


# Does fire affect the temporal pattern of trophic resource supply to pollinators and seed-dispersing frugivores in a Brazilian savanna community?

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**Abstract** In tropical savannas, such as the *campo cerrado* in Brazil, fire plays an important role, affecting plant species' life history. Since fire has the potential to modify the structure of savanna communities as a whole, it is expected that it may influence the resource supply for mutualists by altering the pattern of investment in sexual reproduction. We used an experimental approach to test if fire alters trophic resource availability to pollinators (nectar, pollen, and oil) and seed-dispersing frugivores (fleshy fruits) by altering the seasonality of reproductive phenophases in a savanna community. We sampled all individuals of 60 species that were common to both control and experimental fire treatments. Each month we recorded

the number of reproductive individuals to test whether fire affected the temporal resource offered by the plant assemblage as a whole, and by each specific plant group supporting distinct groups of pollinators and seed-dispersing frugivores. We noticed that fire advanced the nectar, pollen, and fleshy fruit offered by the whole assemblage. Additionally, fire affected the temporal pattern of nectar and pollen available to various pollinator groups, and of fleshy fruits available to all seed-dispersing frugivores. In general, fire seems to have a neutral or even a positive effect on resource availability to mutualists. Nevertheless, there were differences in the availability of the resource utilized by each guild of mutualists.

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## Introduction

Fire is a key ecological disturbance that can influence nutrient cycling (Miranda et al. 2002), shape plant growth forms, plant and animal population distribution, and even biome distribution (Smith 2000; Bond 2014); it can present a positive or negative impact on food webs, affecting plant and animal dynamics, species richness and abundance, as well as biotic interactions (Bowman et al. 2016). It disturbs great areas worldwide every year (Goldammer and Mutch 2001; Pyne 2001), affecting large extensions of savannas (Lavorel et al. 2007; Bond 2014). Fire, ignited by man or lightning, has occurred in savannas for thousands of years (Bond 2014) and, in Brazilian savanna indigenous people have used fire to stimulate fruiting (Coutinho 1990 and references therein). The effect of fire on biological processes can be complex and contrasting, influencing vegetation distribution, structure, and dynamics (Chapin et al. 2002; Bowman et al. 2009), and consequently, plant–animal interactions (Keane et al. 2007).

Many plant species commonly found in fire-prone biomes, like savannas, present strategies that may allow them to survive even if their entire aboveground biomass is destroyed by fire (Coutinho 1982; Hoffmann et al. 2002). Some plants may even be favoured by the physical and chemical effects of fire (Coutinho 1982; Hoffmann et al. 2002) and by the reduction of local competition due to the initial post-fire decrease in the number of ramets (Coates et al. 2006; Coates and Duncan 2009). However, the effects of fire on plant communities vary according to its severity (Wright et al. 2016; Hammill and Bradstock 2006) and frequency of incidence (Barlow and Peres 2006; Ponisio et al. 2016).

Additionally, fire may affect plant species phenology, and thus plants' functional traits associated with persistence strategies, such as post-fire resprouting ability (Pausas et al. 2004). Flowering may be stimulated by fire (Lamont and Downes 2011), especially due to the increase in soil nutrient load from the ashes (Lamont and Runciman 1993; Bond and van Wilgen 1996; Coates et al. 2006). Fire-induced increases in soil fertility may lead to a greater number of flowering species or individuals (Miranda et al. 2002; Lamont and Downes 2011), particularly in species that lose little biomass due to fire and can remobilise remaining resources to reproduce rapidly

(Bond and Van Wilgen 1996). Moreover, fire can trigger synchronized fruit dehiscence and seed dispersal in some savanna species (Coutinho 1982; Munhoz and Felfili 2007; Pivello 2008). However, flowering, as well as fruiting, in some savanna species, may be negatively affected by fire due to the destruction of flower buds, fruits, and seeds (Hoffmann 1998). Also, in flammable communities, fire may stimulate seed release, germination, and seedling recruitment (Bond and Van Wilgen 1996; Marod et al. 2002; Pausas et al. 2004; Causley et al. 2016; Wright et al. 2016). Post-fire seed recruitment may be associated with the efficiency of seed-dispersing frugivores considering that they can bury seeds so that they escape being damaged by fire (Moore and Vander Wall 2015; Peterson and Parker 2016). Additionally, Barlow and Peres (2006) show that a post-fire decrease in fruiting species leads to a decline in large frugivore species.

