



Does fire disturbance affect ant community structure? Insights from spatial co-occurrence networks

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Abstract

The coexistence of several species involves a complex mix of positive and negative interactions that can be represented as networks. As much as other ecological features, patterns of multispecies co-occurrence are susceptible to anthropogenic disturbance. In ant communities, wildfires may enhance competitive interactions by benefiting active, aggressive species, and by increasing encounter probabilities through decreased space availability. We explored ant co-occurrence patterns by analysing the macro and microscopic structure of their interaction networks in burned and unburned habitats. We built co-occurrence networks using significant aggregations and segregations between species pairs as positive and negative interactions, respectively. We described aggregate network properties and microscopic structural changes by comparing species and interactions turnover between burned and unburned sites. We found no differences in the macroscopic structure of co-occurrence networks between different fire regimes. However, we detected changes in the composition of both species and negative interactions. Interaction turnover between networks of different habitats was mostly explained by rewiring of interactions between shared species rather than by species replacement. Our results reflected changes in ant communities in response to fire although there were no changes in global structural patterns. These changes in species and negative interactions suggest modifications in species roles translated into changes in the spatial distribution of ant species. The analysis of species co-occurrence networks is a useful tool to detect and visualize patterns in ant communities and to understand the mechanisms underlying the effects of disturbance on biodiversity.

Keywords Coexistence · Formicidae · Interactions turnover · Interspecific interactions · Network structure

Introduction

A central assumption of the concept of biodiversity is that several species coexist in the same place at the same time (Hubbell 2001). Co-occurrence patterns could reveal not only shared habitat preferences but also the existence of reciprocal influences between species (Gotelli 2000; Cazelles et al. 2016). Accordingly, at small spatial scales

in homogeneous habitats, there should be an intrinsic tension between positive and negative interactions when multiple species that co-occur in space and time exploit similar resources (Allesina and Levine 2011). The complex mix of interactions involved in coexistence patterns can be represented as networks in which segregations between each pairwise species are represented by links of negative sign and aggregations as positive links (Kéfi et al. 2012; Morueta-Holme et al. 2016). The structure of co-occurrence networks can reveal patterns of species organization achieved to avoid conflicts (e.g., Saiz et al. 2016) or to exploit resources more efficiently (e.g., Bronstein 2009). In addition, as any other interaction networks, co-occurrence networks are susceptible to be altered by human disturbances (Kay et al. 2018).

There are several ways to explore the role of species in ecological networks. Species centrality, indicate which members of the community are more important, influencing other species persistence and ecological functions (Borrett 2013). Therefore, centrality allows us to identify keystone

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species that in the case of being extinct, its effect could propagate through the community affecting biodiversity (Saavedra et al. 2011; Borrett 2013). For example, in pollination networks, central species provide a more efficient pollination service than less central species (González et al. 2010). Moreover, it is known that a few dominant ant species, with superior competitive power, have a central role structuring ant–plant interaction networks (Dáttilo et al. 2014; Costa et al. 2016).

Ants are dominant organisms in most terrestrial ecosystems in terms of biomass and ecological function (Hölldobler and Wilson 1990; Lach et al. 2010; Griffiths et al. 2017), and have been frequently used to evaluate the relevance of competitive interactions in determining community structure (e.g., Savolainen and Vepsäläinen 1988; Cerdá et al. 2013; Soares 2013; Stuble et al. 2017). On this regard, ant species distribution was commonly studied based on the ‘ant mosaic theory’ that postulates that competition leads to species exclusion by dominant species (i.e., those that have aggressive behavior, occupy larger areas, and use diverse resources), which can coexist with subordinate and subdominant species (Majer 1972; Blüthgen and Stork 2007). Nevertheless, the definition of ant mosaics is highly contentious, since it depends on the criteria applied in the selection of dominant species and the kind of habitat studied (Sanders et al. 2007; Blüthgen and Stork 2007; Fayle et al. 2013).

In dry forest ecosystems, anthropogenic wildfires are one of the major threats to biodiversity affecting vegetation physiognomy and species diversity (Pyne et al. 1996; Pausas 2015). Wildfire long-term effects on arthropods are mediated by modifications in the plant community which result in changes in resources availability and micro-climatic conditions (Moretti et al. 2004; Kral et al. 2017; Paolucci et al. 2017). In the long-term, wildfires benefit ants adapted to open-areas and those with active and aggressive behavior over other species (Andersen 1995; Andersen et al. 2014; Farji-Brener et al. 2002; Arnan et al. 2013). Furthermore, the reduction of vegetation vertical structure under post-fire conditions enhances encounter probabilities between ant species (Blüthgen and Stork 2007), reinforcing competitive interactions in burned areas (Andersen 1995; Arnan et al. 2013). Accordingly, if dominant ants have a patchy distribution in burned habitats, subdominant or submissive species could occupy empty niches leading to species coexistence (“interstitial hypothesis”, Andersen 2008; Arnan et al. 2011). Therefore, behavioral dominant ant species could influence richness, structure and dynamics of local ant communities (Arnan et al. 2011, 2018).

