PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Structural resilience and high interaction dissimilarity of plant–pollinator interaction networks in fire-prone grasslands

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Abstract

Fire is a frequent disturbance in most grasslands around the world, being key for the structure and dynamics of the biodiversity in such ecosystems. While grassland species may be resilient, little is known on how plant–pollinator networks reassemble after fire. Here, we investigate the structure and dynamics of plant–pollinator networks and the variation in species roles over a 2-year post-fire chronosequence on grassland communities in Southern Brazil. We found that both network specialization and modularity were similar over the chronosequence of time-since-fire, but in freshly burnt areas, there were more species acting as network hubs. Species roles exhibited high variation, with plant and pollinator species shifting roles along the post-disturbance chronosequence. Interaction dissimilarity was remarkably high in networks irrespective of times-since-fire. Interaction dissimilarity was associated more with rewiring than with species turnover, indicating that grassland plant and pollinator species are highly capable of switching partners. Time-since-fire had little influence on network structure but influenced the identity and diversity of pollinators playing key roles in the networks. These findings suggest that pollination networks in naturally fire-prone ecosystems are highly dynamic and resilient to fire with both plants and pollinators being highly capable of adjusting their interactions and network structure after disturbance.

Keywords Mutualism · Modularity · Post-fire · Rewiring · Specialization

Introduction

Grassland ecosystem dynamics are often related to disturbances caused by fire (Bond 2008; Lehmann et al. 2014). Fire may promote biodiversity and is one of the main drivers of ecological and evolutionary patterns on grasslands (Bowman et al. 2009, 2016). However, fire effects can also be negative depending on fire regimes, and the resistance and resilience of the ecosystem (Geldenhuys et al. 2004). While ecosystem resistance is related to the capacity to remain unchanged in the face of disturbance, ecological resilience expresses the capacity to tolerate disturbance without collapsing into a different state, i.e., persistence of an ecologically stable state (Holling 1973). Although measurement and application of the ecological resilience concept to ecosystem management are still very challenging (Standish et al. 2014), it has been mostly assessed through recovery, after a disturbance, to pre-disturbance levels of ecosystem components such as community diversity, composition, and multitrophic interactions (Dell et al. 2019). Plant communities from tropical and subtropical grasslands are highly resilient to (and even dependent on) disturbances such as fire and grazing (Buisson et al. 2019). However, there is still little understanding on how fire affects species interactions and whether (and how) interaction networks reassemble after fire (Brown et al. 2017). Prescribed burning has been used for

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management, and since natural fires are common in certain ecosystems, understanding fire effects on species and ecosystems may inform effective management practices (Valkó et al. 2014; Gillson et al. 2019).

Mutualistic interactions between plants and animals, such as pollination, provide critical ecosystem services (Potts et al. 2016). Because most plants depend on pollinators for reproduction and many animals rely on floral resources, effective conservation strategies should integrate both groups and their interactions (Kearns and Inouye 1997; Ollerton et al. 2011). However, elaboration of such strategies is hampered by the lack of understanding on how fire affects plant–pollinator interactions. In open vegetation ecosystems like grasslands and savannas, fire is thought to benefit floral visitors by increasing flower availability shortly after fire, which suggests that fire can be used as a management tool at local and landscape levels to increase pollinator abundances and diversity (Ponisio et al. 2016; Brown and York 2017; Pyke 2017). In fact, conservation strategies aiming to reduce the ecological and economic consequences of pollinator declines have been increasingly discussed (Kremen et al. 2007), but management of fire regimes has been rarely considered for open ecosystems of South America, where studies on the effects of fire on plant–pollinator interactions are scarce (Beal-Neves et al. 2020; Baronio et al. 2021).

At the community level, plant–pollinator interactions can be described as networks. Recurrent non-random interaction patterns have been documented in plant–pollinator networks and indicate the importance of niche partitioning among coexisting species to shape network structure and dynamics (Bascompte and Jordano 2007; Bascompte 2009; Vázquez et al. 2009; Vizentin-Bugoni et al. 2018). Such niche partitioning often leads to ecological networks with high modularity and specialization (Cordeiro et al. 2020). Modularity consists of the existence of subsets of species that interact preferentially with each other within a network, forming compartments or modules (Olesen et al. 2007; Vizentin-Bugoni et al. 2018), which are thought to increase network stability, since disturbances tend to propagate more slowly across modular networks (Thébault and Fontaine, 2010; Landi et al. 2018). Modules, in turn, emerge as a result of ecological, evolutionary, and/or neutral processes that define specialization and niche partitioning (Cordeiro et al. 2020). For example, modules formed by plants with long tubular corollas and long-billed pollinators suggest "private" niches where these plants experience reduced competition with short-tubed flowers, while these animals avoid competition with short-billed visitors (Maruyama et al. 2014). Furthermore, the number of partners of a species may depend on species abundances as more abundant species have higher chances to encounter and interact with partners than rarer species, thus influencing species specialization (Fort et al. 2016). Also, in specialized and modular networks, species

may play distinct roles depending on how interactions are distributed across partners and can be classified according to their connectivity within and among modules as network hubs, module hubs, connectors, or peripherals (Guimerà and Amaral 2005; Olesen et al. 2007). Evaluating such roles allows identifying key species for network cohesion and how such roles vary across disturbance gradients. However, to our knowledge, no study so far has investigated how species roles are affected by fire disturbance.

Responses of interaction networks to disturbances depend critically on the ability of species to rewire to new partners following species loss, which increases network robustness and, potentially, resilience (Biella et al. 2020; Vizentin-Bugoni et al. 2020). Rewiring seems to be pervasive in mutualistic plant–animal interactions, leading to high levels of interaction dissimilarity across networks (Zhang et al. 2011; CaraDonna et al. 2017; Vizentin-Bugoni et al. 2019). In ecosystems where fire imposes high species turnover across a successional gradient of times-since-fire (Potts et al. 2003; Overbeck et al. 2005), high interaction dissimilarity may be expected, caused by species turnover more than by partner switching. However, a few studies have addressed the effects of fire on plant–pollinator interactions in fire-prone grasslands and savannas (Welti and Joern 2018; Beal-Neves et al. 2020; Baronio et al. 2021). The extent of species turnover and partner switching in causing interaction dissimilarity in plant–pollinator networks affected by fire remains unknown. Filling these gaps may advance our understanding on how plant–pollinator interactions and their networks respond to fire, also informing conservation and management initiatives (Kearns et al. 1998).