The effects of fire have been mainly explored in terms of post-fire changes in the abundance and diversity of plants showing reproductive phenophases (Williams et al. 1999; Lamont and Downes 2011 and references therein). Phenological response to fire may have a direct influence on plant–animal interactions, by altering the period of occurrence of a phenophase, which can lead to the decoupling of species interactions (Williams et al. 1999; Peñuelas and Filella 2001; Solga et al. 2014; Morellato et al. 2016). In the field of pollination biology, there are a growing number of studies that demonstrate that fire can significantly influence plant–pollinator interactions (Ne'eman et al. 2000; Geerts et al. 2012; van Nuland et al. 2013; Brown et al. 2016a, b; Ponisio et al. 2016). Regarding resource availability, Potts et al. (2003) showed that nectar volume and concentration reach their highest levels immediately after fire in bee-pollinated species. However, in Brazilian savanna communities, approximately 57% of zoophilous species are pollinated by animal vectors other than bees (Gottsberger and Silberbauer-Gottsberger 2006). Accordingly, the effect of fire on the trophic resources for these other pollination vectors is still unresolved. From the point of view of seed–dispersal, studies have shown that fire may affect a variety of plant–seed–disperser interactions, with animals helping to disperse seeds to safe sites after fire and promoting post-fire vegetation recovery (Parr et al. 2007; Moore and Vander Wall 2015; Oliveira and Aguiar 2015; Peterson and Parker 2016). Hence, information on how fire may alter the

temporal pattern of reproductive phenophases, and how this may affect mutualistic interactions through changes to the availability of floral resources to potential pollinators, still needs to be further explored, especially in the savanna biome, in which fire plays an important role.

In Brazilian savanna, flowering peaks occur at the end of the dry season (Batalha and Martins 2004, Munhoz and Felfili 2007), a period during which there is a high incidence of fire (Oliveira-Filho and Ratter 2002). Immediately after fire, we expect a reduction in the floral resource available to pollinators due to the destruction of reproductive structures. And following on from the latter, we expect to observe a stimulation of flowering and fruiting, mainly due to an increase in the soil nutrient load provided by the ashes from fires. Considering that fire can affect the temporal pattern of floral resource availability to distinct groups of pollinators and seed-dispersing frugivores, we examined if fire affects the seasonality and timing of the broad types of trophic resource (nectar, pollen, oil, and fleshy fruits) supply to mutualistic animals in a savanna community.

## Methods

### Study site

We carried out this study in the ‘Santa Bárbara Ecological Station’, a 2712 ha conservation unity located in Águas de Santa Bárbara municipality, at 22°46′–22°41′S and 49°16′–49°10′W. The reserve comprises both cerrado and seasonal semi-deciduous forest (Melo and Durigan 2011). The cerrado comprises three biomes: seasonal forest (‘cerradão’ physiognomy), savanna (‘cerrado’ sensu stricto, ‘campo cerrado’, and ‘campo sujo’ physiognomies), and tropical grassland (‘campo limpo’ physiognomy) (Batalha 2011). We carried out this study in ‘campo cerrado’, which is one of the most widespread savanna physiognomies in the study site. According to Köppen’s classification, climate is Cwa, with rainy summers and dry winters (Cunha and Martins 2009). Total annual rainfall varies from 1000 to 1300 mm (Melo and Durigan 2011). Frost and natural fire occurrence are common (Brando and Durigan 2004; Gottsberger and Silberbauer-Gottsberger 2006).

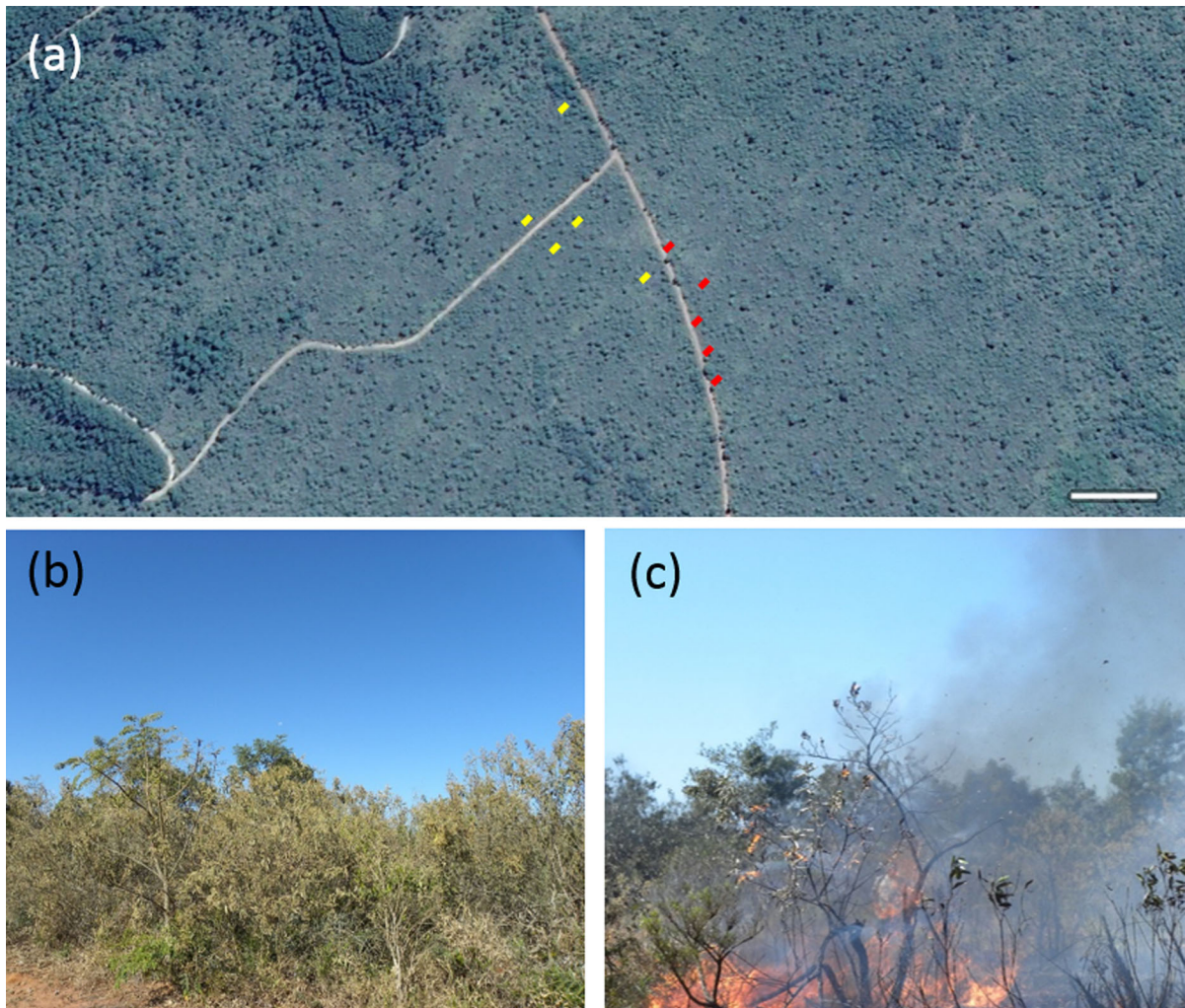
In July 2013, we randomly placed ten 25 m<sup>2</sup> plots in a ‘campo cerrado’ area, at least 5 m one from the

