ORIGINAL PAPER

Changes in plant community structure and decrease in floral resource availability lead to a high temporal β-diversity of plant–bee interactions

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Abstract

Biological communities are subject to spatiotemporal variations in community structure, i.e., species composition, richness, and abundance. Plant–pollinator interactions are affected by species composition and abundance, so that rapid changes in plant community structure can lead to critical impacts on plant–pollinator interactions at the community level. The extent of these impacts depends on how plants respond to different kinds of stressors, such as the disturbance caused by invading species. In this research, we conducted a before-and-after study to evaluate the potential effects of an invasive fast-growing alien grass species on the structure of a plant–pollinator interaction network. We described the changes in community structure and plant–pollinator interactions over two sampling periods, through the temporal β-diversity of plant and bee species, plant–bee interactions, and plant functional traits. Our results showed that changes in plant community composition (especially the plants in the network core) and decrease in plant species richness, as well as in floral resources availability impacted plant–pollinator interactions of a grassland community after the growth of a fast-growing alien grass species. These changes were accompanied by a decrease in plant–bee interaction diversity, and a high β-diversity of species interactions mainly due to interaction rewiring. However, we found no effect on the functional diversity of flowers. In conclusion, our study showed that a short-term change in plant species composition and floral resource abundance impacted plant–bee interactions, which markedly changed network structure and dynamics.

Keywords Functional diversity · Interaction turnover · β-diversity · Invasive species · Pollination network

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Introduction

Community-level interactions between plants and pollinators have a crucial role in the functioning of biological communities (Memmott and Waser 2002), not only because plants provide essential food resources for many groups of animals that visit flowers, but also because the reproductive success of most flowering plants depends on the biotic services provided by animals (Ollerton et al. 2011). Plant reproductive success depends on community trophic interactions mediated by both plant and pollinator species composition and functional traits (Biella et al. 2019). Therefore, changes in community structure, i.e., species composition, richness, and abundance, may affect pollinator visitation patterns, and by consequence, plant reproductive success itself (Karron et al. 2009; Biella et al. 2019). At the community level, this process can lead to changes in plant–pollinator interactions due to the changes in pollinator resource usage patterns (Valdovinos et al. 2013, 2018; Potts et al. 2016;

Hiraiwa and Ushimaru 2017; Biella et al. 2019), which has both ecological and evolutionary consequences (see Vanbergen et al. 2018).

The breadth of these impacts depends on how plants respond to different kinds of stressors, such as the disturbance caused by invading species (see Vanbergen et al. 2018). One of the key ecological processes that mediate plant response to invading species is competition among plants for biotic and abiotic resources (Craine and Dybzinski 2013). In open ecosystems, such as the Cerrado vegetation (Neotropical savannas of Brazil), plants may be more susceptible to intensified competition for light, since a slight difference in plant height and leaf area can confer a significant advantage, limiting the growth and development of shorter neighboring plants (Silvertown 2004; Martin et al. 2009). Therefore, alien plant species can affect the establishment of native plants by limiting their growth (due to the effect of shading) and decreasing their abundance within a given community, which in turn may decrease the overall community diversity and reduce the availability of floral resources for pollinators, eventually changing plant–pollinator interactions (Pivello et al. 1999a, b; Hendrickx et al. 2007; Almeida-Neto et al. 2010).

The introduction of alien grasses is widespread in the Brazilian savannas, where many species of fast-growing African grasses were introduced in the last century (Williams and Baruch 2000). Some of the most common and widely distributed alien species in grassland ecosystems in Brazil belong to the genus *Brachiaria* (Poaceae), which are aggressive grasses that grow rapidly and spread easily (Pivello et al. 1999a). Despite the wide distribution of African grasses in Brazil, the ecological effects of their occurrence on plant–pollinator interactions in natural grassland communities are not well known. Previous studies have shown that *Brachiaria decumbens* Stapf. outcompete native plant species and impoverish Cerrado communities in Brazil (see Pivello et al. 1999a, b; Almeida-Neto et al. 2010). Hence, it may be expected that alien species will affect the dynamics of plant–pollinator interactions, increasing interaction β-diversity because these plants can change species richness, composition, and abundance of natural plant communities (Pivello et al. 1999a, b; Almeida-Neto et al. 2010).

However, undisturbed communities are also prone to experience turnover in plant–pollinator interactions due to the natural changes in community structure (see Souza et al. 2018). These changes may also reduce the overall amount of floral resources to pollinators, as well as functional traits within a given community (De Bello et al. 2006; Pakeman 2011). Alteration in the overall resource availability and functional traits of flowers is known to promote changes in pollinator dietary niche breadth (Hiraiwa and Ushimaru 2017). Dietary niche breadth of pollinators can be highly variable depending on resource availability because it

directly affects pollinator foraging behavior (see Fontaine et al. 2008). In this sense, changes in plant community structure can readily trigger pollinator responses and, as consequence, alter the degree of pollinator specialization within plant–pollinator interaction networks (Fontaine et al. 2008; Hiraiwa and Ushimaru 2017; Lara-Romero et al. 2019).

Considering that alien species of grasses are known to impact plant community structure and that pollinators can be affected by resource availability, in this research we conducted a before-and-after study to evaluate the potential effects of an invasive fast-growing alien grass species on the structure of a plant–pollinator interaction network. We assessed the temporal changes in plant–pollinator interactions in a grassland community invaded by *B. decumbens*, and how the changes in plant species richness, composition, abundance, and availability of floral resources affected plant–pollinator interactions in this community. Since bees are the most common group of pollinators at the Brazilian Cerrado (Oliveira and Gibbs 2000), and can readily respond to variations in resource availability by changing their forage behavior (Fontaine et al. 2008), we used bee–plant interactions to test whether a decrease in floral resource availability for pollinators could lead to a decrease in plant–pollinator network-level specialization, as well as make the network less modular due to an increase in niche overlap between pollinator species sharing floral resources. To test this, we also analyzed the bee species roles, as well as the β-diversity of plant and pollinator species composition over time, and the temporal changes in plant–pollinator relationships through the β-diversity of interactions and plant functional traits.