Co-occurrence networks could be a suitable alternative to study the spatial organization of ant species, allowing to detect structural patterns and different species roles in the community. In this study, we evaluated changes in ant

communities by comparing the structure of species co-occurrence networks from burned and unburned sites. We expect changes in the role and identity of central species in post-fire scenarios since large, aggressive ants could be favoured by the open space (Andersen 1995; Andersen et al. 2014; Farji-Brener et al. 2002; Arnan et al. 2013). Regarding network topology, we expect that changes in species roles leads to more connected (of both positive and negative links) and centralized co-occurrence networks. Nevertheless, the macroscopic features of networks may hide variability occurring at fine-grained level, even if global properties remain stable (Dupont et al. 2011; Aizen et al. 2012; Trøjelsgaard and Olesen 2016). On this regard, we expect the changes in species roles would lead to changes in species and interaction composition between burned and unburned sites, contributing to the dissimilarity between local communities (Poisot et al. 2012; Trøjelsgaard and Olesen 2016; Kemp et al. 2017).

Methods

Study area

The Sierras Chicas in central Argentina encompasses the south-eastern portion of Chaco Serrano District (Cabrera 1976), stretching in a north–south direction (from 31°05'S, 64°28'W to 32°05'S, 64°28'W), with an altitude range between 500 and 1947 m.a.s.l. Climate is temperate semi-arid, with a mean annual temperature of 16.8 °C and a monsoonal rainfall regime. Average annual rainfall is 960 mm, concentrated between October and March (spring and summer) (Argañaraz et al. 2015a). The Sierras Chicas vegetation corresponds to the lower stratum of the mountains, dominated by *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae) and *Zanthoxylum coco* Gillies ex Hook. f. Et Arn. (Rutaceae) (Luti et al. 1979; Giorgis et al. 2011).

In this ecosystem, fire is one of the most important disturbances caused by climate (Argañaraz et al. 2015b) and anthropogenic activity, principally due to the use of fire to remove vegetation for cattle raising (Abril and González 1999), urbanization and tourism (Argañaraz et al. 2015a). In the Sierras Chicas, fire is the main factor associated with changes in vegetation physiognomy, floristic composition and soil properties (Giorgis et al. 2013; Carbone and Aguilar 2017; Carbone et al. 2017). As a result, sites that have had fire events in the last years are characterized by the dominance of shrub woody species such as *Acacia caven* (Mol.) Mol. and *Colletia spinosissima* J. F. Gmel. (both Fabaceae), whereas unburned forests are characterized by a developed vertical structure (Giorgis et al. 2013).

Field study

To represent a contrasting scenario of fire disturbance, we selected sites with different fire history in the oriental slope of the Sierras Chicas that included unburned and burned areas (Fig. 1). The unburned sites were located in three areas with no recent history of fire events (at least since the existence of records in 1991), and the burned sites were located in five areas where the last fire events were recorded in 2010 and 2011 (3–4 years since the last fire event). In addition, these burned sites had been subjected to one to four fire events since 1991 (Giorgis et al. 2013; Argañaraz et al. 2015a). All areas belong to the same phytogeographic district and had similar slope exposure (N, NE, and NW), livestock pressure and altitudinal range (Carbone et al. 2017).

In each site, we selected eight permanent plots separated from each other by at least 20 m (8 per site, 64 in total), and visited each area on four occasions during the period of highest insect activity (between November and April in 2013–2014 and 2014–2015). Each plot consisted of a 25 m² area divided into a grid of 1 m² cells (Fig. 1). At each plot, two operators manually sampled ants foraging on vegetation and soil and recorded their location within the grid. The ants collected were sorted to species

or morpho-species level in the laboratory, and voucher of specimens were deposited in the collection of the Entomology Department, Universidad Nacional de Córdoba, Argentina.

Considering that the study sites may have different land use and fire history (e.g., fire intensity), we evaluated whether they were comparable vegetation units according to their physiognomy, richness and species composition. Accordingly, we performed vegetation surveys (November–December 2013) on the plots for ant sampling, recording the number and identity of plant species in each plot. As a surrogate of habitat structural complexity, we estimated vegetation height every 0.5 m along two perpendicular lines crossing each plot and calculated the average height per plot. We compared vegetation height and plant species richness between burned and unburned sites with Generalized Mixed Models (GLMM), considering plots, as experimental units, nested in sites as random factor using nlme package (Pinheiro et al. 2016) in R (R Core Team 2016). In addition, we used Bray–curtis dissimilarity index to compare plant species composition among fire regimes with analysis of similarities (ANOSIM) in the vegan package (Oksanen et al. 2007) in R (R Core Team 2016) (Supplementary S1).