other, at the same altitude (642–643 m a.s.l.) (Fig. 1a). On August 5th, 2013, we burnt half of the plots (fire treatment) and retained the unburnt plots as controls (Fig. 1b, c). We set fire to each of the five plots, one at a time. Fires were allowed to consume all the flammable biomass in a plot. If a fire did not extinguish on its own, it was put out after approximately 1 h.

We considered ramets, at least five centimetres apart from each other, as individuals, since in ecological terms, they may be considered different individuals in spite of sharing the same genome (Allaby 2010). For this study, we selected plant species that were common in both the fire and control treatments and that were reproductively mature, i.e. flowering or fruiting individuals during the study period. We classified pollination and seed dispersion vectors according to the current literature (Online Resource 1). When such information was not available, we determined the most probable vectors based on flower and fruit attributes according to Faegri and van der Pijl (1979) and van der Pijl (1969). If a plant species was used by more than one guild of pollinators or seed-dispersing frugivores, it was included as supporting all interacting guilds. We excluded all the anemophilous and anemochorous, autochorous and epizoochorous individuals (Gottsberger and Silberbauer-Gottsberger 2006), since they do not offer any resources to pollinator or dispersal vector. However, species used only by pollinators or by seed dispersers were still included in this study.

From September 2013 (30 days after fire) to August 2014 (360 days after fire), we conducted monthly counts of the total number of flowering and fruiting individuals (ramets) per species, which were used to indicate the timing and the amount of food resource supply to pollinators and seed-dispersing frugivores.

To test whether our selected plant assemblage was representative of a savanna community, we compared the proportion of species that supported each guild of pollinators and seed-dispersing frugivores in our assemblage with the proportion of species offering resources to each pollinator and seed-dispersing frugivore guild described by Gottsberger and Silberbauer-Gottsberger (2006). For that, we used the Mann–Whitney test, after checking non-normality of the data. We found that the proportions of plant species supporting each group of pollinators and seed-dispersing frugivores in our study site were similar to those recorded for cerrado ( $P = 0.9397$ , for species



**Fig. 1** General aspect of the studied savanna area and sampling design. **a** Satellite image from ‘Santa Bárbara Ecological Station’, in Águas de Santa Bárbara municipality, São Paulo state, Brazil. The *yellow marks* indicate the approximate location of each

control plot and the *red marks* indicate the approximate location of the burned plots. The *scale bar* represents 100 m (adapted from [Google Earth 2016](#)). Examples of **(b)** control and **(c)** experimentally burnt plots. (Color figure online)

supporting pollinators;  $P = 1.0000$ , for species supporting seed-dispersing frugivores; see the specific proportions in Online Resource 2).

We also evaluated if the seasonality of nectar, pollen, and oil supply to pollinators (small-sized bees, medium- and large-sized bees, butterflies, beetles, flies, wasps, moths, bats, hawkmoths, and hummingbirds) and of fleshy fruits to seed-dispersing frugivores (birds, non-flying mammals, lizards, bats, beetles, and ants) was affected by fire by analysing the phenology and availability of these food resources throughout the year. To determine the phenological patterns, we applied circular statistics to the raw number of

flowering and fruiting individuals offering resources, in both control and fire treatment. To test whether floral resources and fruits were uniformly or seasonally distributed throughout the year, we applied the Rayleigh test (Zar 2010) to each treatment. For this test, each month corresponded to  $30^\circ$ , meaning that January corresponded to  $0^\circ$ , February to  $30^\circ$ , and so on. Result of this test is significant when  $P < 0.01$  and  $r > 0.5$ , as proposed by Morellato et al. (2010), indicating the occurrence of a peak. To test whether the mean periods of nectar, pollen, and oil supply to pollinators and of fleshy fruits supply to seed-dispersing frugivores were altered by fire treatment, we used

the Watson–Williams test (Zar 2010). We carried out all statistical analysis in R v.3.2.1 (R Development Core Team 2016) with standard and additional packages: plotrix (Lemon 2006) and circular (Agostinelli and Lund 2013).