Material and methods

Study site

The data were collected in a Neotropical grassland, known as *campo cerrado* (sensu Oliveira-Filho and Ratter 2002), located in the highest point (about 900 m a.s.l.) of the Municipality of Botucatu, São Paulo State, southeastern Brazil (22° 53′ 35.98″ S 48°9′ 25.78″ W). The total area of the study site is about 2 ha, and vegetation has a few scattered trees and shrubs with a dominant grassy herbaceous layer. The climate is warm-temperate (Cwa according to the Köppen classification, see Kottek 2006) with two distinct seasons, a cold dry winter from March to September, and a hot wet summer from October to April. The study was conducted from 2016 to 2018, and the data were collected in two sampling periods during the flowering peak that occurred from November to January. Weekly temperature ($F_{1,157}=0.17$; $p=0.68$), rainfall ($F_{1,157}=2.17$; $p=0.14$), and humidity ($F_{1,157}=0.26$; $p=0.61$) did not differ among the

three years (2016, 2017, and 2018) that englobed the two sampling periods (Fig. S1).

To prevent the risk of fire, in most years, during the driest months (June–July), the area that includes the study site is mowed to control the grass. However, before the second sampling period, which started in November 2017, the area was not mowed, allowing the rapid growth of the alien grass *B. decumbens*, which yield us the opportunity to conduct a before-and-after study to assess the changes in plant community structure (i.e., species richness, composition, abundance, and functional diversity of floral traits) and plant–bee interaction network over the two sampling periods (November 2016 to January 2017 and November 2017 to January 2018). Our study site represents a relictual grassland occurring in the peri-urban zone of Botucatu Municipality, so we have no other habitats under similar conditions allowing replicability.

Community composition and interaction sampling

To sample the community composition and interactions between plants and bees, 5 transects (50 m × 2 m) were drawn uniformly, to cover the entire study area. During each sampling period, plant–bee interactions were sampled weekly on alternate days. To include the daily time-dependent variations, these interactions were recorded at different times of day, from 07:00 to 10:00 h in the morning and from 15:00 to 18:00 h in the afternoon. During the sampling days, interactions of every focal plant species were recorded simultaneously by three observers (each one observing a different species) for about 30 min at different times of the day alternating transects in distinct days. We recorded only legitimate interactions, defined as when the visitor touched the reproductive structures of the plant, indicating potential pollination. Since bees were the most abundant group of floral visitors and made a significant number of legitimate interactions, we refer to bees as "pollinators." Interactions were sampled at night (19:00 h to 23:00 h) if any plant with nocturnal flowers was blooming. On rainy days, the sampling was shifted to the following day. Since the flowering period varies according to the species phenology, the sampling effort depended on the duration of the species flowering season across the sampling periods, which resulted in different observation times for each plant species in the two sampling periods: 4970 min, $\bar{x} = 191 \pm 165$ min per plant species from 2016 to 2017; and 6500 min, $\bar{x} = 342 \pm 272$ min per plant species from 2017 to 2018.

We calculated plant species richness on the transects and, to estimate plant abundance, we counted the number of individuals and the total number of flowers per plant. Plants were collected and taken to the Herbarium of São Paulo State University (Herbarium BOTU) for identification, and classification followed APG IV (Chase et al. 2016).

Flower-visiting bees were collected with entomological nets and euthanized in killing jars with a 10% ammonia solution. They were mounted and identified using identification keys (Silveira et al. 2002) and with the aid of specialists.

Plant–pollinator interaction networks and metrics

To describe network topology in the two sampling periods, we constructed two quantitative interaction matrices using the visitation frequency of bees on flowers. Each plant or bee species was regarded as a node in the interaction network, and the interaction frequency as links. To illustrate the structural differences between the resulting interaction networks from each sampling period, we calculated several network metrics, prioritizing the quantitative indices, which are less influenced by sampling effort (see Vizentin-Bugoni et al. 2016). The metrics calculated were as follows: (1) connectance (*C*), which represents the proportion of the potential interactions that are realized; (2) weighted nestedness, which quantifies whether specialized species interactions represent subsets of the more generalist species interactions, evaluated by the wNODF (nestedness based on overlap and decreasing fill) index (Almeida-Neto and Ulrich 2011). Higher values of wNODF demonstrate whether species of the network core (see Bascompte et al. 2003) also establish higher frequencies of interactions (Almeida-Neto and Ulrich 2011); (3) network-wide specialization, represented by the H_2' index, which describes how a species restrict their interactions from those expected based only on the availability of partners (Blüthgen et al. 2006) and therefore demonstrates the degree of interaction exclusiveness or selectiveness; (4) niche overlap (R_0), which measures the similarity of interaction patterns between species of the same level, calculated by Horn's index (Horn 1966). Lower values of R_0 indicate that bee species are partitioning the floral resources available in the community; and (5) weighted modularity (Q_w'), an index that quantifies how interactions are structured within network modules (which are a subset of interactions), relative to interactions occurring between modules. Higher values of Q_w' indicate the existence of pollinator interaction preferences for a particular subset of plant species, i.e., niche specialization. We calculated the modularity of the networks using the DIRTLPAwb+ algorithm (Beckett 2016). Because the value of Q_w' might vary slightly between the algorithm runs, we ran the algorithm 10 times to find the optimal module conformation with the highest value of Q_w', and the number of Markov Chain Monte Carlo (MCMC) moves was set to 10^9 steps (as in Maruyama et al. 2015; Araujo et al. 2018; but see also Dormann and Strauss 2014). All the network-level metrics were calculated using the package *bipartite* in R (Dormann 2008).

To assess the significance of each network metric, we compared the observed values to those generated by a

null model, after 10,000 randomizations, and estimated the one-tailed 95% confidence intervals (CIs) from the null distributions of each network metric. To generate the null matrices, we used the Patefield algorithm (Patefield 1981), which maintains the total number of interactions by fixing the marginal totals, thus maintaining the network size and species richness.

