinator interaction networks, modifying the structure and function of communities.
2. Some pollinators, such as wood-nesting bees, may be particularly affected by fire events due to damage to the nesting material and its long regeneration time. However, it remains unclear whether fire influences the structure of bee–plant interactions.
3. Here, we used quantitative plant–wood-nesting bee interaction networks sampled across four different post-fire age categories (from freshly-burnt to unburnt sites) in an arid ecosystem to test whether the abundance of wood-nesting bees, the breadth of resource use and the plant–bee community structure change along a post-fire age gradient.
4. We demonstrate that freshly-burnt sites present higher abundances of generalist than specialist wood-nesting bees and that this translates into lower network modularity than that of sites with greater post-fire ages. Bees do not seem to change their feeding behaviour across the post-fire age gradient despite changes in floral resource availability.
5. Despite the effects of fire on plant–bee interaction network structure, these mutualistic networks seem to be able to recover a few years after the fire event. This result suggests that these interactions might be highly resilient to this type of disturbance.

KEYWORDS

generality, modularity, Monte desert, pollinator, post-fire, species degree, trap-nests, wood-nesting bee

1 | INTRODUCTION

Most flowering plants need to be pollinated by insects or other animals to reproduce (Ollerton, Winfree, & Tarrant, 2011). Therefore, plant–pollinator interactions are of great importance for the maintenance of biodiversity (Allen-Wardell et al., 1998; Biesmeijer et al., 2006) and for food production world-wide (Garibaldi et al., 2013; Rader et al., 2016). In a strongly human-modified world, plant–pollinator assemblages and

the services they provide are threatened by multiple environmental changes (Potts et al., 2010), such as climate change (Forrest, 2015; Memmott, Craze, Waser, & Price, 2007), alien species (Aizen, Morales, & Morales, 2008) and land-use change (Brown & Paxton, 2009; Winfree, Aguilar, Vázquez, LeBuhn, & Aizen, 2009).

In many ecosystems, fire represents the most frequent disturbance and the main cause of habitat conversion (Argañaraz, Pizarro, Zak, & Bellis, 2015; Bond, Woodward, & Midgley, 2005), affecting the plant and pollinator assemblages therein. Previous studies have shown that while plant–pollinator assemblages can be drastically affected by

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fire events (Potts et al., 2003), they exhibit high resilience, recovering rapidly after fire (Capitanio & Carcaillet, 2008; Moretti, Duelli, & Obrist, 2006; Turner, Romme, & Tinker, 2003; Van Nuland et al., 2013). Furthermore, the effects of fire on pollinator diversity exhibit substantial spatial variation (Grundel et al., 2010; Lazarina et al., 2016, 2017; Moretti, Obrist, & Duelli, 2004; Potts et al., 2003), potentially because the relative importance of fire as a disturbance varies according to the type of ecosystem studied. As most studies up to date focus on mediterranean scrubland and forests, we still do not know how plant–pollinator communities in more climatically extreme ecosystems, such as drylands, respond to fire events.

Apart from the direct effects of fire on plant communities, and hence on flower feeding resources for pollinators, the variability in the dispersal ability of pollinators, their different requirements of nesting resources and their degree of generalism can influence their response to fire events. For instance, generalist pollinators might cope with human disturbances, including fire, better than specialist pollinators, presumably because generalists are more likely to switch partners if necessary (Lazarina et al., 2016), such that generalist pollinators can be dominant in sites with recurrent fire events (Grass, Berens, Peter, & Farwig, 2013; Lazarina et al., 2016; but see Vázquez & Simberloff, 2002). Furthermore, a change towards higher generalism within pollinator species might be observed in sites that have recently suffered from fire events, potentially resulting from a change in the feeding behaviour of species to resource scarcity and habitat disturbance (Goverde, Schweizer, Baur, & Erhardt, 2002).