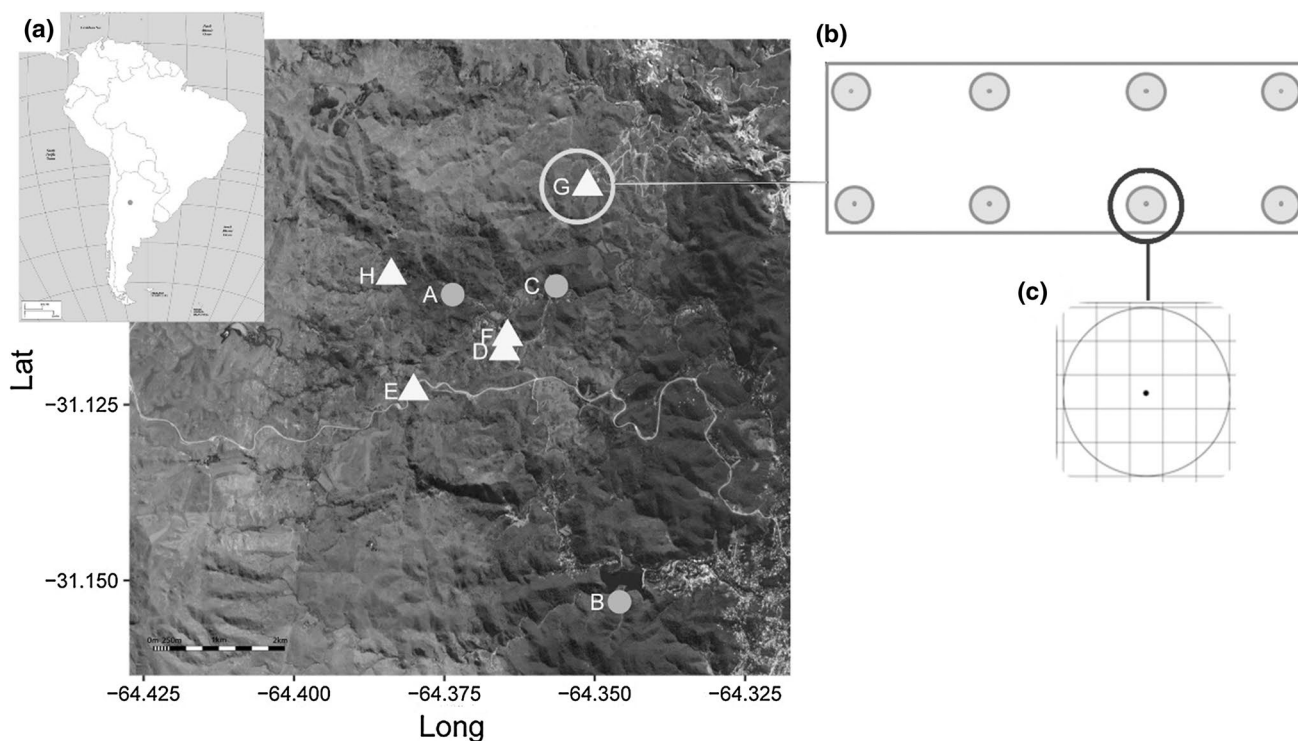


Fig. 1 Location of burned (triangles) and unburned (circles) sites in the Chaco Serrano forest from central Argentina (a). At each site, we delimited eight permanent plots (b) in which we located ant species occurrences in a 1 m² grid (c)

Data analysis

Construction of co-occurrence networks

To maximize the possibility of species encounters, we focused on the smallest spatial scale possible. Accordingly, we used a *grid cell* × *ant species* matrix of each site on each visit date to assess species co-occurrences. We calculated two metrics: the Checkerboard score (C-score) and the Sørensen index (Sør) to evaluate whether species pairs distributed in a segregated or aggregated fashion, respectively (Arita 2017). The C-score represents the normalized mean number of checkerboard combinations [i.e., submatrices of the form (1, 0, 1, 0)] in an $i_{\text{species}} \times j_{\text{sites}}$ matrix (Stone and Roberts 1990). However, in this study we used the C-score to evaluate co-occurrence between each pair of species as $\text{C-score} = (a - c) / (b - c)$, where a is the total number of occurrences of one species, b is the total number of occurrences of a second species, and c is the number of sites that contain both species (Ulrich 2008; Camarota et al. 2016). Values of C-score close to 1 indicate segregation or negative co-occurrence and values close to 0 aggregation or positive co-occurrence. Contrarily, the Sørensen index (Dice 1945) measures the mean number of shared sites (i.e., grid cells in our study) between a species pair, calculated as $\text{Sør} = 2c / (2c + a + b)$, where a , b and c are defined as above. In this case, values close to 1 indicate aggregation. We used both metrics in a complementary way, and as a means of double-check for interactions.

Since co-occurrences can be a product of random distribution over a homogeneous space, we compared observed values with distributions generated by equiprobable-fixed null models for each matrix. In this way, we obtained pairwise species that segregate or aggregate beyond expectation by chance. The equiprobable-fixed null model considers the original species abundance on each matrix (fixed row sums) but gives an equal probability of occurrence in each cell (SIM 2, Gotelli 2000). We selected this null model among all possible models because it is appropriate to compare standardized samples from homogeneous habitats, such as those considered here (Gotelli 2000). We obtained the significance levels of the C-score and Sørensen index from the lower and upper 95% confidence limits of the null model distributions. We also calculated the standardized effect sizes (SES) to quantify the direction and degree of deviation from the null model as $\text{SES} = (\text{observed index value} - \text{mean null value}) / \text{standard deviation of null values}$ (Gotelli 2000). For each species pair in a matrix, significant ($p < 0.05$) and positive SES values of the C-score indicate negative co-occurrence of a species pair (i.e., segregated distribution of a species pair), whereas the Sørensen index indicates positive co-occurrence (i.e., aggregated distribution of a species pair). The opposite

(i.e., significant and negative SES values) indicates positive co-occurrence in the case of the C-score and negative co-occurrence in the case of the Sørensen index (Ulrich 2008).

Based on the significant negative and positive co-occurrences of species pairs in each site, we constructed ant–ant co-occurrence networks in a way that nodes represent ant species, links represent significant positive and negative co-occurrences, and SES values represent interaction strength (details of the estimation of interaction weights are in the supplementary S2). Since the interpretation of network patterns may be different depending on the interaction sign (Sauve et al. 2014), we analyzed positive and negative co-occurrence networks separately for each of the eight study sites. With this information, we described the ant community structure by analysing the macro- and microscopic structure of these networks (Trøjelsgaard and Olesen 2016) as described below.