Species roles of bees in the interaction networks

Since we wanted to know how bee roles within a network changed between the two sampling periods, i.e., with the differences in resource availability and plant species composition, we evaluated two species-level indices that characterize different topological properties of the species: (1) species strength (ss'), which represents the sum of the proportions of interactions realized by a given species across all its interaction partners. Higher values illustrate how plants depend on a specific bee species, and vice versa (Bascompte et al. 2006); (2) species-level specialization (d'), which describes how the frequency of interactions of a given bee species diverges relative to the availability of interaction partners in the network, represented by the plants' marginal totals. Hence, higher values denote high specialization (Blüthgen et al. 2006). We performed paired t-tests to analyze whether d' and ss' differed between sampling periods. For these analyses, we considered only the bee species (10 of 13 species) shared between the 2 sampling periods. Therefore, *Augochloropsis* sp., *Ptiloglossa* sp., and *Monoeca* sp. were excluded from this analysis. To characterize the importance of bee species across both periods to the structure of the modules, we also calculated two indexes based on the modular webs: (1) the within-module degree (z), an index that represents the number of connections that a species has within its module relative to the other species in that module, and (2) among-module connectivity (c), which informs how well a given species is connected to species from other modules (Olesen et al. 2007). Then, following Olesen et al. (2007), we classified species in four categories according to their "c" and "z" values: (i) peripherals, represented by low values of both c and z; (ii) connectors, represented by high c and low z; (iii) module hubs, represented by high z and low c; and (iv) network hubs, represented by high values of both c and z. The threshold values for c and z were defined following Dormann and Strauss (2014). For this we calculated the expected c and z values using null models based on the original networks, and then we used 95% quantiles as critical values (Dormann and Strauss 2014). Therefore, the threshold values used were 0.77 for c and 1.15 for z.

Floral resource availability and floral trait diversity

Resource availability and floral trait diversity were sampled twice a week on all transects. As we were interested to describe the changes in resource availability and floral diversity between the two sampling periods, we used the richness of the blooming species as well as their floral abundance as a proxy for resource availability. To measure the functional diversity of plant species, we recorded floral traits using four distinct measures (both qualitative and quantitative, see Table S1): (i) the flower morphology, classified as poricidal, tubular, dish, bell-funnel, brush, flag, and gullet (according to Souza et al. 2018, modified from Machado and Lopes 2004); (ii) operative flower length, measured from the base of the corolla to the highest floral whorl; (iii) floral width, measured from the most peripheral floral structure to the opposite end; and (iv) floral reward, defined as pollen, nectar, pollen/nectar, and/or oil.

Changes in community structure and functioning over sampling periods

To describe the changes in community structure and functioning over sampling periods (before-and-after the growth of *B. decumbens*), we assessed the changes in flower abundance, as well as the β-diversity of the plant and bee communities, and the changes in the structure of plant–bee interaction network. Also, to analyze how such changes may affect community functioning, we first used Hill numbers to assess the changes in the pairwise interaction pattern over sampling periods through rarefaction and extrapolation analyses (Hsieh et al. 2016; but see also Chacoff et al. 2012; Ramírez-Burbano et al. 2017). Second, we assessed the β-diversity in plant–bee interactions over sampling periods (Poisot et al. 2012; Carstensen et al. 2014) and the β-diversity of plant functional traits (Anderson et al. 2006).

To assess the species turnover (β-diversity) of plants and bees over sampling periods, we used three different indexes: $\beta_{Whittaker}$, which assesses species turnover based on the presence and absence of species shared by communities (Whittaker 1960); and the uncorrected probability version of the abundance-based Chao–Jaccard and Chao–Sørensen indexes, i.e., $\beta_{Chao–Jaccard}$ and $\beta_{Chao–Sørensen}$ (see Chao et al. 2006, but see also Barwell et al. 2015). All indexes vary from 0 to 1, where values close to 1 indicate high species turnover between years, and were computed using *CommEcol* and *vegan* packages in R (Melo and Melo 2019; Dixon 2003).

To calculate individual-based rarefaction and extrapolation curves of interactions (see Chao et al. 2014), we used Hill numbers of the diversity orders of $q = 0$ (richness of pairwise interactions), $q = 1$ (Shannon diversity of interactions) and $q = 2$ (Simpson diversity of interactions). To make

these comparisons, we extrapolated the smaller reference sample (2017 to 2018) up to the same number of interactions recorded in the larger reference sample (2016 to 2017). Then, we obtained 95% confidence intervals for all rarefied and extrapolated curves by using a bootstrap method with 200 replications (for details see Hsieh et al. 2016). Rarefaction and extrapolation analyses were performed using the package iNEXT in R (Hsieh et al. 2016).

To calculate the β-diversity of interactions, we first used a model proposed by Magrach et al. (2017), which applies a quantitative measure of β-diversity using the Ruzicka distance coefficient. This coefficient is based on the shared pairwise interactions between the sampling periods and is weighted by the interaction frequencies. Three components of the β-diversity were calculated: (i) the total β-diversity of interactions (β_{WN}), which describes the total interaction turnover (i.e., interaction dissimilarity) between the networks from both sampling periods; (ii) the interaction rewiring (β_{OS}), which describes the portion of the interaction β-diversity that occurred due to the changes in the interactions realized by the shared species; and (iii) the portion of the interaction β-diversity that occurred due to the dissimilarity in species composition between sampling periods (β_{ST}, see details in Poisot et al. 2012). These values range from 0 to 1, with 1 representing the higher temporal β-diversity in plant–pollinator interactions.

However, despite the robustness of these metrics, it is widely understood that plant–pollinator interaction networks may be affected by sampling (Vizentin-Bugoni et al. 2016), since not all interactions are actually recorded, especially the rarer ones. Hence, considering that rarer interactions are less likely to be sampled, β-diversity analyses of interaction networks may be subject to significant biases due to an uneven sample probability of pairwise interactions, which may lead to misinterpretations. Hence, to assess the β-diversity of interactions and overcome the effect of potential sampling biases, we used the corrected version of the abundance-based Chao–Jaccard and Chao–Sørensen indexes, which takes into account the occurrence of "unseen" shared species, considered in our analysis as "unrecorded" pairwise interactions (see Chao et al. 2005; Chao et al. 2006). For this, we decomposed the interaction matrices into pairwise interactions and considered each interaction pair as a single species. We used the version "rare" of the function *dis.chao* in *CommEcol* R package to calculate the Chao–Jaccard and Chao–Sørensen β-diversity indexes, considering the effect of "unrecorded" plant–pollinator interactions. To assess the significance of the corrected $\beta_{Chao–Jaccard}$- and $\beta_{Chao–Sørensen}$-diversity indexes, we used the R package *vegan* to produce a null distribution of both β-diversity indexes using the Patefield null model (Patefield 1981). The $\beta_{Chao–Jaccard}$- and $\beta_{Chao–Sørensen}$-diversity indexes also range from 0 to 1, with 1 representing the higher β-diversity.