Here, we investigated the structure, species roles, and interaction dissimilarity in plant–pollinator networks across a chronosequence of grassland patches with different times-since-fire in Southern Brazil. As grassland ecosystems have a long evolutionary history of fire disturbance, plants and pollinators are expected to be highly resilient to fire, changing roles in the network and flexibly switching partners. Plant–pollinator networks should be resilient and reassemble quickly after disturbance. Specifically, we asked: (1) how does network structure (i.e., modularity and complementary specialization, i.e., the degree of exclusiveness of the interactions between plants and pollinators considering the entire community) vary among grasslands with different times-since-fire? (2) How does species specialization and species roles (i.e., species contribution to connectivity within and among modules) change across the chronosequence? And (3) how much does interaction dissimilarity vary among plots with the same or different times-since-fire? Considering that fire has been shown to promote short-term increases in flower availability and density (Fidelis and Blanco, 2014; Mola and Williams, 2018; da Silva et al. 2020; Goldas et al. 2021) and at least in one instance, an increase in network

generalization (Welti and Joern 2018), we hypothesize that freshly burnt grasslands would present lower complementary specialization (network-level specialization) and modularity. Also, due to high generalization, we expect more species acting as network hubs in freshly burnt areas (da Silva et al. 2020). We expect higher levels of interaction dissimilarity across areas of distinct times-since-fire (compared to areas with same time-since-fire), with this dissimilarity mainly associated with species turnover across the chronosequence. Conversely, in areas with longer time-since-fire, we expect higher specialization and modularity, a reduced number of species playing network hub roles, and lower interaction dissimilarity.

Materials and methods

Study area

Our study was carried out in grassland areas within the Saint' Hilaire Municipal Park (30° 5′ 11.39″ S, 51° 5′ 39.00″ W) in Viamão municipality, Brazil. This protected area has 1148.62 hectares of native grassland and forests amidst the urban environment. Campos Sulinos are natural grassland ecosystems, relics of Holocene climate, resisting forest expansion over grassland, and shrubby ecosystems after the increase in humidity of the Late Holocene (Behling and Pillar 2007). Paleoecological studies carried out in the grasslands suggest that natural fire events were rare during the Late Quaternary glacial period (ca. 40,000 years BP), becoming frequent in the early Holocene (Behling et al. 2004, 2005). This increase in fire frequency coincides with the initial occupation of the area by humans (Dillehay et al. 1992). More recently, grasslands have been used for cattle breeding and managed with fire since the introduction of European cattle in the eighteenth century (Porto 1954).

Campos Sulinos grasslands are maintained largely due to grazing by cattle and management by farmers who mow and burn grasslands after winter to increase resprouting (Behling and Pillar 2007; Behling et al. 2007; Fidelis and Pivello 2011). Campos Sulinos are highly diverse ecosystems, composed of C4 and C3 grasses, forbs, and shrubs, with high diversity of Poaceae, Asteraceae, Fabaceae, and Rubiaceae species (Overbeck et al. 2006; Overbeck and Pfadenhauer 2007). However, land conversion to agriculture, forestry, and other land uses have reduced natural grassland cover by over 50% (Cordeiro and Hasenack 2009; Staude et al. 2018). Only 0.8% of these grasslands are within protected areas (Oliveira et al. 2017), illustrating the underrepresentation of non-forest environments among protected areas in Brazil (Overbeck et al. 2015).

Grasslands at the study site are not formally managed with a prescribed burning regime or grazing animals. Saint' Hilaire Municipal Park is surrounded by urban areas and has several conflicts with local residents, such as improper use by people and pets, burning, and garbage dumping in some areas. Owing to anthropogenic action, the Park faces a regular burning regime with random patches being occasionally burnt from late winter and early spring, through summer. In terms of fire frequency, these grassland areas are usually burned every 2 or 3 years. These fire events are not uniformly distributed in space and time, which results in a mosaic of grassland patches with different post-disturbance stages (i.e., times-since-fire). Fire intensity in this region is classified as low in comparison with other grassland ecosystems, because the disturbance regimes do not allow for flammable biomass to accumulate (Fidelis et al. 2010).

Sampling design

We selected 12 burned grassland patches (sites) classified in three time-since-fire categories: freshly burnt (less than 6 months since the last fire), intermediate-burnt (about 1 year after fire), and old-burnt grasslands (2 years since fire). Information regarding the fire history of each studied site was provided by park rangers, and further validated with satellite images (when available). Burns were all accidental or deliberate uncontrolled anthropogenic fires occurring between September and December. Sampling of freshly burnt sites started 2 months after the fire, which is the minimum time necessary for vegetation to recover and start blooming again. Burned patches varied from 0.60 to 7.74 hectares, but did not significantly differ among time-since-fire categories (Goldas et al. 2021). Proximity to urban areas, and proportion of grasslands and forest surrounding the burned patches also did not vary with the fire treatments, indicating that site selection was unbiased (Goldas et al. 2021).

Data collection

Sampling was carried out during two growing seasons: one in 2015/2016 (6 sites), and another in 2016/2017 (six different sites), and replicated in three rounds per growing season (i.e., spring: November/December, summer: January/February, and autumn: March/April), thus encompassing the seasonal variation of the system. In each growing season, we sampled two sites (burned patches) within each time-since-fire category.

In each site, we established six 10 × 10 m plots inside which interaction observations were carried out. First, we recorded all flowering plant species in the plots (further details in Goldas et al. 2021). Then, we observed floral visitors for a 15 min period in one individual of each plant species per site. This focal plant individual was selected within one among the six plots per site. The total observation time

spent per site was thus dependent of its flowering plant species richness. For each round, we repeated observations in three periods of the day: 08–11 h, 11–14 h, and 14–17 h. Up to two plant species were observed concomitantly if they were closely located. For plants that were not easily identifiable in the field, vouchers were collected and identified by specialists. All floral visitors that contacted reproductive parts of the flowers (i.e., legitimate visits) and, therefore, acted as potential pollinators were collected with entomological nets. The pollinators were killed in a lethal chamber containing ethyl acetate, labeled, and stored. At the lab, they were pinned and identified by specialists to species level when possible or assigned to morphospecies. We considered an interaction every time a pollinator was observed on a flower (regardless of the number of flowers visited) and performed a legitimate visit. For other details on sampling in general, refer to Goldas et al. (2021).