## Results

### Resource availability to pollinators

Most of the 60 plant species provided more than one type of resource to pollinators and some of them offered all three types of resource (42 offered nectar, 41 offered pollen, and three offered oil to their pollinators) (Online Resource 1).

The resources were seasonal in their availability to all the pollinator guilds in the control with the exception of nectar to flies, butterflies, and moths, and pollen to flies and beetles (Fig. 2a–s; see Table 1 for statistics). Fire did not affect the seasonality of the resources offered by the whole assemblage (nectar, pollen, and oil) (Fig. 2a–c) and to small-sized bees (nectar and pollen) (Fig. 2d, e) (Table 1). However, resources used by flies (nectar and pollen) (Fig. 2f, g) were seasonally available post-fire but not in the control (Table 1). The opposite pattern was observed for resources favoured by wasps (nectar and pollen) (Fig. 2i, j), medium- and large-sized bees (nectar and pollen) (Fig. 2k, l), and beetles (nectar) (Fig. 2n), which were seasonal in the control, but showed no seasonality in the fire treatment (Table 1).

The nectar availability to butterflies (Fig. 2h), moths (Fig. 2q), hawkmoths (Fig. 2r), and bats (Fig. 2s) was not seasonal after fire (Table 1). There was no nectar available to hummingbirds after fire (Fig. 2p), whereas nectar for hawkmoths and bats was only available after fire (Fig. 2r, s).

Based on the mean angle ( $\alpha$ ), we observed that resource availability to most groups was advanced with fire (Table 1). The nectar availability by the whole-plant assemblage advanced by approximately 20 days in the fire treatment (Fig. 2a), as did the nectar availability to small-sized bees (12 days), flies (90 days), butterflies (80 days), wasps (170 days), and beetles (11 days) (Fig. 2d, f, h, i, n; Table 1). The pollen availability by the whole-plant assemblage advanced by approximately 13 days in the fire treatment (Fig. 2 b), as did pollen availability to small-

sized bees (12 days), flies (90 days), and wasps (166 days) (Fig. 2e, g, j). Pollen availability to medium- and large-sized bees (Fig. 2l), and to beetles (Fig. 2o), was delayed by fire by approximately 6 and 90 days, respectively (Table 1).

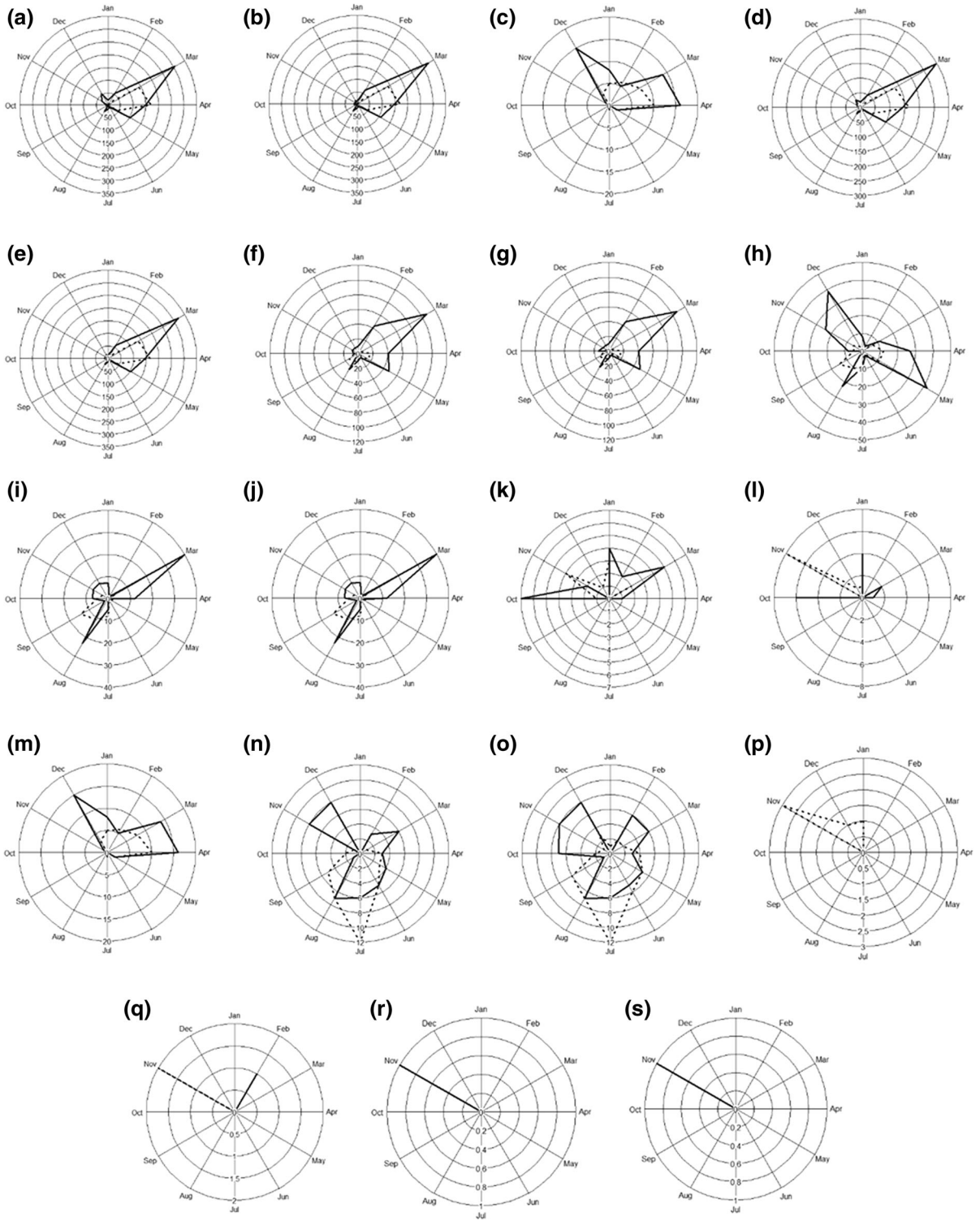
### Resource availability to seed-dispersing frugivores