Finally, to calculate the temporal β-diversity of plant functional traits in the community, we used the model proposed by Anderson et al. (2006), as follows: first, we constructed a functional trait matrix for each sampling period, and then we computed the distance matrices using the Gower dissimilarity coefficient (Gower 1971). Each distance matrix was submitted to a principal coordinates analysis (PCoA), and then, using the function *betadisper* in the *vegan* package, we performed an analysis of multivariate homogeneity of group dispersions to calculate the average trait distance of species from each sampling period to a group centroid in the principal coordinates trait space (Anderson et al. 2006). To assess the significance of the distance difference between each group (sampling period), we performed a permutation test for homogeneity of multivariate dispersions using the function *permutest* in *vegan* (Legendre et al. 2011). We also used the combination of plant functional traits to calculate two metrics of functional diversity: functional evenness (FEve, Villéger et al. 2008) and functional dispersion (FDis, Laliberté and Legendre 2010). FEve ranges between 0 and 1 and measures the regular distribution of individual species abundances in the trait space. Higher values of FEve indicate a more equally spaced distance between species, which can be interpreted as a low functional diversity (Villéger et al. 2008). FDis is calculated by projecting one community centroid in a trait space and then calculating the mean distance of species to the community centroid. High values indicate the presence of functionally distinct species (Laliberté and Legendre 2010). Both metrics evaluate the difference in species abundance and weight for species relative abundances, represented here by the total number of flowers. We calculated these metrics using the package *FD* in R (Laliberté and Legendre 2010).

Results

Community composition and interactions sampling

During the 2 sampling periods, 399 interactions were recorded for 33 species of plants in 16 families, and 13 species of bees in 9 tribes. The first sampling period (November 2016 to January 2017) had higher flower abundance and species richness (26 species, of which 14 occurred exclusively in this period, Fig. 1; Table S1), along with 11 species of bees (Fig. 2). In the second sampling period (November 2017 to January 2018), both flower abundance and plant richness (19 species, of which 7 were exclusive, Fig. 1; Table S1) were lower. The number of bee species was similar in both periods (11 and 12 species, respectively, Table S2). Among plant families, members of Asteraceae had the highest frequency of visits (28% of total interactions), followed by Myrtaceae (24%) and Rubiaceae (8%). The tribe of bees
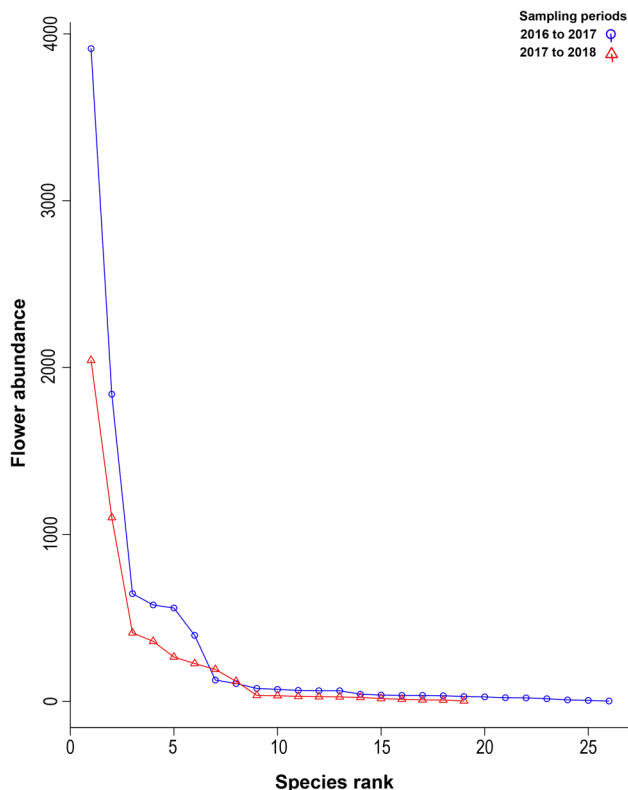
Fig. 1 Rank–abundance curve showing the change in floral resource availability over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado

with the highest frequency of interactions was Apini (41% of interactions, represented by 1 species), Meliponini (25% of interactions, represented by 4 species), and Augochlorini (14% of interactions, represented by 3 species). The alien honeybee, *Apis mellifera* Linnaeus, was the most frequent flower visitor in both years (24% of all interactions in 2016 and 50% in 2017, Fig. 2).

Plant–pollinator interaction networks and metrics

Specialization (H_2') and modularity (Q_w') were higher in the first sampling period (Table 1; Fig. 3). On the other hand, connectance (C), nestedness (wNODF), and niche overlap (R_0) were higher in the second period (Table 1). In the first sampling period (2016 to 2017), the network was less nested than expected by chance, revealing a non-nested structure (Table 1).

Bee roles in networks

We found no difference in bee species strength (ss′) between sampling periods ($t = 1.37$, $p = 0.19$, Table S2); however, bee

species specialization (d') differed over sampling periods, with an overall decrease in bee species specialization in the second period ($t = 2.69$, $p = 0.02$, Fig. S2; Table S2). According to bee c and z values (Fig. 4), all bee species were classified as "peripherals" in the first sampling period. In the second period, in turn, *A. mellifera* changed its species role from "peripheral" to "module hub" (Fig. 4).