Statistical analyses

For each of the 12 sites, we built a weighted interaction matrix by pooling plots, periods of the day, and within-site rounds. A matrix has plant species as rows, pollinator species as columns, and the intersection between rows and columns representing the number of legitimate visits observed by each pollinator on each plant species. To evaluate network resilience, we explored variation in network metrics (modularity, network-level complementary specialization [H_2', Blüthgen et al. 2006]) and species-level metrics (species-level specialization index d', species roles) across grasslands from different time-since-fire categories. We further evaluate interaction dissimilarity between different time-since-fire categories and within the same category. All statistical analyses were performed using *R* (R Development Core Team 2020).

Network level

To calculate modularity, we used the Q metric and the DIRTLPAwb + algorithm which searches for the optimal division of weighted bipartite networks into modules (Beckett 2016). Modules emerge when subsets of species interact more strongly among themselves than with other species in the network. Q ranges from 0 (lowest modularity possible) to 1 (highest modularity possible). Q was calculated using the *computeModules* function of the package *bipartite* (Dormann et al. 2008). As Q values may be slightly variable across runs owing to the stochastic nature of the optimization algorithm, we ran ten repetitions for each network (or null matrix, see below) and accepted the highest value obtained. We also calculated the specialization (H_2') which quantifies the deviation between the realized interaction frequencies and the expectation from a null model that assumes

that all partners interact in proportion to their availability, where marginal totals of the interaction matrices are used as proxies for availability. Thus, H_2' represents an estimation of the degree of niche partitioning in the network and ranges from 0 for the most generalized to 1 for the most specialized networks (with exclusive interactions).

To evaluate the significance of modularity (Q) and complementary specialization (H_2') for each network, we produced 1000 random networks generated by the Patefield null model (*r2dtable* function in *bipartite*)—which reshuffles interactions producing random networks with the same dimensions (i.e., number of species in each trophic level) and marginal totals as the observed network (Blüthgen et al. 2008). We considered a network significantly modular or specialized when the observed values of these metrics were higher than the 95% confidence interval generated by the null model. We also used null models to improve comparability across networks with varying dimensions and connectance. Specifically, we calculate a z-score, which is the difference between Q (or H_2') in the observed matrix and the mean Q (or mean H_2') obtained with the null models (Dalsgaard et al. 2017).

We used Generalized Linear Models (GLM) to compare z-score values of Q and H_2' (response variables) among time-since-fire categories (predictor variable). Response variables followed a Gamma distribution, and models were built using the *stats* package. Year of sampling was considered the first term in the models, as a blocking variable, to control for potential variation in the effects of time-since-fire in the response variables. We further performed likelihood-ratio tests comparing fitted models with null models (i.e., including only year of sampling as predictor). Tukey HSD post hoc tests were used to compare effects between pairs of time-since-fire categories, when needed.

Species level

We also calculated species-level specialization (d' index), which describes the deviation of realized interactions in comparison to a null model that assumes that all partners are used in proportion to their availability, having marginal totals as proxies for partner availability (Blüthgen et al. 2006). This metric ranges from 0 for the most generalized to 1 for the most specialized species. We then fitted GLM (Gamma distribution) and used likelihood-ratio tests as already described to test whether species-level specialization (d') for pollinators and plants differed among the three time-since-fire categories. For these tests, we used the averaged d' value of each taxon (species/morphospecies) obtained for each of the 12 networks. For pollinators, we performed an analysis considering all species and, separately, considering each taxonomic group (bees, beetles, flies, wasps, and butterflies).

We classified species based on their roles for within-module connectivity (z) and among-module connectivity (c) following Guimerà and Amaral (2005) (adapted by Olesen et al. 2007). Species were classified among four roles: *network hubs* (high c and high z, meaning that a species is highly linked both within its own module and with other modules in the network), *module hub* (low c and high z, when a species is highly connected within its own module but weakly connected to species in other modules), *peripheral* (low c and low z, when a species has few links both within or among modules), or *connectors* (high c and low z, when a species connects distinct modules, but has few links within its own module (Olesen et al. 2007). The reference values for each classification of roles in the network followed Olesen et al. (2007).

Interaction dissimilarity

We then calculated the interaction dissimilarity between pairs of networks both *within* and *between* categories of times-since-fire. We used the function *network_betadiversity* of the package *betapart* (Poisot et al. 2012) which calculates interaction dissimilarity using Whittaker's (1960) equation

$$\beta_{WN} = \frac{a+b+c}{\frac{(2a+b+c)}{2}} - 1,$$

where a is the number of shared interactions between networks A and B, b is the number of interactions unique to network A, and c is the number of interactions unique to network B. β_{WN} represents the total interaction dissimilarity and ranges from 0 (when all interactions are shared) to 1 (when no interaction is shared). β_{WN} was then decomposed into two additive components: *species turnover* (β_{ST}) which is the proportion of interactions that are not shared due to differences in species composition between two networks, and *rewiring* (β_{OS}) which is the proportion of interactions that only occur in one network despite the occurrence of both partners in both networks (Poisot et al. 2012).

Results

Across all networks, we detected 284 pollinator taxa and 70 plant species that performed 1646 interactions (Supplementary Material 1). Most pollinators' taxa were bees (36%), followed by beetles (29%), flies (18%), wasps (10%), and butterflies (6%). Twenty-six plant families were recorded, with Asteraceae being the richest (37 species) and most-visited plant family, receiving 24% of all visits, followed by Rubiaceae and Fabaceae with 22% and 21% of all visits, respectively. Network sizes varied as follows: freshly burnt had 156 pollinator species (61.7 ± 11.4; mean $\pm$ s.d. across all four

sites within each site type), 49 plant species (25.2 ± 4.3), and 672 interactions (168 ± 52.9; Fig. 1A); intermediate-burnt had 134 pollinator species (49.7 ± 8.3), 35 plant species (18 ± 2.4), and 472 interactions (118 ± 24.6; Fig. 1B); and old-burnt had 152 pollinator species (51.2 ± 7), 44 plant species (20.7 ± 2.5), and 501 interactions (125.2 ± 38.5; Fig. 1C). Sampling coverage was similar across sites and categories of time-since-fire (see Supplementary Material 2).