Besides effects on plant and pollinator species, fire could also affect their interactions (Brown, York, Christie, & McCarthy, 2017), as interactions depend not only on species presence and abundance but also on phenology, behaviour and physiology of the multiple interacting species (Forrest, 2015; Memmott et al., 2007), which can also be altered by fire events (Platt, Evans, & Davis, 1988; Van Nuland et al., 2013). Furthermore, interactions can change and even cease to occur before species are lost (Aizen, Sabatino, & Tylianakis, 2012; Tylianakis, Didham, Bascompte, & Wardle, 2008), which can affect ecosystem structure and functioning. For instance, if fire increases the abundance of generalist species, plant–pollinator interaction network generality could also increase, and with it the cohesion of the network (i.e. the extent to which different parts of the network interact with each other). Increased generalism and network cohesion could impact community fragility, as effects of other disturbances could spread faster across the entire community (Stouffer & Bascompte, 2011). Despite the great importance of these network properties for the persistence and resilience of communities (Thébaud & Fontaine, 2010), it still remains unknown whether fire events affect interaction networks of plant–pollinator assemblages.

In this study, we investigated how the abundance and degree of generalism of pollinators and the plant–pollinator interaction network structure change across post-fire successional age gradient categories (from freshly-burnt to unburnt sites) in the Monte Desert of Argentina. To this end, we used bipartite plant–bee networks constructed from pollen contents in brood cells of wood-nesting bees, that is, pollen collected by female bees to feed their offspring. Specifically, we tested

three hypotheses. Our first two hypotheses relate to the idea that generalist wood-nesting bee species could cope better with fire disturbances than specialists, because they can take greater advantage of increased post-fire floral diversity, particularly of herbaceous species. Thus, our first hypothesis posits that the abundance of wood-nesting bees across the post-fire gradient depends on their regional specialization (their overall degree of generalism across the post-fire gradient, that is, the species plasticity in pollen resource use), leading to higher abundance of generalist bees in freshly-burnt sites compared to sites with greater post-fire age. Our second hypothesis posits that wood-nesting bees change their feeding behaviour, that is, local (site-specific) resource specialization, in response to post-fire age due to changes in the diversity of floral resources available. We therefore expect that site-specific bee generalism increases in freshly-burnt sites compared to other sites. Our final hypothesis is that the effects of post-fire age on wood-nesting bees lead to changes in the structure of plant–bee networks. Consequently, we expect that an increase in the abundance of generalist bees and/or in the generalism of bee species in freshly-burnt sites compared to other sites leads to higher network generality and cohesion.

2 | MATERIALS AND METHODS

2.1 | Study region and sampling

Our study area was located in the Monte Desert of Villavicencio Nature Reserve, Mendoza, Argentina (32°32'S, 68°57' W), between 1100 and 1500 m.a.s.l. The Monte is a xeric biome (Cabrera, 1953) with a long history of human-induced fire (Rostagno, Defossé, & del Valle, 2006; Villagra et al., 2009). In Villavicencio, fire occurrence is highly spatially heterogeneous, which allowed us to select 14 sites within four contrasting post-fire age categories (from 1–2 to over 50 years since last fire) (Table 1). The minimum and maximum distances between sites were 1.11 km and 14.13 km, respectively, (see Table S1 in Supporting Information).

At each site, we used trap-nests to sample quantitative interactions between wood-nesting bees and the plant species they interact with under standardized nesting conditions (Tscharrntke, Gathmann, & Steffan-Dewenter, 1998). We established six plots at each site, separated by 100 m (forming a 100 m × 200 m rectangle; Figure S1). At each plot we set up groups (packages) of wooden trap-nests of different length and hole diameter to maximize the diversity of species nesting in the traps. At each plot, we set up two bundles of 16

TABLE 1 Number of sampling sites assigned to different post-fire age categories according to time since last fire

Post-fire category	Post-fire age (years)	Number of sites
Freshly-burnt	1–2	2
Intermediate-burnt	7–8	4
Old-burnt	15–22	4
Unburnt	>50	4

trap-nests (with holes 150 mm long and 5 and 8 mm of diameter) and two bundles of 8 trap-nests (with holes 280 mm long and 11 mm of diameter), that is, 288 traps per site (Figure S2). We checked the traps weekly from the beginning of October to the end of December 2008, the period of maximum bee activity. Occupied traps were taken to the lab and replaced by empty ones. Each trap constituted a bee nest, usually formed by multiple cells; only rarely were two nests of different bee species found in the same trap. In the laboratory we extracted one cell of each nest for pollen identification, which we identified based on a reference collection prepared with flowers sampled on the same sites. From these nest cells we also measured the proportion of pollen grains from each plant species as an estimate of plant–bee interaction weights. We used this proportion as an estimate of how much pollen of each plant species each bee species is using in its nest. The remaining nest cells were kept in the laboratory under ambient conditions until adult emergence, which allowed the morphological identification of the bee species.