Changes in community interactions and functional traits over time

Rarefaction analysis showed higher interaction richness, Shannon, and Simpson interaction pairwise diversity in the first sampling period (Fig. 5). However, extrapolation analysis showed no difference in interaction richness between years, but Shannon and Simpson interaction diversity were both higher in the first sampling period, even considering extrapolation analysis (Fig. 5). The total β-diversity of interactions (β_{WN}) was 0.88, of which 93% ($\beta_{OS} = 0.83$) was due to the rewiring of bee–plant interactions (see Fig. 2), and only 7% ($\beta_{ST} = 0.06$) occurred due to the dissimilarity in species composition between sampling periods. β-Diversity in plant–bee interactions over time was still very high even when we considered the effect of "unrecorded" shared interactions, since the corrected versions of $\beta_{Chao–Jaccard}$ and $\beta_{Chao–Sørensen}$ were as high as 0.76 and 0.61, respectively. The observed values of both β-diversity indexes were significantly higher ($p < 0.0001$) than expected from random pairwise interactions generated by the Patefield null model (Fig. S3). The β-diversity of plant functional traits did not differ between sampling periods (Fig. 6, pseudo-$F = 0.41$, $p = 0.52$), and showed similar values of functional evenness and dispersion for both sampling periods (2016 to 2017: FEve = 0.46, FDis = 0.44; 2017 to 2018: FEve = 0.46, FDis = 0.52).

Discussion

Our results showed that both plant community composition (especially the plants in the network core) and floral resource availability have changed over sampling periods, impacting plant–bee interactions in a grassland community. These changes were followed by a decrease in plant–bee interaction diversity, along with a high β-diversity in plant–pollinator pairwise interactions. It is widely known that plant–pollinator interactions are highly variable through time (Chacoff et al. 2018) and space (Carstensen et al. 2014), and these variations are an intrinsic property of interaction network dynamics (Poisot et al. 2015). Natural changes in environmental conditions and, by consequence, in species composition are important factors affecting spatiotemporal dynamics in interaction networks (Traveset et al. 2018; Lara-Romero
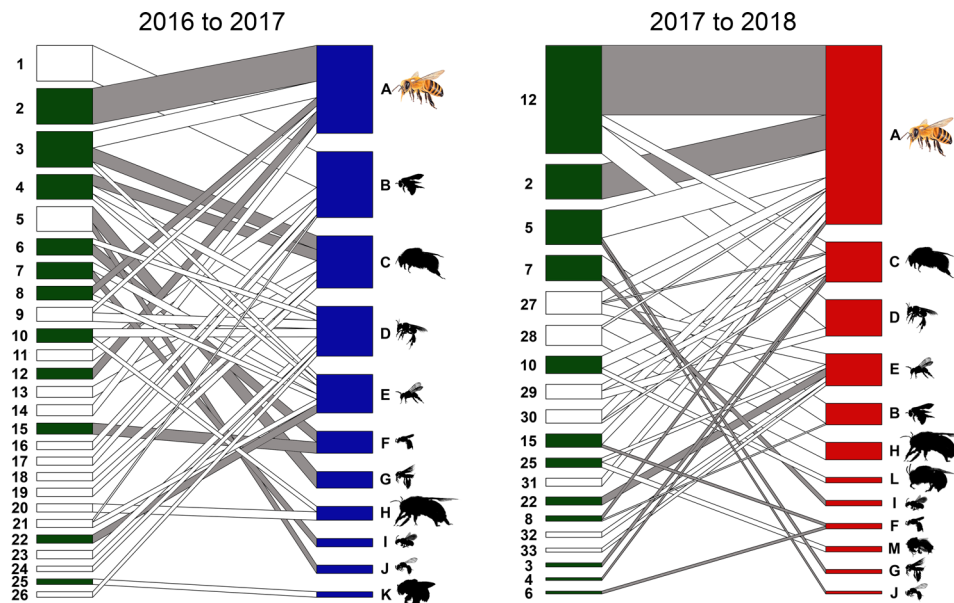
Fig. 2 Plant–bee interactions over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado. Bar thickness represents the interaction frequencies for each pairwise interaction. Vertices and links in white color represent plants and interactions occurring in only one period of sampling, highlighting the *β*-diversity of species and interactions. Numbers and letters represent, respectively, plant and bee identities, as follow: 1: *Psidium grandifolium*, 2: *Cosmos sulphureus*, 3: *Borreria poaya*, 4: *Solanum* sp., 5: *Chromolaena laevigata*, 6: *Commelina erecta*, 7: *Acisanthera quadrata*, 8: *Trichogonia attenuata*, 9: Fabaceae 2, 10: *Caryocar brasiliense*, 11: *Richardia grandiflora*, 12: *Myrcia bella*, 13: *Mimosa debilis*, 14: *Hyptis* sp., 15: *Borreria capitata*, 16: *Waltheria communis*, 17: *Trimezia juncifolia*, 18: *Polygala violacea*, 19: *Mimosa dolens*, 20: *Mandevilla emarginata*, 21: *Cambessedesia espora*, 22: *Byrsonima intermedia*, 23: Asteraceae 2, 24: Fabaceae 1, 25: *Banisteriopsis campestris*, 26: Asteraceae 1, 27: *Aspilia foliacea*, 28: *Kielmeyera variabilis*, 29: *Palicourea rigida*, 30: *Lessingianthus grandiflorus*, 31: *Erythroxylum cuneifolium*, 32: *Byrsonima pachyphylla*, 33: *Eriope macrostachya*, A: *Apis mellifera* (highlighted in the image), B: *Augochloropsis* sp., C: *Bombus morio*, D: *Trigona spinipes*, E: *Plebeia* sp., F: *Augochlorella* sp., G: *Tetrapedia* sp., H: *Xylocopa brasilianorum*, I: *Nannotrigona testaceicornis*, J: *Augochlora* sp., K: *Centris* sp., L: *Ptiloglossa* sp., M: *Monoeca* sp.

et al. 2019). Despite being highly dynamic, the structure of plant–animal interaction networks remains stable due to the persistence of a relatively unchanged core group of interacting species (Chacoff et al. 2018).

In our study system, however, the plant species in the network core have markedly changed over the two sampling periods, and it is not likely that variations in abiotic conditions, such as rainfall, temperature, and humidity, have affected plant composition and interaction network in such a manner. Similarly, the variations in community structure cannot be attributed to natural demographic fluctuation due to seed bank dynamics, since most plants in our study site are perennial (hemicryptophyte) species, and despite belonging to the herbaceous strata, they present xylopodium, an underground woody carbohydrate storage organ very common in Cerrado plants (see Appezzato-da-Glória and Cury 2011; Pausas et al 2018). Hence, we suggest that the growth of *B. decumbens*, an invasive fast-growing grass species, which is known to affect plant community structure (species composition, richness, and abundance) and impoverish Cerrado vegetation in Brazil (Pivello et al. 1999a, b;

Almeida-Neto et al. 2010), may have contributed to the temporal change in the structure of plant–bee interaction network in our study area.