Among the 60 plant species, only 30 provided fleshy fruits to seed-dispersing frugivores (Online Resource 1). In general, fruit availability was not seasonal to seed-dispersing frugivores in the control, with the exception of ants (Fig. 3a–g; Table 2). Fire promoted the seasonality of fleshy fruits eaten or taken by lizards, bats, and beetles (Fig. 3d–f; Table 2).

Based on the mean angle ( $\alpha$ ), we observed that fruit availability to most frugivore guilds was advanced with fire (Table 2). Fleshy fruit availability by the whole-plant assemblage advanced by 13 days in the fire treatment (Fig. 3a), and fruit availability advanced to lizards (34 days), bats (97 days), beetles (50 days), and ants (21 days) (Fig. 3d–g), whereas to birds (Fig. 3b) and non-flying mammals (Fig. 3c) fruit availability was delayed by fire by approximately 12 and 11 days, respectively (Table 2).

## Discussion

In the absence of fire, the availability of nectar and pollen from the whole-plant assemblage was seasonal, due to flowering seasonality, which reflected climate seasonality as suggested by Batalha and Martins (2004). There was a peak of nectar and pollen availability at the end of the rainy season that lasted for approximately three months, which is a narrow period of resource availability to pollinators in the community. Thus, the coexistence of pollinators during the dry season may be characterised by intense diffuse competition for scarce nectar and pollen resources in savanna (Birch 1957; Ford 1979; Goulson and Sparrow 2009). Alternatively, if these animals' home ranges comprise not only savanna, but also the adjacent seasonal forest, competition for resource may be less during the dry season, which may enable the coexistence of these animals in this season (Henderson and Southwood 2016). In contrast, fruiting occurred over most of the year and was not seasonal, representing a long period of fleshy fruit supply to seed-



◀ **Fig. 2** Number of individuals offering resource to pollinators in each of the sampled months for both control (*dotted line*) and fire treatment (*full line*), regarding **a** nectar, **b** pollen, and **c** oil offered by the whole assemblage of plants; **d** nectar and **e** pollen offer to small-sized bees, **f** nectar, and **g** pollen offer to flies; **h** nectar offer to butterflies; **i** nectar, and **j** pollen offer to wasps; **k** nectar, **l** pollen, and **m** oil offer to medium- and large-sized bees; **n** nectar, and **o** pollen offer to beetles; **p** nectar offer to hummingbirds; **q** nectar offer to moths; **r** nectar offer to hawkmoths; and **s** nectar offer to bats in a savanna area, Águas de Santa Bárbara municipality, São Paulo state, Brazil

dispersing frugivores. In fact, fruiting commonly occurs in the wet period of the year, which prolongs the availability of fleshy fruits attractive (Batalha and Mantovani 2000; Batalha and Martins 2004; Gottsberger and Silberbauer-Gottsberger 2006).