Network structure

All networks were significantly modular when compared with null models ($p < 0.01$): (Q values old-burnt $= 0.72 \pm 0.03$; intermediate-burnt $= 0.68 \pm 0.02$; freshly burnt $= 0.68 \pm 0.04$; mean $\pm$ s.d.). Based on the z-score values, modularity did not differ significantly among time-since-fire categories (deviance $= 0.16$; df $= 2, 11$; $p = 0.72$; Fig. 2A).

All networks presented higher specialization than expected by the null model ($p < 0.01$), being highest in the old-burnt network ($H_2' = 0.65 \pm 0.07$), followed by intermediate-burnt ($H_2' = 0.57 \pm 0.04$), and freshly burnt ($H_2' = 0.49 \pm 0.06$). However, based on the z-score values, complementary specialization did not differ significantly among time-since-fire categories (deviance $= 0.11$; df $= 2, 11$; $p = 0.82$; Fig. 2B).

Species-level specialization and species roles

Specialization (d') of plant species (deviance $= 0.06$; df $= 2, 11$; $p = 0.24$) and total pollinator species (deviance $= 0.09$; df $= 2, 11$; $p = 0.19$) did not differ among time-since-fire categories (Fig. 3A and B). Analyses performed for each pollinator group separately showed that butterflies in freshly burnt grasslands were less specialized than those in intermediate-burnt and old-burnt grasslands (deviance $= 1.21$; df $= 2, 11$; $p < 0.01$; Tukey, $p < 0.01$; Fig. 3C). Specialization of bees (deviance $= 0.04$; df $= 2, 11$; $p = 0.59$), beetles (deviance $= 0.05$; df $= 2, 11$; $p = 0.41$), wasps (deviance $= 0.22$; df $= 2, 11$; $p = 0.62$), and flies (deviance $= 0.11$; df $= 2, 11$; $p = 0.79$) did not differ among categories (Fig. 3D–G).

Values for c and z showed that, while most species act as connectors or peripherals, the role played by the main pollinator species (network hubs and module hubs) is dynamic across networks with variable time-since-fire (Figs. 1 and 4). Most of the network hub species were bees (Fig. 4) and the number of pollinator species acting as network hubs did not significantly differ among freshly burnt (5 species), intermediate-burnt (1 species), or old-burnt (2 species) networks, with similar results for module hubs (Fig. 4, and Supplementary Material 3). Among plants, no species acted as network hub or module hub, all species being classified as

(A) Freshly-burnt

(B) Intermediate-burnt

(C) Old-burnt

Legend

■ Plants   ■ Pollinators

Network hubs   Module hubs   Peripherals/connectors
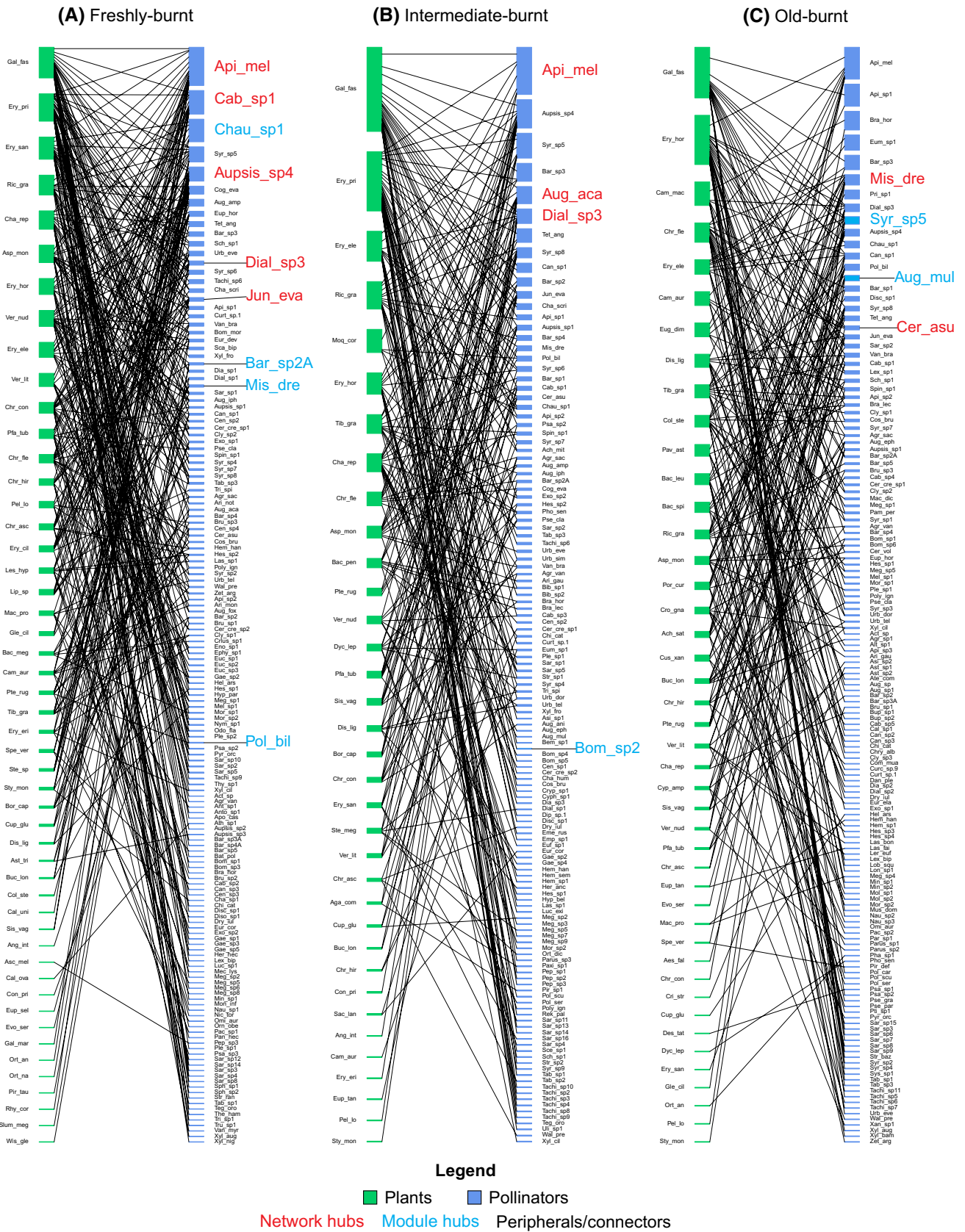
◄**Fig. 1** Interaction networks for grassland pollinator and flower species on different times-since-fire: **A** freshly burnt areas (6 months or less after fire); **B** intermediate-burnt (1 year); **C** old-burnt (2 years). Green rectangles represent plant species nodes and blue rectangles insect pollinator nodes; rectangle sizes reflect interaction frequency. Black lines connecting rectangles are pollination interaction links among species. Acronyms beside nodes are for species names; for full names and roles, see Supplementary Material 3. Acronyms in red are for species with a network hub role in the network; those in blue for the module hub role; names in black are for connectors/peripheral species. Networks represent data from four sites per category distributed in 2 sampling years

either peripherals or connectors regardless of the time-since-fire (Fig. 4 and Supplementary Material 3).