Aggregate network metrics

We registered the number of species present in sites as a measure of network size. Also, we described each positive and negative network by their number of links, and the mean degree per species (i.e., average number of links from all interacting species in a network) as a measure of network centralization (Wasserman and Faust 1994). Species degree is the number of direct links of each species to other species, and we consider more connected species to be more central than less connected ones (Borrett 2013). It is important to note that in this study, species of high degree of negative and positive interactions could be considered as behaviorally dominant since they segregate and aggregate with many other species in the community. We used these network metrics as response variables to evaluate the differences in network structure between burned and unburned habitats using General Linear Models (GLMs). In these GLMs, fire regime (burned and unburned) was the factor and ant species richness was included as co-variable since network size can affect network properties (except for network size) (Dormann et al. 2009). For number of species and links we used Poisson distribution to meet assumptions of the analysis.

Microscopic network metrics

Microscopic network metrics reflect properties at node and link levels, providing insights into the roles of species and interactions within the network (Lewinsohn and Cagnolo 2012). Considering that network macroscopic structure may remain constant under different environmental conditions while the identity of nodes and interactions may change (Trøjelsgaard and Olesen 2016; Kemp et al. 2017), we compared ant species and interaction composition between burned and unburned sites. We

performed an Analysis of Similarity (ANOSIM) and a Non-Metric Multidimensional Scaling (NMDS) ordination using Bray–Curtis dissimilarity distance with the *vegan* (Oksanen et al. 2007) package in R (R Core Team 2016). These analyses considered both ant species incidences and interaction frequency, calculated as the sum of observations in each grid-cell on the different survey dates for species and interaction composition in each site, respectively.

We also explored the mechanisms involved in interaction turnover (i.e., interaction dissimilarity) of positive and negative interaction networks separately by estimating Beta diversity (β) between all possible pairs of burned and unburned networks (15 combinations in total). To estimate each β value, we used Whittaker's dissimilarity index (Whittaker 1960), $\beta_{WN} = ((a + b + c) / ((2a + b + c) / 2)) - 1$, where β_{WN} is the interaction turnover between each pair of burned–unburned networks, a is the number of interactions shared between both networks, and b and c are the numbers of unique interactions in each network. Whittaker's dissimilarity index uses presence–absence data to explore the absolute gain or loss of interactions, with values ranging from 1 (high turnover) to 0 (low turnover).

To assess whether interactions turnover is explained by species turnover or by interaction rewiring, we partitioned this metric in two components: $\beta_{WN} = \beta_{ST} + \beta_{OS}$, where β_{WN} is the dissimilarity of interactions, β_{ST} is the dissimilarity of interactions due to species turnover, and β_{OS} is the dissimilarity of interactions established between shared species (i.e., interaction rewiring). Given that β_{OS} (dissimilarity of interactions between shared species) is a component of β_{WN} , the inequality $\beta_{OS} - \beta_{WN}$ is always satisfied, and β_{ST} takes values between 0 (dissimilarity between two networks is entirely explained by shared species interacting differently), and β_{WN} (the shared species interact with the same species, and the difference between the two networks is explained by differences in species composition). Because differences in network structure can arise either by species or interactions turnover, there is no obvious analytical solution for β_{ST} , which is found by removing the effect of β_{OS} on β_{WN} between networks (Poisot et al. 2012). The Beta diversity analyses were performed using the *betalink* package (Poisot et al. 2012) in R (R Core Team 2016). To assess the contribution of interaction rewiring and species turnover to global interaction turnover (β_{WN}) between burned and unburned sites, we compared β_{OS} and β_{ST} values using a non-parametric Wilcoxon signed-rank test for paired samples. In this case, we compared β_{OS} with β_{ST} values calculated for each pairwise of burned–unburned sites using a paired test because of metrics dependency, since β_{OS} and β_{ST} are the additive component parts of β_{WN} . To discard spatial autocorrelation in the species and interactions composition, as well as in the distribution of fire frequency between sites we

performed Mantel tests using *vegan* package (Oksanen et al. 2007) in R (R Core Team 2016) (Supplementary S3).

We calculated species centrality, measured as node degree, to define the role of species within networks (Newman 2003), expecting species to have a higher degree of both negative and positive interactions in burned habitats compared to unburned ones. We applied a Generalized Linear Mixed Model (GLMM) to compare ant species degree (response variable), using fire regime and the sign of interaction networks as explicatory variables (fixed factors), and using species identity as a random factor. We also evaluated changes in the role of each species through line graphs looking for changes in the identity of central species.

Results

We found 36 mellivorous and omnivorous ant species, ranging from 27 to 17 species per site; however, there were no differences in the number of species between burned and unburned sites (GLM, $F_{1,6} = 0.042$, $P = 0.844$). Across all sites, we found 122 positive and negative non-random interactions among ant species, with aggregations ($n = 85$) prevailing over segregations ($n = 37$) (Supplementary S2).

We built positive and negative co-occurrence interaction networks for each site (Fig. 2), which showed no differences in the number of links (positive networks: $F_{1,4} = 0.311$, $P = 0.607$; negative networks: $F_{1,4} = 1.360$, $P = 0.308$), and centralization (positive networks: $F_{1,6} = 0.463$, $P = 0.522$; negative networks: $F_{1,6} = 0.053$, $P = 0.825$) (Supplementary S5).