Fire did not drastically alter the duration of resource availability to pollinators and seed-dispersing frugivores in this community. However, it promoted the availability of nectar, pollen, and fleshy fruit earlier in the year, which corroborates the idea that fire may stimulate plant reproduction (Munhoz and Felfili 2007; Pivello 2008; Lamont and Downes 2011); ensuring earlier availability of resources to animals, favouring an earlier recovery of the plant community after fires (Menz et al. 2011; Oliveira and Aguiar 2015). Even though the mean dates of nectar, pollen, and fleshy fruit offer were altered by fire, the shift was only 13–20 days earlier than usual in the season. Thus, the post-fire nectar and pollen availability overlapped with the period of availability of these resources in the control. This shift to earlier flowering comprised a relatively short period of time, when compared to the four months of which flowering occurs, and the shift may not be long enough to affect plant–pollinator interactions. So, the overall patterns observed for the whole-plant assemblage did not indicate any drastic post-fire change in the timing of resource availability to pollinators and seed-dispersing frugivores. However, different pollination and seed-dispersing guilds did demonstrate distinct response patterns.

Similar to the findings for the whole assemblage, in the post-fire scenario, plants offering nectar and pollen to small-sized bees, and nectar to beetles showed a small advance (12 and 11 days, respectively) in timing of these resources, whereas the plants supporting medium- and large-sized bees with pollen delayed pollen production by six days. In both cases, the

changes in the mean period of resource availability were slight compared to long period of resource availability after fire. Additionally, the period of nectar and oil availability to medium- and large-sized bees remained unaltered by fire. The lack of change in the period of availability of oil could be a key to the maintenance of this specialized mutualism between oil-collecting bees and their flowers (Mello et al. 2013) in fire-prone ecosystems. The short advances and delay observed for several guilds of pollinators probably do not represent any risk to the maintenance of the interactions between those plants and pollinators. However, the greater advances were observed in the availability of resources to flies (nectar and pollen), butterflies (nectar), and wasps (nectar and pollen); and the greater delay in the availability of resource to beetles (pollen) indicate a stronger influence of fire on plant–animal pollination interactions. In fact, it is possible that a temporal mismatch may occur between plant and pollinator phenologies (Peñuelas and Filella 2001; Memmott et al. 2007; Solga et al. 2014), since both nectar and pollen availability may not coincide with the period of natural pollinator activity (Bawa 1990; Hegland et al. 2009). It is notable that there were virtually no flowering individuals in the month after fire, which may represent a transient negative effect of fire on resource availability to those pollinator groups caused by the destruction of flower buds (Hoffmann 1998).

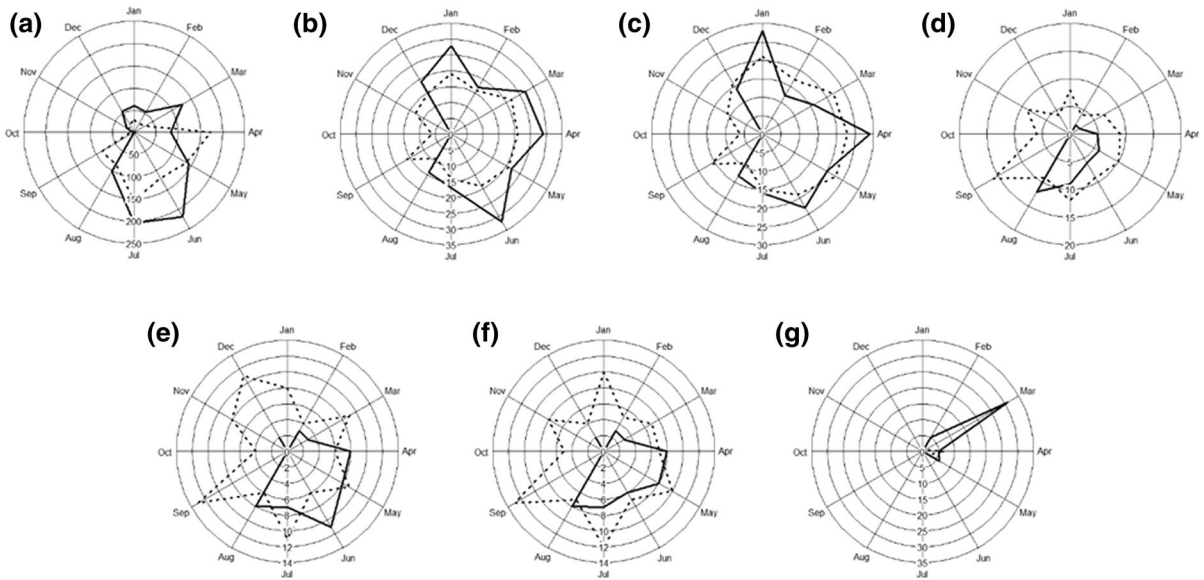
The absence of nectar for hummingbirds in the fire treatment could result in no floral food resources for hummingbirds for at least one year after fire, possibly breaking the natural synchrony between plant and pollinator phenology by causing either a temporal or spatial mismatch (Hegland et al. 2009). This situation could have two outcomes, either the abandonment of the area or an increase in the competition among hummingbirds and other pollinators, since the first might act as cheaters on non-ornithophilous plant species (Maloof and Inouye 2000). Thus, hummingbirds may switch diets and deplete nectar from plant species pollinated by other animal groups, which may eventually result in novel plant–pollinator interactions (Hegland et al. 2009). In fact, Geerts et al. (2012) observed that nectarivorous birds stopped visiting burnt areas even if there were abundant post-fire resources available to them, because of the greater predation risk in burnt out and exposed vegetation.