Interaction dissimilarity

Total interaction dissimilarity (β_{WN}) was high and mostly associated with interaction rewiring (βOS) rather than species turnover (βST) (Table 1). These results were consistent both for comparisons among networks between distinct categories (Fig. 5A) and within the same category of time-since-fire (Fig. 5B). Specifically, for networks of the *same* category of time-since-fire, the total dissimilarity varied from 0.90 to 0.95 on average, with 0.64–0.77 associated with rewiring and only 0.17–0.26 associated with species turnover. Similarly, between networks of *distinct* time-since-fire categories, total dissimilarity varied from 0.88 to 0.95 on average, with 0.68–0.75 associated with rewiring and only 0.20–0.25 associated with species turnover.

Discussion

Contrary to our predictions, plant–pollinator networks presented similar complementary specialization and modularity, and species-level measures of specialization across time-since-fire categories for plants and all groups of pollinators, except butterflies. More species appeared to act as network hubs in freshly burnt grasslands, but this trend was not significant. Interaction dissimilarity was remarkably high and associated more with rewiring than with species turnover. Surprisingly, interaction dissimilarity between networks of the same category of time-since-fire was as high as between networks of distinct times-since-fire. These findings indicate that fire has little influence on the structure and specialization of plant–pollinator interaction networks, but the identity and diversity of pollinators playing key roles in the networks vary across the chronosequence. We found that grassland species are highly flexible in their interaction partners, but that this flexibility is not necessarily associated with post-fire succession, since interactions were highly dissimilar due to rewiring (i.e., species co-occurring in both areas but

interact in only one) even across areas with the same time-since-fire. Altogether, these results indicate that grassland pollination networks are resilient to fire, maintaining overall network structure and specialization, which is probably possible due to rapid flowering responses from plants and the ability of plants and insect pollinators to switch partners.

Our findings contrast with other similar ecosystems, such as North American tallgrass prairies (Welti and Joern 2018) and Argentine Monte Desert scrubland/grasslands (Peralta et al. 2017), where plant–pollinator networks tend to increase specialization with time-since-fire, although longer times-since-fire were involved in these cases. We indeed found a general trend (although not statistically significant) for lower specialization in freshly burnt sites for plants and bees, and for all pollinators taken together, especially when contrasting freshly burnt against old-burnt sites. We found that plant and pollinator species tended to have similar niche breadths regardless of time-since-fire, which also led to similar complementary specialization and modularity over time. This is unexpected, considering that abundance and richness of grassland flowering plants increase shortly after fire (Fidelis and Blanco, 2014; Pyke, 2017; Goldas et al. 2021) and resource availability tends to decrease as post-fire dynamics progresses (Potts et al. 2003). In this scenario, both plants and pollinators would be expected to become more specialized over time as a consequence of higher competition for scarce resources. However, we found that within 6 months after fire network structure presented similar levels of specialization and modularity (both metrics translating patterns of niche partitioning) as networks of 2 years after fire. This is in line with the previous studies considering a longer post-fire chronosequence in open savanna in Cerrado (Baronio et al. 2021) and Southern Brazilian grasslands (Beal-Neves et al. 2020), which also found pollination networks with consistent structure over time. Such structural consistency was also recorded in pollination networks across a gradient of grazing intensity in the latter ecosystem (Oleques et al. 2019). Together, these results suggest that plant–pollinator interactions in this system present high resilience, rapidly reassembling after disturbance and maintaining their structure over the late-successional stages. This resilience may be due to different aspects of these communities and the fire disturbance endured in ecological and evolutionary terms, such as the long history of fire in these ecosystems, generally low fire intensity, fire-adaptive traits present in many plants, and the patchiness of fire events allowing pollinators to easily move to (or recolonize from) adjacent unburnt patches (Overbeck et al. 2018).