Ant species composition differed between burned and unburned sites (ANOSIM, $R = 0.733$, $P = 0.02$) (Fig. 3a). Although the identity of positive co-occurrences (i.e., “which species co-occur together”) was unaffected by fire regimes ($R = -0.036$, $P = 0.622$) (Fig. 3b), negative co-occurrence interactions (i.e., “which species segregate each other”) differed between burned and unburned sites ($R = 0.621$, $P = 0.015$) (Fig. 3c). Accordingly, we found high interaction turnover for both positive and negative co-occurrence networks between burned and unburned sites (Fig. 4). The identity of interactions can change between sites because of changes in species composition and because of interaction rewiring. For both positive (Wilcoxon signed-rank test, $V = 120$, $P < 0.001$; Fig. 4a) and negative (Wilcoxon signed-rank test, $V = 120$, $P < 0.001$; Fig. 4b) networks, interaction rewiring (β_{OS}) was the main driver of changes in ant–ant interaction composition between burned and unburned sites.

Ant species degree varied between networks according to the sign of interactions (GLMM, $F_{1,154} = 24.363$, $P < 0.001$), with those of positive networks being higher than those of negative interactions (GLMM, $Z = 0.151$,

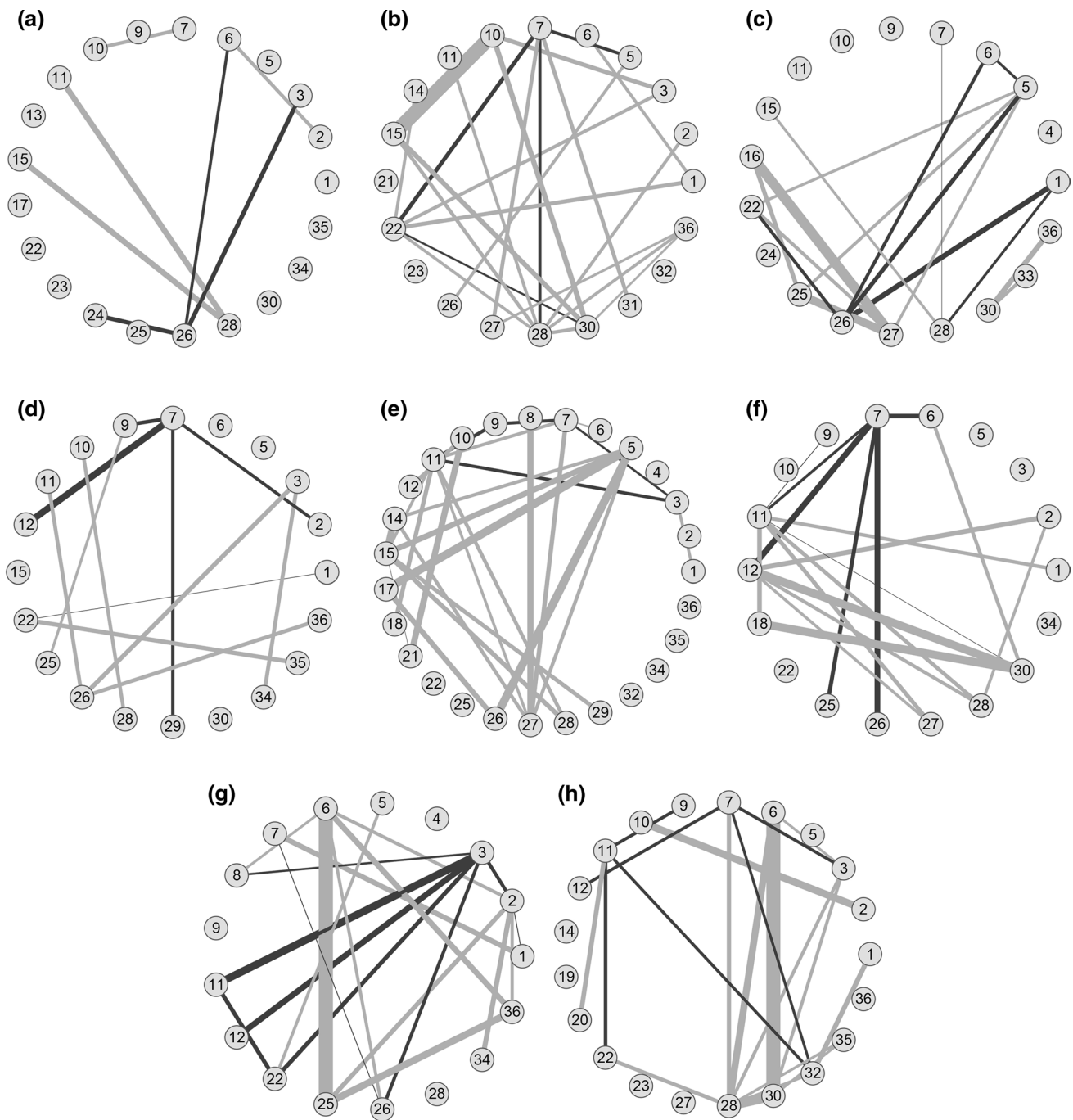


Fig. 2 Co-occurrence networks showing positive (grey lines) and negative (black lines) interactions between ant species from unburned (a–c) and burned (d–h) sites. The width of lines represents the stand-

ardized effect size of interactions. Species codes and names can be found in Table S4

$P < 0.001$). Nevertheless, we found no differences in species degree between burned and unburned sites ($F_{1,6} = 0.344$, $P = 0.579$) nor a differential effect of fire regime according to interaction sign ($F_{1,154} = 0.054$, $P = 0.817$). Although fire regime did not affect ant species degree, we noticed a replacement of the species in the central core of negative interaction networks between burned and unburned sites:

Pheidole cordiceps was replaced by three species (*Camponotus mus*, *C. rufipes*, and *Brachymyrmex patagonicus*) that interacted with at least two other species (i.e., with a degree value above 2) in burned sites (Fig. 5b). Regarding positive interactions, three out of seven species with degree values above 2 remained in the central core of burned and unburned sites (Fig. 5a).