The information from all the traps within each site was combined to obtain one plant–wood-nesting bee interaction network per study site. Each interaction network was represented as a matrix, with bee species as columns, plant species as rows and each cell containing the sum of pollen proportions of a particular plant species found in all the trap-nests of a particular bee species in that site. Hence, the column sums of each interaction matrix represent the number of nests built by each bee species (as in Vázquez et al., 2012). A list of the plant and bee species involved in this study and locations where voucher specimens have been deposited can be found in Table S2.

Because differences in floral resources available for bees could explain changes in bee abundance, behaviour and plant–bee interactions, we measured the diversity of floral resources available at each site. During the trap-nest sampling period we registered weekly all the flowering plant species, and the number of flowers of each species, that were assumed to be animal pollinated (excluding grass species) at four 8 m × 20 m plots and two 2 m × 50 m transects per site (Figure S1). Floral resource diversity per site was calculated using all the floral records across the entire sampling period.

2.2 | Analyses

As fire can modify the diversity of floral resources available for pollinators, we used an ANOVA to determine whether floral Shannon diversity of sampling sites changed across post-fire age categories. Also, to assess whether floral resource diversity available for bees at each site affected the diversity of pollen diversity found on the traps, we used a linear model with trap-pollen (Shannon) diversity (calculated based on the pollen collected in all the traps of each site) entered as the response variable and floral diversity of each site as the predictor variable. We calculated the Shannon diversity index using the function `diversity` from the `vegan` R package (Oksanen et al., 2017).

We tested whether bee abundance changed across a post-fire age gradient, whether it was affected by floral diversity and whether bee species with higher degree of generalism (i.e. regional

specialization) were more abundant in sites that recently suffered from fire events. To this end, we used a generalized linear mixed-effects model (GLMM) with Poisson error distribution. We entered bee abundance (number of traps occupied by each bee species) as the response variable, and floral diversity, bee normalized degree (calculated from the entire dataset, $N_{d_{ed}}$), fire regime (factor with four levels) and the interaction between normalized degree and fire regime as fixed factors. To estimate the overall degree of generalism of each bee species ($N_{d_{ed}}$), that is, their regional specialization, we used the data of all sites combined. This overall degree of generalism represents the fraction of all plant species connected to each bee species, and was calculated using the species-level function of the bipartite R package (Dormann, Gruber, & Fründ, 2008). We included bee species names as a random factor to remove between-species variability, although excluding this random factor did not qualitatively affect the results.

Because fire could affect the feeding behaviour of wood-nesting bees, specifically increasing their site specialization degree of generalism in freshly-burnt sites, we compared bees' normalized degree across post-fire ages (i.e. site specialization) only for those bee species that were present in all post-fire age categories. In this case, we calculated the normalized degree of each bee species on the different fire regimes (ND_{pfa}) by pooling data from different sites within the same post-fire age. Hence, ND_{pfa} was then number of plant species each bee species interacts with in the different post-fire ages, normalized to account for differences in the number of partners available in the different post-fire ages (i.e. degree for each bee species divided by the number of potential partners – 1). We then built a linear mixed-effects model with the normalized degree of each species on the different post-fire ages (ND_{pfa}) as the response variable and post-fire age and floral (Shannon) diversity as the predictor variables. We included bee species names as a random variable to compare changes in generalism within species.

Finally, we evaluated whether fire affects the structure of plant–wood-nesting bee networks, particularly increasing network generality (relative generalism of bees) and cohesion. As a measure of network cohesion we used modularity, a measure of the extent to which subsets of a network interact among themselves, such that lower modularity would reflect higher cohesion. We calculated generality based on both presence–absence of interactions (the mean number of plant species with which bees interact) and quantitative pollen usage (the mean effective number of plants per bee weighted by their marginal totals), as qualitative and quantitative network generality elucidate different aspects of network structure and how species abundance and generalism aggregate into network-wide patterns. We calculated both qualitative and quantitative generality (Bersier, Banasek-Richter, & Cattin, 2002) and quantitative modularity (Dormann & Strauss, 2014) of the fourteen interaction networks, using the network-level function from the bipartite R package (Dormann, Fründ, Blüthgen, & Gruber, 2009; Dormann et al., 2008). We then used three ANCOVAs, with qualitative generality, quantitative generality and modularity as the response variable, respectively. Floral diversity was used as a continuous predictor and post-fire age as a categorical predictor in all the models.