With the exception of butterflies, all pollinator groups showed similar specialization across grasslands. Butterflies are known to be sensitive to disturbances (Brereton et al. 2011; Van Swaay et al. 2015). While fire-suppressed areas are essential refuges for habitat-specialist butterflies
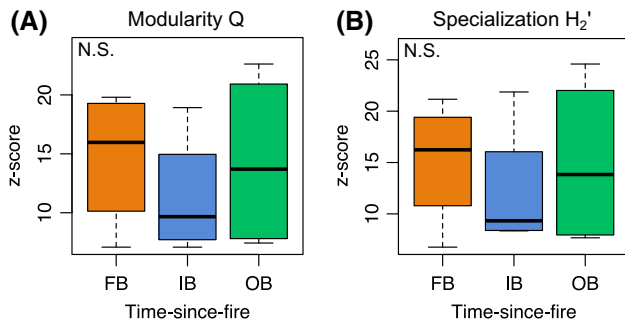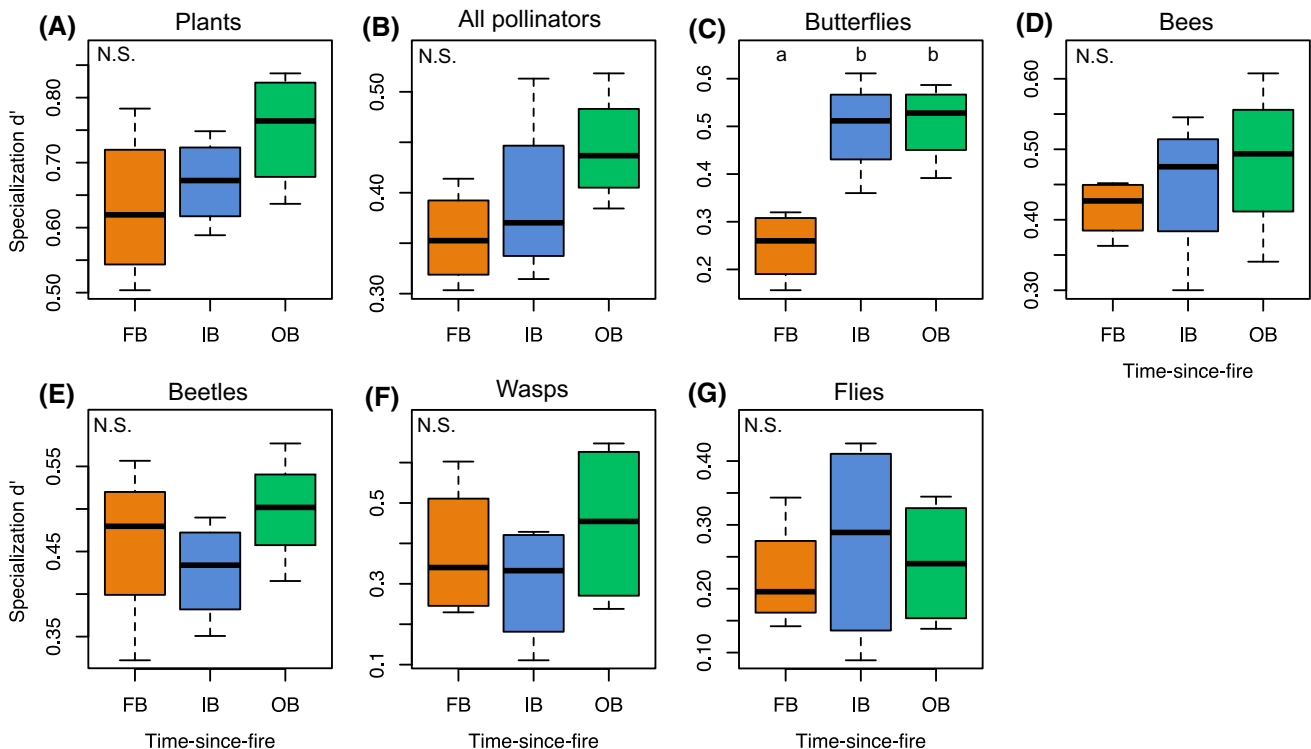
Fig. 2 Interaction network modularity Q **A** and complementary specialization H_2' **B** among grasslands with different time-since-fire categories (*FB* freshly burnt, *IB* intermediate-burnt and *OB* old-burnt). Boxplot components are the median (solid black line), first and third quartiles (box limits), and whiskers (maximum and minimum values). *NS* non-significant differences

(Swengel and Swengel, 2007; Swengel et al. 2011), freshly burnt grasslands may be highly attractive to butterflies due to resprouting of forbs and enhanced floral availability (Swengel et al. 2011; Vogel et al. 2007, 2010) which may explain the observed increasing abundance and lower specialization of this group soon after burning (but without changes in species richness or composition, Goldas et al. 2021). Our

results indicate that distinct groups of pollinators respond differently to fire, which is likely linked to its effect on the spatial heterogeneity of floral resources that, ultimately, shape plant–pollinator interactions.

As in other pollination networks, we also found that a few pollinator species act as network hubs while most species are peripherals (Olesen et al. 2007; Watts et al. 2016). Most of these network hubs were generalist bees indicating the disproportional role of this group in structuring these networks. Furthermore, pollinator species occurring in grasslands at distinct times-post-fire presented plasticity in their roles. For example, the introduced *Apis mellifera* acted as a network hub in freshly burnt and intermediate-burnt networks but was a connector in old-burnt grasslands. The ability of *Apis mellifera* to change network roles has been reported previously (Watts et al. 2016) and highlights its potential to drive network structure and dynamics in disturbed communities. Importantly, native bees also acted as network hubs, such as *Dialictus* sp. in both freshly burnt and old-burnt grasslands, *Augochloropsis* sp. in freshly burnt areas and *Augochlorella acarinata* and *Ceratina asunciana* in old-burnt areas, indicating that despite being surrounded by urban areas and suffering from anthropogenic disturbances, native


Fig. 3 Specialization, *d*', for **A** plants, **B** all pollinators, **C** butterflies, **D** beetles, **E** bees, **F** wasps, and **G** flies among grasslands with different time-since-fire categories (*FB* freshly burnt, *IB* intermediate-burnt, and *OB* old-burnt). Different letters denote significant differences ($p < 0.01$) based on a post hoc Tukey test, and NS, non-significant differences. Boxplot components are the median (solid black line), first and third quartiles (box limits), and whiskers (maximum and minimum values)