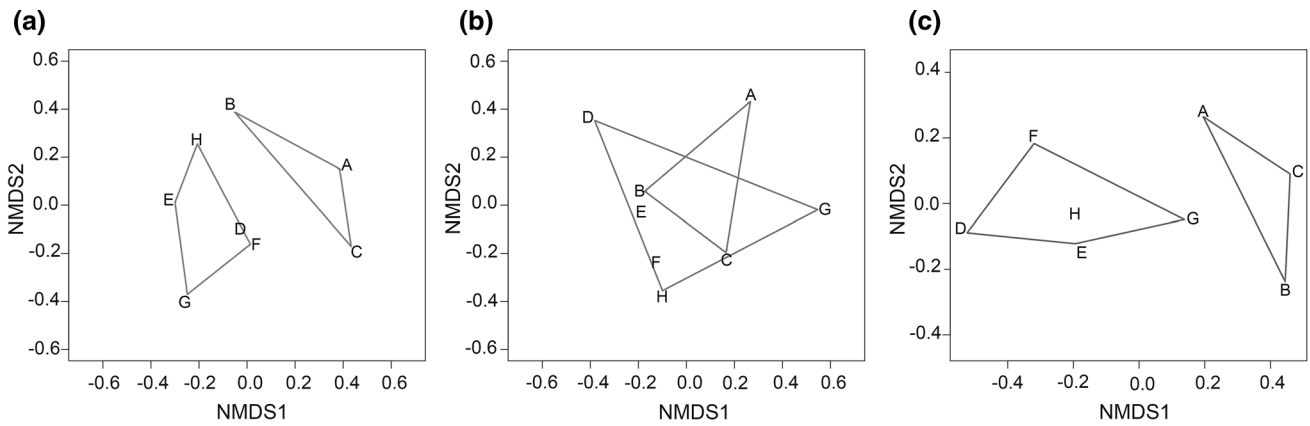


Fig. 3 Non-metric multidimensional scaling ordination (NMDS) based on ant species (a) composition (two dimensional stress = 0.1322), ant-ant positive interactions (b) (two-dimensional stress < 0.001) and

negative interactions (c) (two-dimensional stress < 0.001). Letters indicate unburned (A–C) and burned (D–H) sites, polygons link sites with the same fire regime

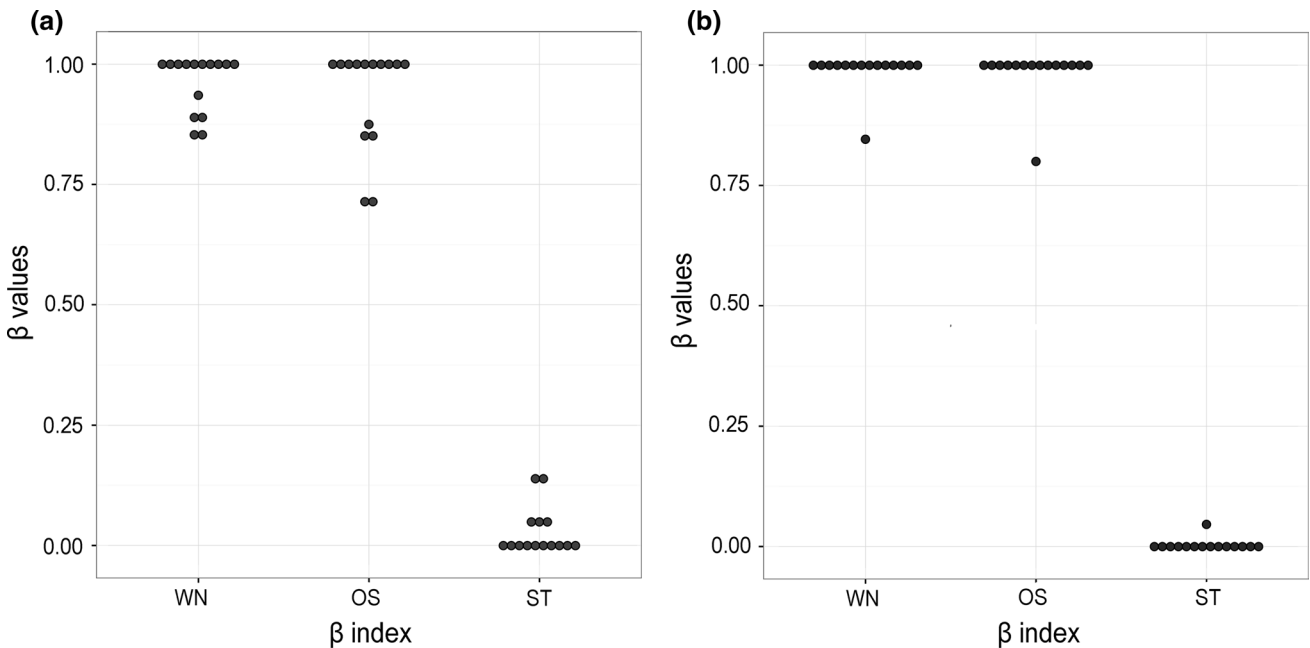


Fig. 4 Turnover of positive (a) and negative (b) interactions between all possible combinations of burned and unburned sites according to the total interaction turnover (β_{WN}) and its two components: interac-

tion turnover between shared ant species (or rewiring, β_{OS}) and interaction turnover due to species turnover (β_{ST})

Discussion

To understand how biodiversity is lost, we should ask how species assemble into interactive communities (Connor and Simberloff 1979; Bascompte and Stouffer 2009), and how this organization changes under disturbance pressure (Tylianakis et al. 2007). In this study, we evaluated changes in ant community structure in relation to wildfire disturbance by examining their co-occurrence networks.