We used the `glmer` and `lmer` functions of the `lme4` R package (Bates, Maechler, Bolker, & Walker, 2015) for the Poisson and Gaussian mixed models, respectively, and the `glm` function for the ANCOVA models. We tested their corresponding assumptions (overdispersion, normality and homoscedasticity) and log transformed modularity to meet the assumptions. The best fitting model was selected in all analyses by running the full model as well as all possible simpler models, and selecting the model with the lowest Akaike information criterion (AIC) value as the final one (Burnham & Anderson, 2002). All analyses were performed in the R 3.3.1 environment (R Development Core Team 2016).

3 | RESULTS

Over 290 trap-nests (14% of the traps established) were occupied by 10 wood-nesting bee species during our sampling period (Table S2), with 70% of the bee species present across the entire post-fire age gradient. Normalized degree of bee species calculated from the entire dataset, that is, considering the pollen from all the nests across all fire regimes (ND_{ed}), varied from 0.04 to 0.62 ($M \pm SD = 0.293 \pm 0.188$). Overall, trap-nests contained pollen from 45 plant species (Table S2). In particular, trap-nests from freshly-burnt sites contained pollen from 31 plant species, 74% of which were present in the surrounding area (i.e. they were part of the 76 plant species found flowering on freshly-burnt sites). In intermediate-burnt sites, traps had pollen from 26 plant species, 65% of which were part of the 50 plant species found flowering in those sites. Old-burnt sites trap-nests contained pollen from 26 species, 73% of which were part of the 83 plant species flowering in those sites, while trap-nests from unburnt sites had pollen from 28 species, 54% of which formed part of the 54 plant species flowering assembly of those sites.

Although the diversity of floral resources available for pollinators was higher in recently burnt sites (Figure 1), there were no significant differences across post-fire age categories ($F = 0.892$, $p = .479$). Furthermore, despite the high percentage of trap-nests pollen species found in the surrounding areas, we found no relationship between the diversity of floral resources available at the sampling sites and

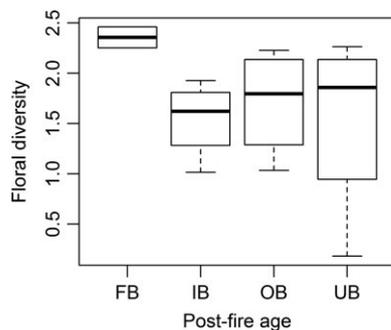


FIGURE 1 Floral (Shannon) diversity across post-fire ages (FB, freshly-burnt; IB, intermediate-burnt; OB, old-burnt; UB, unburnt). Floral diversity did not change significantly across post-fire age categories (see Results)

the diversity of pollen collected from the nesting traps ($t = -1.652$, $p = .124$).

We found that wood-nesting bee species with higher normalized degree were more abundant than specialists across all fire regimes (Figure 2). The slope of this abundance–generalism relationship was significantly higher in freshly-burnt sites compared to intermediate-burnt (interaction term: $Z = -3.370$, $p = .001$), old-burnt (interaction term: $Z = -4.424$, $p < .001$) and unburnt sites (interaction term: $Z = -4.987$, $p < .001$) (Figure 2, Table S3). Furthermore, there was a significantly negative effect of floral diversity on bee abundance ($Z = -2.577$, $p = .010$).