We know from previous studies that indirect effects caused by the introduction of alien species in plant–pollinator interaction networks can disrupt network structure and stability (see Vanbergen et al. 2018; Valido et al. 2019). Also, the reduction in the abundance or loss of plant species with high interaction frequency decreases interaction richness in plant–pollinator networks (see Biella et al. 2019). Although *B. decumbens* is not integrated into plant–bee interaction network, it may have affected network dynamics by limiting the growth of native plant species, decreasing community diversity and species abundances (Pivello et al. 1999a, b; Silvertown 2004; Martin et al. 2009; Almeida-Neto et al. 2010). Such changes reduced the availability of floral resources to bees, leading to a high temporal *β*-diversity in plant–bee interactions, mainly due to the interaction rewiring.

Across the two sampling periods, the plant–bee interaction network became less modular and specialized, showing

Table 1 Changes in community composition and structure over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado

Community composition	Sampling period		
	2016 to 2017		2017 to 2018
Plant richness	26		19
Flower availability	8830		4950
$\beta_{\text{Whittaker}}$ diversity of plants		0.44	
$\beta_{\text{Chao–Jaccard}}$ diversity of plants		0.32	
$\beta_{\text{Chao–Sørensen}}$ diversity of plants		0.19	
Bee richness	11		12
$\beta_{\text{Whittaker}}$ diversity of bees		0.13	
$\beta_{\text{Chao–Jaccard}}$ diversity of bees		0.04	
$\beta_{\text{Chao–Sørensen}}$ diversity of bees		0.02	
Network metrics	Observed value (95% confidence interval)		
Connectance (C)	0.13		0.15
Nestedness (wNODF)	4.14 (12.37–18.94)		11.8 (0.76–0.79)*
Specialization (H'_2)	0.80 (0.16–0.26)*		0.66 (0.07–0.13)*
Niche overlap (R_0)	0.05 (0.22–0.32)*		0.23 (0.39–0.62)*
Modularity (Q'_w)	0.69 (0.25–0.33)*		0.46 (0.12–0.17)*

*Significant values based on a null distribution using the Patefield null model
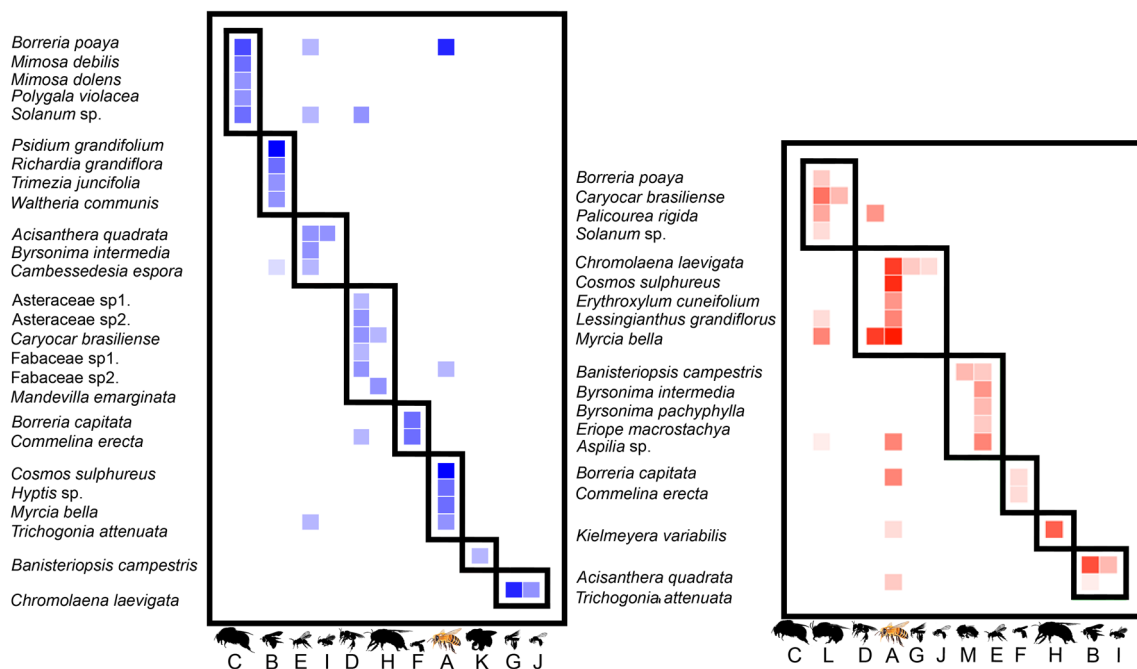
Fig. 3 Changes in module conformations (niche specialization pattern) of plant–bee interactions network over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado. *Apis mellifera* is highlighted in the image, and identities of bee species follow as in Fig. 2

higher connectance, nestedness, and niche overlap among bee species. These changes may be related to the rewiring of plant–pollinator interactions due to shifts in the bee resource usage pattern through pollinator adaptive foraging (see Valdovinos 2019 and references therein), together with a potentially intensified competition among bee species