The study of these co-occurrence networks may allow filling the gap between detailed species-centered studies and broad scale community ones, since it reveals the interdependencies that link species responses with community-wide patterns.

We found 122 positive and negative interactions between ant species that departed from randomness. The non-random patterns of species spatial distribution could be under the influence of several factors, including species traits such as body size and diet (e.g., Gotelli and Ellison 2002; Blüthgen

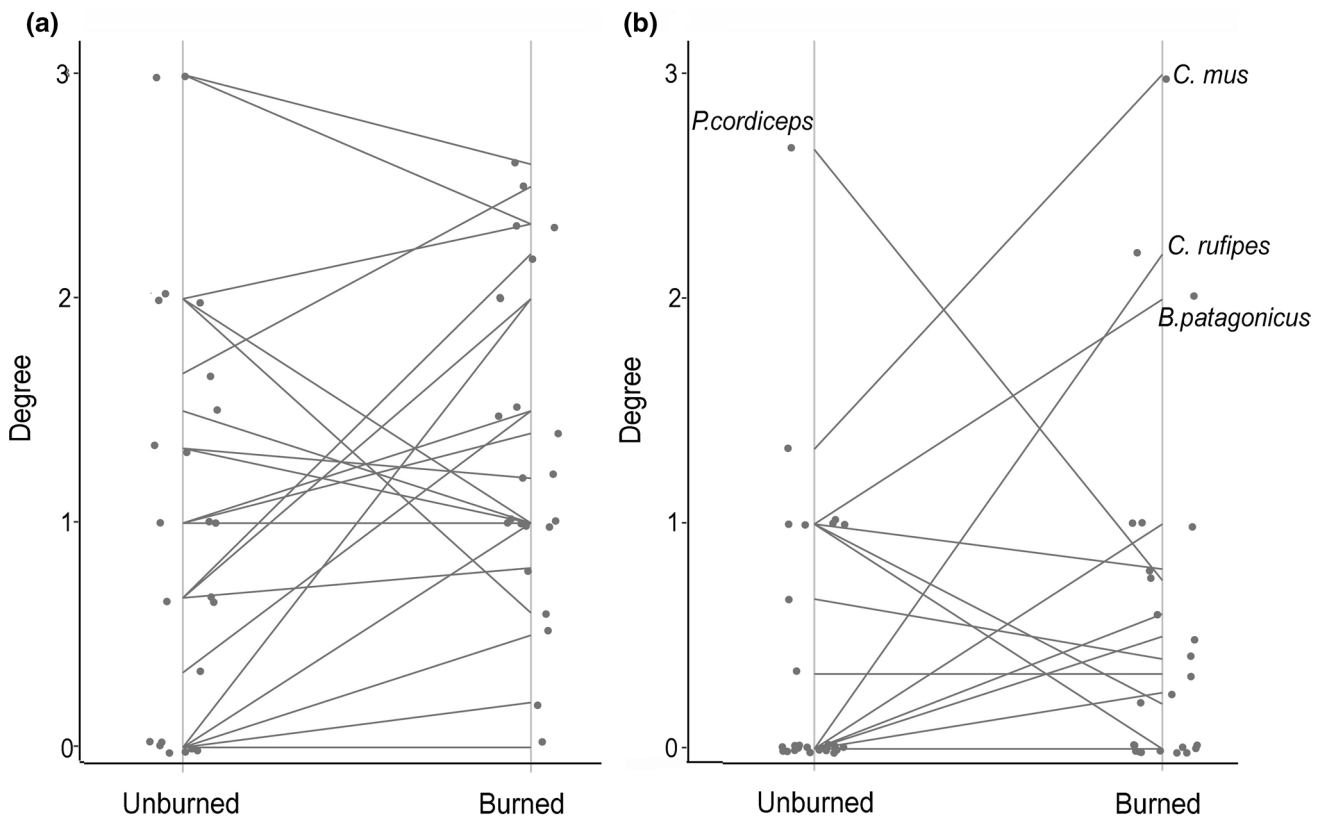


Fig. 5 Ant species positive (a) and negative (b) degree in co-occurrence networks from burned and unburned sites. Lines connect the same species in burned and unburned habitats

et al. 2004; Houadria et al. 2015), stochastic processes (Ribas and Schoereder 2002) and habitat requirements (Powell et al. 2011). In the past, the study of spatial patterns of ant communities were focused on species segregations, reinforcing the idea that competitive interactions were the main driving force determining species distribution (Blüthgen and Stork 2007; Sanders et al. 2007; Calcaterra et al. 2016).