Despite changes in the abundance of wood-nesting bees across post-fire age, bee species did not seem to change their behaviour towards higher generalism in freshly-burnt sites compared to intermediate-burnt ($t = -1.142$, $p = .258$), old-burnt ($t = -0.307$,

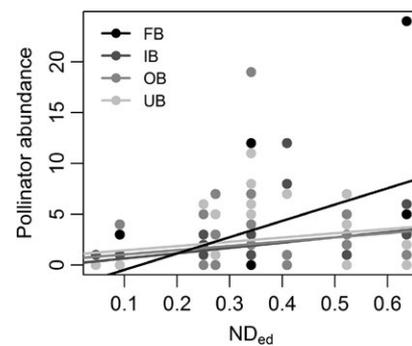


FIGURE 2 Relationship between wood-nesting bee species abundance in the different post-fire categories and bee's normalized degree calculated from the entire dataset (ND_{ed}). Post-fire age: FB, freshly-burnt; IB, intermediate-burnt; OB, old-burnt; UB, unburnt. Although a generalized linear mixed-effects model was used to evaluate changes in the abundance–generalism relationship across the post-fire gradient (Table S3), the least squares trend lines are shown to illustrate the direction of the relationships

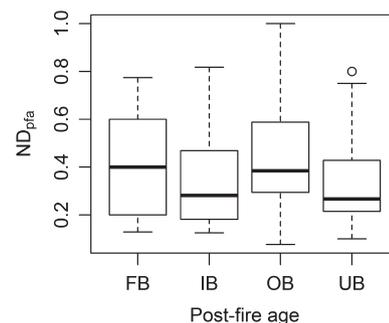


FIGURE 3 Wood-nesting bees' normalized degree (ND_{pfa}) across post-fire ages (FB, freshly-burnt; IB, intermediate-burnt; OB, old-burnt; UB, unburnt). ND_{pfa} was calculated for each bee species on each of the different post-fire ages. Only bee species that were present in all the different post-fire age categories were used for comparisons. In each box plot, the middle line indicates the median, bottom and top box limits are the first and third quartiles, respectively, whiskers indicate most extreme points 1.5 times the interquartile range, and circles indicate outliers

$p = .760$) and unburnt ($t = 0.736$, $p = .465$) sites (Figure 3, Table S4). Furthermore, post-fire age was not even retained in the best fitting model (Table S4), where only floral diversity was retained as a predictor with no significant effects on bees' generalism ($t = 1.086$, $p = .282$).

Finally, when comparing plant–wood-nesting bee interaction network structure from different post-fire ages (Figure 4, Figure S3), we found significant differences both in generality and modularity of the networks (Figure 5). In particular, we found that qualitative generality was significantly higher in freshly-burnt sites compared to intermediate-burnt ($t = -2.658$, $p = .024$), old-burnt ($t = -2.482$, $p = .032$) and unburnt ($t = -2.407$, $p = .037$) sites (Figure 5a, Table S5), while floral diversity was not retained in the best fitting model (Table S5). Network quantitative generality, however, did not differ across post-fire ages, nor was this variable retained in the best fitting model (Figure 5b, Table S5). Even though floral diversity was the only predictor variable retained in this model, it did not have a significant effect on quantitative generality ($t = -0.642$, $p = .533$). Meanwhile, interaction network modularity from freshly-burnt sites was significantly lower than that of intermediate-burnt ($t = 2.934$, $p = .015$), old-burnt ($t = 2.616$, $p = .026$) and unburnt ($t = 2.475$, $p = .033$) sites (Figure 5c, Table S5). Floral diversity was not retained in this best fitting model either (Table S5).

4 | DISCUSSION

In many areas, including our study region, fire represents the most common and widespread anthropogenic disturbance (Argañaraz et al., 2015; Bond et al., 2005; Ponisio et al., 2016; Rostagno et al., 2006). Here, we have shown that the time of recovery since the last fire event not only influences wood-nesting bee communities but also the structure of interaction networks formed by these bees and the plant species they interact with.