Fig. 4 Distribution of pollinator and plant species across distinct network roles (module hubs, network hubs, peripherals, and connectors) in grasslands with different times-since-fire in Southern Brazil. **A** Overall distribution of network roles. **B** Relative contribution of plant and pollinator groups in each role. For full species (or morphotype) names and roles, see Supplementary Material 3
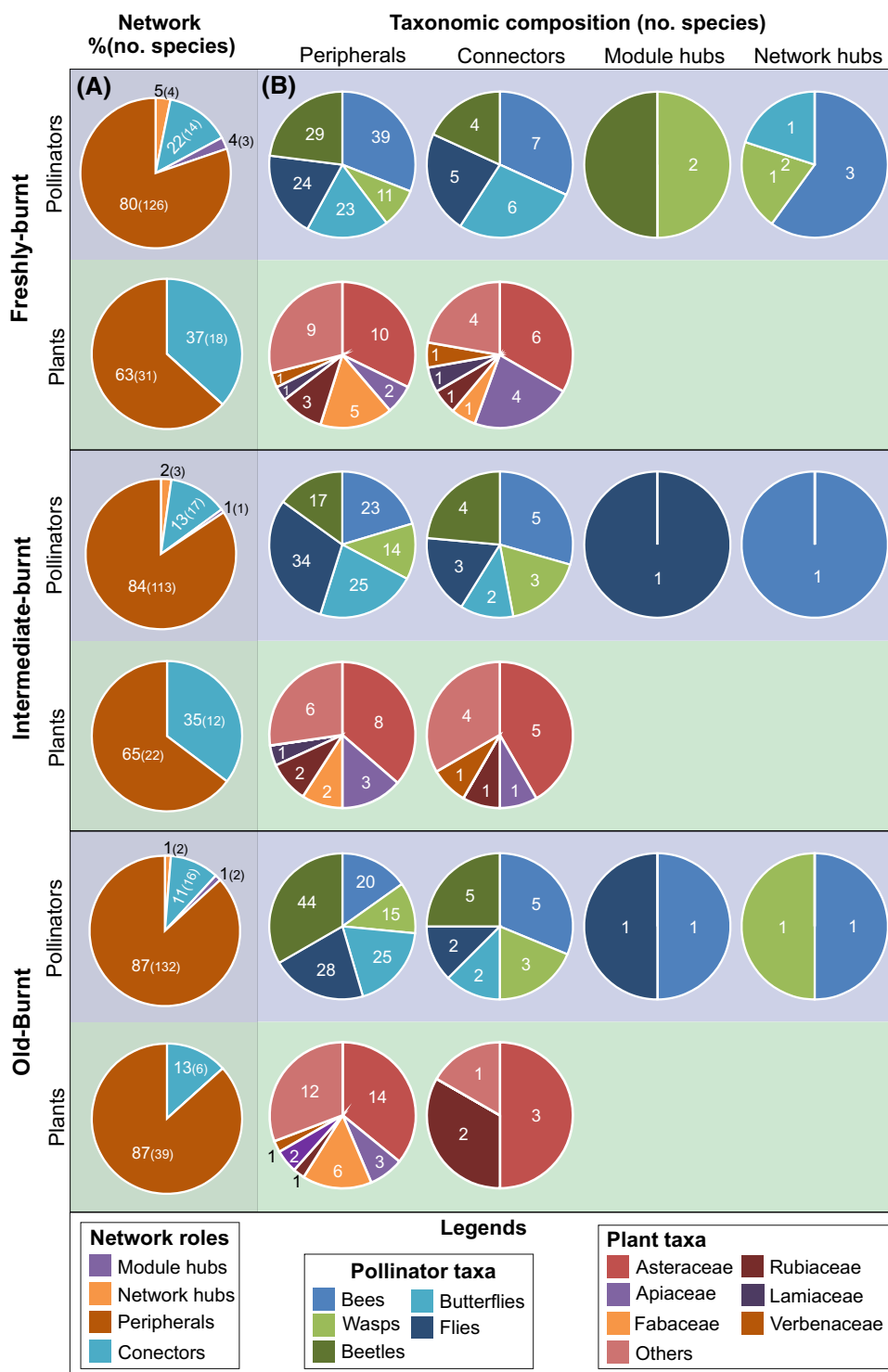

species still play key roles structuring local pollination networks. Other groups (butterflies, wasps, beetles, and flies) also had representatives as network hubs and module hubs, increasing the taxonomic and functional diversity of species important to network structure. Species from different taxonomic groups varied their roles in the network with the time-since-fire categories, probably influenced

by their intrinsic preferences, tolerances, or necessities regarding grassland habitat structure, which may affect their flower-visiting performance and competitive abilities in the environment (da Silva et al. 2020; Bruninga-Socolar et al. 2021). Unfortunately, information on the biology of the hub species is scarce in the study region, either for native bees or other insects, and although a

Table 1 Total interaction dissimilarity (βWN) and the proportion of the dissimilarity associated with species turnover (βST) and rewiring (βOS) across networks of the same or distinct categories of time-since-fire in Southern Brazilian grasslands

Comparison	Time-since-fire category	β_{WN}	β_{ST}	β_{OS}	N (pairs of areas)
Same category	Freshly burnt	0.94 ± 0.04	0.17 ± 0.08	0.77 ± 0.11	6
	Intermediate-burnt	0.90 ± 0.05	0.26 ± 0.06	0.64 ± 0.08	6
	Old-burnt	0.95 ± 0.05	0.20 ± 0.16	0.75 ± 0.21	6
Distinct categories	Freshly vs. intermediate-burnt	0.88 ± 0.21	0.20 ± 0.09	0.68 ± 0.21	16
	Intermediate vs. old-burnt	0.94 ± 0.04	0.25 ± 0.08	0.69 ± 0.12	16
	Freshly vs. old-burnt	0.95 ± 0.03	0.20 ± 0.10	0.75 ± 0.12	16

$N = 12$ sites sampled; 4 sites per category
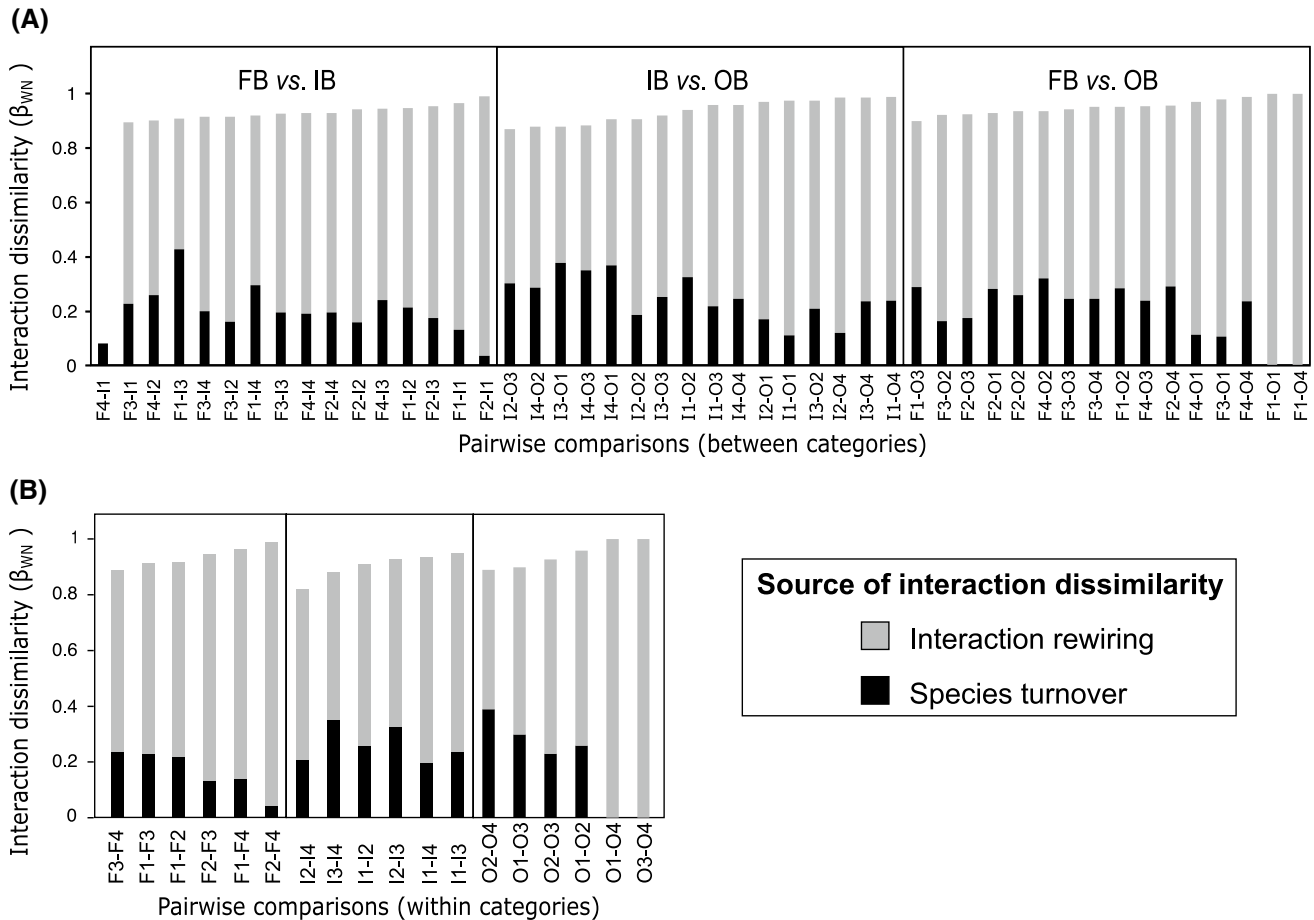
Fig. 5 Plant–pollinator interaction dissimilarity (β_{WN}) between (**A**) and within (**B**) categories of time-since-fire (*FB* freshly burnt, *IB* intermediate-burnt, and *OB* old-burnt). The total dissimilarity (β_{WN}; full bars) is composed of dissimilarity caused by species turnover (β_{ST}; darker shades) and rewiring (i.e., species not interacting despite both being present in the two areas considered) (β_{OS}; lighter shades)