We found positive interactions (i.e., species aggregation) prevailing over negative ones (i.e., segregations). Although the ant mosaic concept focuses on segregation between dominant species, it also involves the co-occurrence of dominants with sub-dominant or submissive species, leading to a more aggregated distribution than expected by chance when all species are included in the analysis (Ribas and Schoereder 2002; Blüthgen and Stork 2007). However, we should not discard the possibility that the number of negative co-occurrences could be underestimated by the presence of rare species, less likely to be detected in co-occurrence with other species (Saiz and Alados 2012).

Our surveys confirmed a reduction in vegetation height and a turnover of plant species between burned and unburned sites (Supplementary S1). It is known that the response of ant communities vary according to the vegetation and matrix type and, also, to the intensity and

frequency of disturbance events (Folgarait 1998; Paolucci et al. 2017). Here, we hypothesized that a less structurally complex vegetation in burned sites would increase encounter probabilities between ant species, increasing their co-occurrence interactions. In addition, we expected fire disturbance to change ant species composition (Neves et al. 2016), favouring open-area adapted ants, with active and aggressive behavior (Farji-Brener et al. 2002; Andersen et al. 2014; Arnan et al. 2013). Both mechanisms could lead to an increase in the centralization of both positive (for example, through the co-occurrence of dominants and subordinates) and negative (for example, through the segregation between dominants) co-occurrence networks. Nevertheless, our results did not reveal differences in the macro-structure of co-occurrence networks between burned and unburned sites. There are several examples in the literature of changes in the structure of interaction networks in relation to land use change (e.g., Tylianakis et al. 2007), habitat fragmentation (e.g., Valladares et al. 2012) and habitat loss (Laliberté and Tylianakis 2010); nevertheless, other studies revealed a stable structure across different vegetation physiognomies (Nielsen and Totland 2014). Consequently, the macroscopic effects of disturbance on networks could be idiosyncratic of each

interaction type and the kind of environmental gradient under study (Trøjelsgaard and Olesen 2016).

Despite no changes in network macroscopic structural patterns, the microscopic features of ant–ant co-occurrence networks differed between burned and unburned sites. On this regard, the number of ant species registered did not vary according to fire regime but species composition did. Changes in species composition after fire events were frequently reported (e.g., Farji-Brener et al. 2002; Parr et al. 2004; Arnan et al. 2006; Albuquerque et al. 2017), indicating a replacement of original assemblages with species associated to hot environments and open areas (Arnan et al. 2013; Paolucci et al. 2017). In this study, these changes translated into a consistent interaction turnover between burned and unburned sites for negative networks, but not for positive ones.

Interaction turnover between networks from sites with different fire regimes could be related to changes in species composition as well as to the interaction rewiring between shared species (Lewinsohn and Roslin 2008; Poisot et al. 2012). In our comparison of ant co-occurrence networks between burned and unburned sites, we found that interaction turnover was mostly explained by interaction rewiring rather than by species turnover. The changes in the core of central species according to fire regime could be the cause of such rewiring of interactions. Accordingly, when we considered the five most frequent species, only one (*Linepithema humile*) was shared between burned and unburned sites. Coincidentally, interaction rewiring due to phenological changes in the relative abundance of species was the main driver of interaction turnover in a plant–pollinator network (CaraDonna et al. 2017). Overall, these results agree with previous studies that found a stable structure of ecological networks, whereas individual pairwise interactions experience spatial and temporal switches (Dupont et al. 2009; Trøjelsgaard and Olesen 2016; Kemp et al. 2017).

Ant species degree also varied between networks of different interaction sign, being higher in those of positive interactions. Moreover, negative interactions tend to be dominated by few species, whereas positive ones were evenly distributed. Although there are no previous records of spatial co-occurrence networks, other studies demonstrated that interactions in which none partner is negatively affected (i.e., mutualisms, commensalisms) tend to be less restricted than antagonistic ones, leading to differences in degree distributions (Lewinsohn et al. 2006; Fontaine et al. 2009; Thébault and Fontaine 2010).

Species roles changed between burned and unburned networks but only for negative interactions. We found that the central ant *P. cordiceps* in unburned networks were replaced by *C. mus*, *C. rufipes* and *B. patagonicus* in unburned sites. *Camponotus* species demonstrated to be

the most aggressive ants in the region when confronted with other species in arena experiments (Alvarez Pringles, Tavella, and Cagnolo, unpublished data). Moreover, *Camponotus* species showed to be central species in myrmecophilic networks from other ecosystems (Costa et al. 2016; Fagundes et al. 2016), suggesting that these species may exert aggressive dominance over available resources. Our results suggest that negative interactions were monopolized by central species that differed between burned and unburned conditions. On the other hand, positive interactions may result from opportunistic interactions between submissive species that tolerate each other (Sanders et al. 2007), regardless of the environmental condition. Taken together, these results could provide new insights on the role of competitive interactions in the organization of ant assemblages at small spatial scale, between species that share micro-habitat preferences.

Co-occurrence data are a neglected source of information to investigate species interactions (Cazelles et al. 2016). Although ants are a paradigmatic object of study to evaluate the role of competition in community structure, to our knowledge, this is the first study focused on the analysis of co-occurrence networks of ant species in disturbed habitats. Here we found changes in interaction composition and species roles while species richness and aggregated network properties remained stable. These changes in species roles translated into an interaction turnover of species pairs according to fire regime of sites. Whether or not these changes may affect the rest of the community, including myrmecophilous partners and their associated species, remains to be tested. We expect higher cascading effects on other ecological processes such as parasitism and herbivory on burned sites due to the high fidelity myrmecophilic interactions with the more aggressive ants.

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