In particular, we found that the relationship between abundance and the degree of generalism of wood-nesting bee species was stronger in freshly-burnt sites, suggesting that generalist bees are more

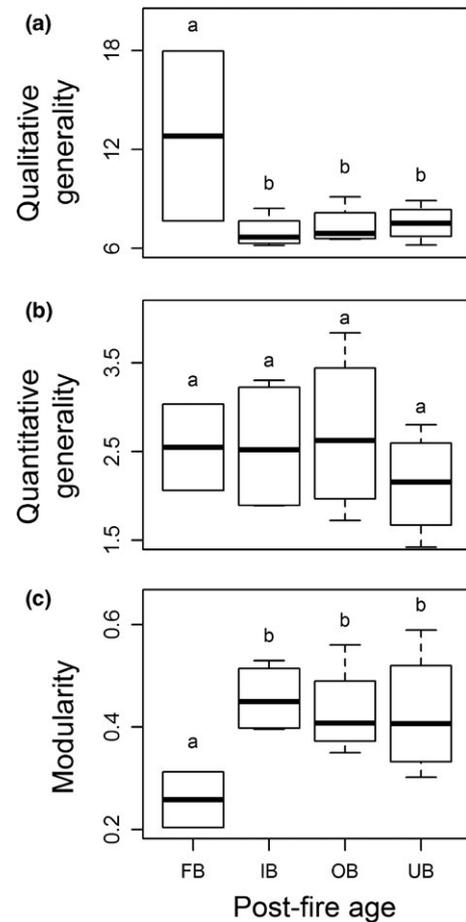


FIGURE 5 Plant–wood-nesting bee interaction network structure across post-fire ages. (a) Qualitative network generality, (b) quantitative generality and (c) modularity. FB, freshly-burnt; IB, intermediate-burnt; OB, old-burnt; UB, unburnt. Other conventions as in Figure 3. Different letters show significant differences at $p < .05$ (see Results)

abundant in these sites compared to sites that had longer time to recover since the last fire. This result could be due to higher flexibility of these species to feed on different resources and hence take

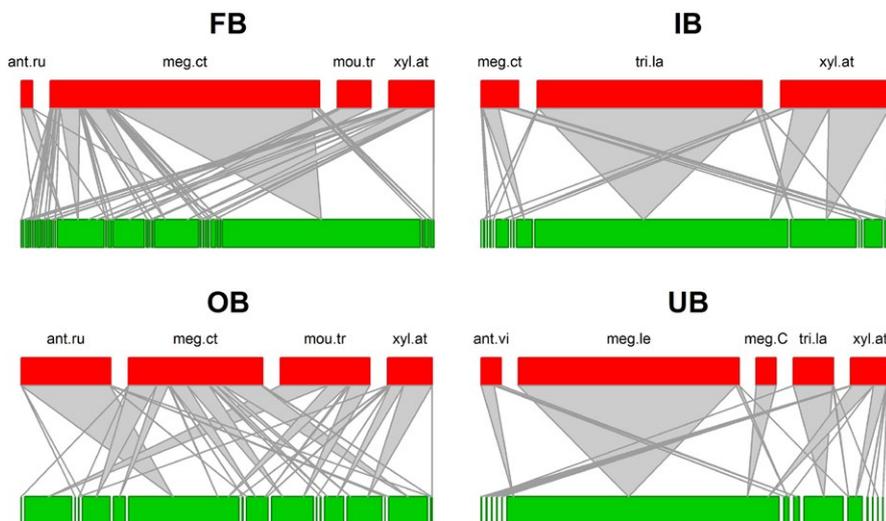


FIGURE 4 Examples of plant–wood-nesting bee networks across post-fire ages. Upper and lower bars represent bee and plant species, respectively, with links among them representing interactions. FB, freshly-burnt; IB, intermediate-burnt; OB, old-burnt; UB, unburnt. Bee species names: ant.ru = *Anthidium rubripes*, ant.vi = *Anthidium vigintipunctatum*, meg.le = *Megachile leucographa*, meg.C = *Megachile* sp. C, meg.ct = *Megachile ctenophora*, mou.tr = *Mourecoctelles triciliatus*, tri.la = *Trichothurgus laticeps*, xyl.at = *Xylocopa atamisquensis* [Colour figure can be viewed at wileyonlinelibrary.com]

advantage of what it is available after the fire event. Nevertheless, bees did not seem to change their feeding specialization behaviour across the post-fire age gradient. A potential explanation of this observation is that bees could find their preferred feeding resources in nearby areas (Gathmann & Tscharntke, 2002). It is important to notice that even though the vegetation of plots that have recently suffered from fire events can change dramatically in the Monte Desert, the plant coverage and composition recover relatively quickly after fire. Also, in this region the landscape mosaic is formed by habitats with different fire histories as well as preserved areas, such that bees could find their preferred offspring-feeding resources in a relatively short flying distance and are hence not forced to change their feeding behaviour. Furthermore, at the species level, it might not be convenient to change the offspring-feeding resources, which would explain the lack of a positive relationship between the local site plant diversity and the pollen diversity of the trap-nests, as the reproductive success of bees does not necessarily depend on local plant diversity (Dorado & Vázquez, 2016).