**Table 1** Circular statistical analysis of the number of individuals offering each type of resource (nectar, pollen and oil) by the assemblage of plants and to each group of pollinator in a savanna community. *n* number of species that offer one or more resources to each group; *NA* data not available

	Treatment Groups										
	Assemblage ( <i>n</i> = 60)	Small-sized bees ( <i>n</i> = 36)	Flies ( <i>n</i> = 22)	Butterflies ( <i>n</i> = 19)	Wasps ( <i>n</i> = 14)	Medium- and large-sized bees ( <i>n</i> = 13)	Beetles ( <i>n</i> = 10)	Hummingbirds ( <i>n</i> = 4)	Moths ( <i>n</i> = 3)	Bats ( <i>n</i> = 1)	Hawkmoths ( <i>n</i> = 1)
<b>Nectar</b>											
Mean angle ( $\alpha$ )	87.90°	84.50°	158.35°	182.59°	220.34°	334.79°	182.88°	317.37°	300.00°	NA	NA
Mean date	68.57° Apr	72.01° Mar	72.74° Jun	102.79° Jul	51.14° Aug	345.42° Dec	171.21° Jul	NA Nov	30.00° Nov	300.00° NA	300.00° NA
Length of mean vector ( <i>r</i> )	0.6439	0.73	0.3088	0.2861	0.5572	0.6899	0.6139	0.9149	1.00	NA	NA
Rayleigh test ( <i>P</i> )	0.6055	0.6955	0.5583	0.0946	0.1816	0.4543	0.0469	NA	1.00	1.00	1.00
Watson-Williams test ( <i>P</i> )	<0.0001*	<0.0001*	0.0001	0.001	<0.0001*	0.0032*	<0.0001*	0.007*	0.1372	NA	NA
	<0.0001*	<0.0001*	<0.0001*	0.1716	0.0241	0.0115	0.8937	NA	0.5122	0.5122	0.5122
	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.05 < <i>P</i> < 0.1	<0.01*	NA	>0.1	NA	NA
<b>Pollen</b>											
Mean angle ( $\alpha$ )	87.48°	84.53°	159.06°	-	220.34°	320.32°	177.39°	-	-	-	-
Mean date	74.60° Apr	72.86° Mar	71.61° Jun	-	53.70° Aug	326.83° Nov	266.41° Jul	-	-	-	-
Length of mean vector ( <i>r</i> )	0.6268	0.7219	0.3122	-	0.5572	0.7434	0.4304	-	-	-	-
Rayleigh test ( <i>P</i> )	0.6859	0.7089	0.5279	-	0.1834	0.4595	0.0689	-	-	-	-
Watson-Williams test ( <i>P</i> )	<0.0001*	<0.0001*	0.0001	-	<0.0001*	0.0005*	0.0001	-	-	-	-
	<0.0001*	<0.0001*	<0.0001*	-	0.0216	0.0616	0.7446	-	-	-	-
	<0.001*	<0.001*	<0.001*	-	<0.001*	<0.001*	<0.01*	-	-	-	-
<b>Oil</b>											
Mean angle ( $\alpha$ )	53.73°	-	-	-	-	53.73°	-	-	-	-	-
Mean date	37.01° Mar	-	-	-	-	37.01° Mar	-	-	-	-	-
Length of mean vector ( <i>r</i> )	0.7145	-	-	-	-	0.7145	-	-	-	-	-
Rayleigh test ( <i>P</i> )	0.6533	-	-	-	-	0.6533	-	-	-	-	-
Watson-Williams test ( <i>P</i> )	<0.0001*	-	-	-	-	<0.0001*	-	-	-	-	-
	<0.0001*	-	-	-	-	<0.0001*	-	-	-	-	-
	0.05 < <i>P</i> < 0.1	-	-	-	-	0.05 < <i>P</i> < 0.1	-	-	-	-	-

\* Statistically significant values. For the Rayleigh test we only highlighted as significant the *P*-values associated with *r*-values >0.5





**Fig. 3** Number of individuals offering fleshy fruits in each of the sampled months for both control (*dotted line*) and fire treatment (*full line*), regarding **a** the assemblage of plants as a

whole, **b** fruit offer to birds, **c** non-flying mammals, **d** lizards, **e** bats, **f** beetles, and **g** ants in a savanna area, Águas de Santa Bárbara municipality, São Paulo state, Brazil

**Table 2** Circular statistical analysis of the number of individuals offering resource (fleshy fruits) by the assemblage of plants and to distinct groups of seed-dispersing frugivores in a savanna community. *n* number of species that offer resource to each group