Fig. 4 Distribution of bee species according to their *c*- and *z*-scores over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado. Species roles of bees in the first period (2016 to 2017) are represented by blue circles, and in the second period (2017 to 2018) by red circles. Circle colors have 30% opacity to highlight the overlying values of *c*- and *z*-scores, and species role of *Apis mellifera* (which has changed over sampling periods) is highlighted
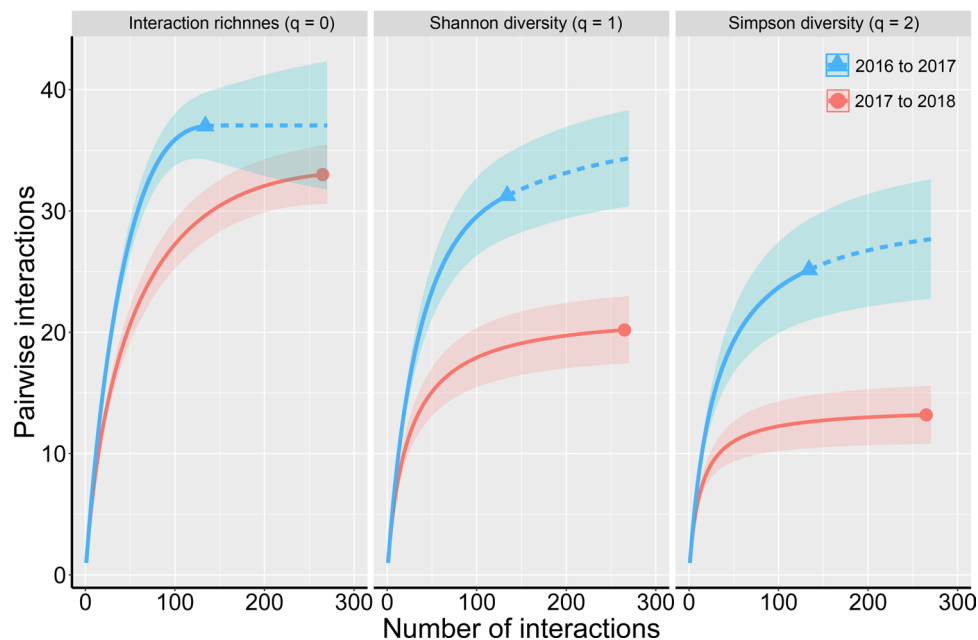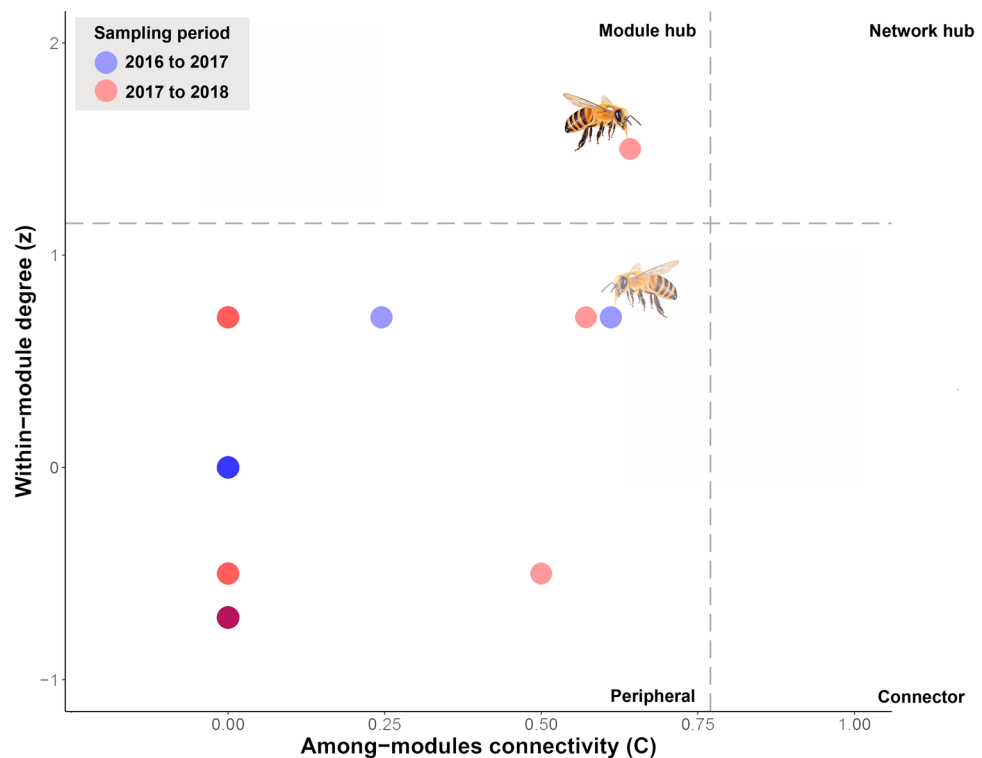
Fig. 5 Rarefaction (continuous lines) and extrapolation (dashed lines) curves with Hill numbers of the diversity order of *q* = 0, 1, and 2 of pairwise interactions over sampling periods, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado. The first sampling period is represented by blue lines, and the second one by red lines. The smallest sample (second sampling period) was extrapolated up to the same number of interactions as the reference sample (first sampling period). Shaded areas represent 95% confidence intervals for each sample after 200 bootstraps

Fig. 6 β-Diversity of plant functional traits over sampling periods, represented in the principal coordinates analysis (PCoA) space, before (November 2016 to January 2017) and after (November 2017 to January 2018) the growth of the invasive alien grass species, *Brachiaria decumbens*, in a grassland community of the Brazilian Cerrado. Blue dots represent functional traits of plants in the first period and red triangles represent functional traits of plants in the second. Red triangles with blue dots inside represent species with equal functional traits. Polygons represent the functional space occupied by overlapping species (pseudo-$F = 0.41$, $p = 0.52$)
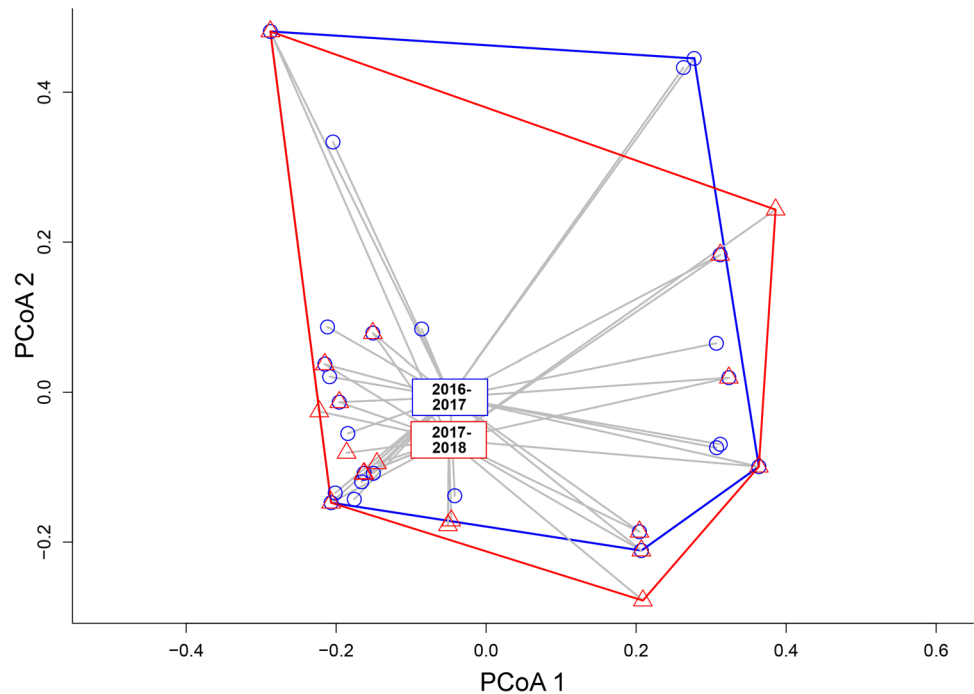
(Valdovinos et al. 2013; Vanbergen et al. 2018). Therefore, it seems that the decrease in floral resource availability may have favored more generalist and abundant bee species, such as *A. mellifera*, that dominated the reduced floral resources (Aizen et al. 2008; Magrach et al. 2017; Valdovinos et al. 2018; Hung et al. 2019). This process may have increased competition between wild bee species and *A. mellifera* (see Magrach et al. 2017; Valdovinos et al. 2018) that changed its topological role within the community, contributing to the nested pattern of the interaction network in the second sampling period. This means that the more generalist bees came to occupy a larger portion of the feeding-niche axis (Dáttilo et al. 2014).