Despite the lack of changes in behaviour at the species level, at the community level freshly-burnt sites had significantly higher qualitative generality (based on the presence-absence of interactions), although there were no differences across post-fire ages in quantitative generality (the average number of plant species with which each bee species interacted at each particular site weighted by the pollen usage). This result could be explained by the fact that all interaction networks from the different post-fire ages had few strong interactions, and that freshly-burnt networks also had many weak interactions. This pattern in the strength of interactions would lead to greater qualitative generality in freshly-burnt networks, as weak and strong interactions contribute equally to generality under such metric; however, because the quantitative version of generality weights the stronger interactions more heavily, the additional weak interactions in the freshly-burnt sites would not make a large enough difference to be significant.

Recent fire occurrence was associated as well with lower network modularity (i.e. higher network cohesion) compared to networks that had longer post-fire ages, suggesting that fire could blur modules, potentially due to the higher abundance of these generalist pollinators (Olesen, Bascompte, Dupont, & Jordano, 2007). Theory predicts that modularity can have stabilizing effects in ecological networks (Grilli, Rogers, & Allesina, 2016), which suggests communities from freshly-burnt sites, that have lower modularity, could be less resilient to perturbations than communities with longer time since fire. Lower modularity in interaction networks could increase community fragility and susceptibility to other disturbances that could spread faster across the entire community (Stouffer & Bascompte, 2011), ultimately impacting on species survival (Thébaud & Fontaine, 2010).

Plant-wood-nesting bee interaction networks were similar at sites that had not been burnt for 7 to over 50 years (intermediate-burnt, old-burnt and unburnt sites), suggesting that in this desert ecosystem, 3–7 years after a fire event plant-pollinator communities

acquire a persistent structure that varies little for many years. Similarly, in Mediterranean forest ecosystems, sites in which fire had occurred at least 4 years before had no differences in pollinator diversity (Lazarina et al., 2016). Taken together, these studies suggest that plant-pollinator assemblages in ecosystems ranging from Mediterranean to drylands recover relatively quickly after fire, suggesting high resilience to this disturbance. Although in our study system wood-nesting bees represent only c. 6% of the pollinator species richness, wood-nesting bees are frequent visitors of many key plant species from the Monte Desert (Chacoff, Vázquez, Lomáscolo, Stevani, & Padrón, 2012). Furthermore, by using the bee-nesting guild as a study system, we avoided the confounding effects of different bees' nesting habits.

Although the effects of fire have been assessed previously for plant and pollinator diversity (Capitanio & Carcaillet, 2008; Grundel et al., 2010; Lazarina et al., 2016; Potts et al., 2003), to our knowledge our study is the first to show that fire can affect plant-bee interaction networks and it is also the first to show fire effects on bee abundance in an arid ecosystem. In particular, we have shown that fire can affect plant-bee interaction network structure. Furthermore, 70% of the bee species were present across the entire post-fire age gradient, which suggests that network changes are driven mostly by interaction re-wiring rather than changes in species composition. Yet, after c. 7 years post-fire these networks exhibit some apparently time-invariant properties (e.g. lower generality and higher modularity). This result suggests that communities can be quite resilient to fire events, although this resilience might depend on the extent of adjoining plant-pollinator source areas, fire frequency and history of fires in the area. Therefore, beyond changes in species diversity, determining the effects of global environmental changes on species interactions and the way in which they assemble forming complex networks of interactions can provide important information on ecosystem function and restoration practices.

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AUTHORS' CONTRIBUTIONS

E.L.S., J.D., N.P.C. and D.P.V. designed the study and collected data. G.P., E.L.S. and D.P.V. conducted analyses. G.P. wrote the manuscript. All authors commented on the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.c7844> (Peralta, Stevani, Chacoff, Dorado, & Vázquez, 2017)

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