trait-based approach of pollinator communities would be useful to further improve our understanding on network ecology of this system (Rader et al. 2014); at this moment, there are too many gaps. Interestingly, no plant species acted as network or module hubs, indicating that no single plant centralizes interactions with pollinators. In this scenario, no keystone plants can be identified in the pollination network, which suggests that to sustain a local

pollinator community, conservation of plant assemblages is necessary.

Interaction dissimilarity was remarkably high across networks, meaning that a few links (i.e., pairwise interactions) occurred repeatedly across multiple areas. Despite the existence of species turnover across time-since-fire categories (plants and bees) (Goldas et al. 2021), most of the dissimilarity (about 70%, on average) occurs due to partner switching,

meaning that even when species co-occur in two areas, they may only be observed interacting in one. This indicates high flexibility of both pollinators and plants to adjust interactions to distinct ecological scenarios which could require rewiring to new mutualistic partners, such as disturbances and varying resource diversity and abundance. This flexibility may represent an important ecological trait to succeed in highly patchy and dynamic ecosystems such as grasslands, whose evolutionary history is closely related to complex grazing and fire disturbance regimes. This also indicates the existence of relatively few constraints imposed by traits such as mismatching between corollas and insect mouthparts (Oleques et al. 2019). Furthermore, this dissimilarity is also remarkably high between networks of the same category of time-since-fire, which may be related to the marked spatial heterogeneity of both the vegetation and floral resources, even among areas of similar times-since-fire. In fact, in this ecosystem, disturbances create a mosaic of heterogeneous vegetation at small spatial scales, leading to floral resources being highly variable in quality, quantity, and flowering plant identity (Overbeck et al. 2005; Fidelis et al. 2012; Podgaiski et al. 2013; Fidelis and Blanco 2014; da Silva et al. 2020). This heterogeneity in turn may promote context-dependent interaction adjustments at this small scale, generating high dissimilarity in pollinator communities interacting caused by partner switching. It is also important to note that, despite sampling coverage being similar across sites (Figure S1), our complementary analyses indicate that a moderate fraction of the links was not detected (Table S1), which is commonplace in species-rich ecosystems (Jordano 2016). While such missing links may, to some extent, overestimate the proportion of interaction dissimilarity caused by partner switching, they may also reflect the opportunistic behavior of pollinators.

One apparent paradox emerges from our contrasting results: how can networks be modular and specialized in a system where species are so flexible to switch partners? In such a scenario, the intuitive expectation would be high generalization and lack of modules as virtually all species are capable of interacting one with another. A potential explanation is that ecological mechanisms, such as competition for floral resources, drive plants and pollinators toward specialization. Thus, a species' realized niche (i.e., resources used at specific sites) is much narrower than its fundamental niche (i.e., the pool of resources used in the entire region) (Hutchinson 1957; Vizentin-Bugoni et al. 2019). The existence of specialization and modularity in highly dissimilar networks has also been reported for mutualistic plant-seed disperser networks in novel ecosystems, where competition and ecological fitting may be at play (Janzen 1985; Vizentin-Bugoni et al. 2019). Modular networks may emerge in new ecological contexts owing to the lack of trait matching, which allows ecological fitting to operate, while competition pushes species toward specialization. In this scenario, specialization and modularity emerge in networks without coevolution between the species observed interacting in the present (Vizentin-Bugoni et al. 2019; Dormann et al. 2017).

In conclusion, our findings suggest that grassland plant–pollinator mutualistic networks are resilient to fire disturbance, and are shaped by plant and pollinator species highly capable of adjusting their roles and switching their interaction partners along post-fire community dynamics. By advancing understanding of how complex mutualistic networks respond to fire disturbance, this study provides basic empirical evidence to foster ongoing discussions on how fire disturbances may contribute to pollinator conservation initiatives. Simply fencing grasslands without fire management, as has been suggested for grasslands in this region and elsewhere, would probably not be an effective conservation initiative in terms of retaining pollinators and pollination functions (Pillar and Vélez 2010; Tylianakis et al. 2010). Thus, prescribed fires should be further evaluated as a management tool to preserve grassland-dependent species and their interactions in South American grasslands.

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Availability of data and materials We agree to archive the data in Harvard Dataverse https://dataverse.harvard.edu/

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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