	Treatment	Groups						
		Assembly ( <i>n</i> = 30)	Birds ( <i>n</i> = 26)	Non-flying mammals ( <i>n</i> = 21)	Lizards ( <i>n</i> = 7)	Bats ( <i>n</i> = 6)	Beetles ( <i>n</i> = 5)	Ants ( <i>n</i> = 2)
<b>Fleshy fruits</b>								
Mean angle ( $\alpha$ )	Control	145.50°	78.57°	79.11°	192.54°	234.70°	185.33°	87.92°
	Fire	132.59°	86.51°	88.80°	158.23°	137.92°	135.45°	66.41°
Mean date	Control	May	Mar	Mar	Jul	Sep	Jul	Mar
	Fire	May	Mar	Mar	Jun	May	May	Mar
Length of mean vector ( <i>r</i> )	Control	0.4827	0.1743	0.1959	0.1756	0.0529	0.1092	0.9186
	Fire	0.4485	0.3882	0.3754	0.6373	0.5827	0.5393	0.8762
Rayleigh test ( <i>P</i> )	Control	<0.0001	0.003	0.0005	0.0417	0.7669	0.322	<0.0001*
	Fire	<0.0001	<0.0001	<0.0001	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Watson–Williams test ( <i>P</i> )		<0.001*	<0.001*	<0.01*	<0.001*	<0.001*	<0.001*	<0.01*

\* Statistically significant values. For the Rayleigh test we only highlighted as significant the *P*-values associated with *r*-values >0.5

This suggests that either way, plant–hummingbird interactions may be negatively affected by fire.

Negative consequences are also associated with plant species supporting moths, of which there were very few individuals that provided suitable nectar, and showed a delay in nectar availability by three months. Moths are seasonally active, which may break the natural synchrony between plant and pollinator

phenologies (Peñuelas and Filella 2001; Memmott et al. 2007; Solga et al. 2014). Also, the small nectar availability to moths is observed all year round in both scenarios (with and without the effects of fire), and moth-pollinated species are not particularly abundant in cerrado, possibly as a consequence of fire affecting this plant–animal mutualism (Bond 1994; Kearns and Inouye 1997; Potts et al. 2010).

Plants supporting hawkmoths and bats only flowered in the fire treatment, and the species supporting this pollinator guild have fire-stimulated flowering (Lamont & Downes Lamont and Downes 2011). Thus, in the post-fire environment, this pollinator guild is favoured, restoring plant–pollinator mutualisms, which is crucial for the restoration of the community as a whole (Menz et al. 2011).

When compared to the number of species that support pollinators, the smaller number of species that support seed-dispersing frugivores highlights the fact that many cerrado plant species do not rely on biological vectors to disperse their fruits or seeds (Batalha and Martins 2004; Gottsberger and Silberbauer-Gottsberger 2006). Among the zoochorous plant species, birds and non-flying mammals were the main seed-dispersing frugivores registered in this study, similar to that described for other cerrado areas (Gottsberger and Silberbauer-Gottsberger 2006). Even though savanna vegetation is known to rely mainly on vegetative reproduction (Higgins et al. 2000), a variety of plants are considered “propagule persisters” (Pausas et al. 2004). Therefore, plant–disperser interactions could contribute to the maintenance of their populations via the seedbank, i.e. seed is buried by the vector. Additionally, birds, bats, rodents, and ants play an important role in dispersing seeds in post-fire scenarios, ensuring species persistence and allowing the recolonization of the burnt areas (Parr et al. 2007; Moore and Vander Wall 2015; Oliveira and Aguiar 2015; Rost et al. 2015; Peterson and Parker 2016). Some rodents and ants may bury heat-sensitive seeds deep enough so they escape damage from fire (Moore and Vander Wall 2015; Peterson and Parker 2016), and shallow enough so that seeds that require heat to germinate do so (Auld 1986).

The initial inhibition of fruiting in plant species that support beetles, lizards, birds, non-flying mammals, and bats during three or more months after fire may be due to the destruction of reproductive structures, as pointed out by Hoffman (Hoffmann 1998). For beetles, lizards, and bats, such inhibition means that fruits that were available all year round in the control were restricted by fire to approximately six months, which can have drastic impacts in animal populations by increasing competition (Willson and Traveset 2000).

In general, nectar, pollen, and oil availability were not uniformly distributed throughout the year and this

is consistent with other cerrado areas (Munhoz and Felfili 2007; Neves and Damasceno-Junior 2011), whereas fleshy fruits were uniformly available throughout the year even in the post-fire scenario, which is similar to the fruiting phenology of zoochorous species in other savanna areas (Munhoz and Felfili 2007). Our results highlight that fire does not filter species offering one specific resource to the detriment of others, and also emphasize that post-fire resource fluctuations in a community are complex. Hence, the severity of the potential effects of phenological mismatches will be determined by the ability of the plant–animal guilds to adapt to changing plant resource availability (Memmott et al. 2007; Geerts et al. 2012; Morellato et al. 2016), and also by the mutualists specificity and dependence on interacting species in the food web (Bond 1994; Waser et al. 1996; Rafferty et al. 2015). Animal species that fly long distances (e.g. birds and mammals) may be more resilient to plant phenology shifts than insects, such as ants, for example (Rafferty et al. 2015). Also, the temporal displacement of plant species’ phenophases may result in complex community-level responses, since they may affect other coexisting plant species through facilitation or competition for pollinators and seed-dispersing frugivores (Fleming and Kress 2013; Albrecht et al. 2015).

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#### Compliance with ethical standards

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

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