These shifts in bee resource usage patterns across sampling periods were highlighted by the decrease in overall bee specialization within the network, which reduced the strength of interactions between bees and plants. In fact, the bee species that compose the community of our study system are polylectic, i.e., they are generalists and use a wide variety of plants as food sources (Michener 2000). Hence, in a scenario of reduced resource availability, polylectic bees may easily change their foraging behavior (Valdovinos et al. 2013, 2018; Souza et al. 2018). Especially, the more dominant bees, such as *A. mellifera*, tend to dominate the most abundant plants (Aizen et al. 2008, 2014; Magrach et al. 2017; Vanbergen et al. 2018), thus decreasing the overall bee specialization within the interaction network after the growth of the alien grass species in the second sampling period. On the other hand, from the plants' perspective, a community-wide decrease in pollinator specialization and an

increase in niche overlap mean a higher risk of interspecific pollen deposition, potentially impairing plant reproduction by decreasing fruit and seed formation (in most cases but not in all, see Maruyama et al. 2018).

The decrease in plant species richness over the two sampling periods did not reduce the functional diversity of floral traits in the short term, similar to observations in other Cerrado/grassland ecosystems in Brazil where natural changes in plant species richness occur due to seasonality (Souza et al. 2018). Hence, our results indicate that the change in plant–pollinator network structure occurred due to the interaction rewiring mediated by the decline in floral resource availability and not by species turnover, or the turnover of plant functional traits. Also, despite the short-term resilience of our community in terms of functional diversity of floral traits, the persistence of invasive species in native communities may lead to cumulative changes (Strayer et al. 2006; Edwards et al. 2019; Yang et al. 2019). Over the long term, such changes can have greater impacts on the community structure, reducing, even more, the species richness and abundance, which eventually will reduce the functional diversity and convert an originally diverse grassland community into a simplified pasture dominated by only a few species (Strayer et al. 2006).

Notwithstanding, the total number of pairwise interactions, i.e., interaction richness, was not affected by the reduction in plant species richness, but the pairwise interaction diversity decreased by about 50%. This reduction in interaction diversity highlights the indirect effect that an invasive species may have on the dynamics and structure

of the plant–bee interaction network, since the reduction in plant richness and floral resource abundance may allow the best bee competitors to dominate the available resources (Magrach et al. 2017). It is remarkable that another alien invasive species, the Africanized honeybee, may have contributed to impoverish the community-wide diversity of plant–bee interactions (Goulson 1999; Valido et al. 2019). In addition to the overall decrease in the species-level specialization of bees, most bees, particularly the less competitive ones, also showed decreased interaction strength, which demonstrates that these interactions were more susceptible to disruption and finally became extinct (see Aizen et al. 2008; Stout and Morales 2009; Morales et al. 2013; Valdovinos et al. 2018; Vanbergen et al. 2018; Valido et al. 2019). Indeed, the extinction of ecological interactions occurs much faster than species extinctions per se and may affect ecosystem functioning more rapidly through cascading effects (Aizen et al. 2012; Valiente-Banuet et al. 2015). Interestingly, our study site in the Municipality of Botucatu, São Paulo, is only 100 km from the Municipality of Rio Claro, São Paulo, where the Africanized honeybees were inadvertently released into South America by Dr. Warwick E. Kerr in 1956 (see Kerr 1957). Hence, the local wild bee community has been facing interference by a highly aggressive alien species of bee for more than 60 years, which may have affected the ecosystem functioning through time, especially in synergy with other invasive species, such as *B. decumbens*.

Concluding remarks and caveats

In this study, we described the short-term change in plant species composition and abundance, along with a decrease in plant species richness and floral resource availability, and their effect on the dynamics and structure of plant–bee interactions in a disturbed grassland community. We acknowledge that the nature of our before-and-after study may preclude us from drawing an intimate cause–effect relationship of the invasive grass, *B. decumbens*, on the structure of plant community and plant–bee interaction dynamics. However, the evidence of the deleterious effect of invasive grass species, including *B. decumbens*, on the diversity, composition, and abundance of natural plant community worldwide is overwhelming (Pivello et al. 1999a, b; Mack et al. 2000; Williams and Baruch 2000; Silvertown 2004; Martin et al. 2009; Almeida-Neto et al. 2010; Edwards et al. 2019). Therefore, it is reasonable to consider that the rapid growth of the invasive grass species in our study site may have contributed to the high interaction rewiring observed due to the changes in floral resource availability. However, future studies are still needed to experimentally access the effect of *B. decumbens*, as well as other invasive species, on the structure

and dynamics of plant–pollinator interaction networks in highly threatened ecosystems in tropics, such as the Brazilian Cerrado.

Compliance with ethical standards

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

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