

Fire? They don't give a dung! The resilience of dung beetles to fire in a tropical savanna

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Abstract. 1. Disturbance is a strong driver of community assembly and fire has long been recognised as one of the main disturbances of terrestrial ecosystems. This study tested the resilience of dung beetles to fire events in *campos rupestres*, which is a tropical savanna ecosystem that evolved under a frequent fire regime, by assessing the resistance and recovery of their communities.

2. Dung beetles were sampled before and after a fire event and the effect of fire on dung beetle richness, abundance, mean community biomass and composition was tested. The effects of time since last fire and fire frequency on the community were also tested.

3. No effect of fire occurrence, time since last fire and fire frequency on any community variable was found.

4. Some non-mutually exclusive mechanisms promoting the resistance and recovery of dung beetles in *campos rupestres* could be acting in synergy. One potential mechanism is the mismatched seasonality between fire events and dung beetle occurrence, as fires occur during the dry season and dung beetles are present above ground during the rainy season. Furthermore, dung beetles are insects that remain buried during most of their lifetime, which could protect individuals from being burned. Another potential mechanism is the replacement of species in burned areas by the movement of individuals from unburned areas, attracted by resources and/or by metacommunity dynamics.

5. It is concluded that in this 'fire-dependent' ecosystem, dung beetle communities are resilient to fire and seem not to be structured by this disturbance.

Key words. campos rupestres, community, recovery, resistance, Scarabaeinae.

Introduction

Disturbances caused by anthropogenic or natural processes are among the strongest drivers of community assembly. Climatic variation (e.g. Araújo & Rahbek, 2006; Lugo, 2008; Peters *et al.*,

2016; Beiroz *et al.*, 2017), intensive single-event disturbance (e.g. Dalsgaard *et al.*, 2007; Lugo, 2008), and land-use modifications (e.g. Audino *et al.*, 2017; Concepción *et al.*, 2017; Sepp *et al.*, 2018) are among the drivers with the strongest effects on community diversity and assembly. However, how biological communities respond to disturbances depends on many conditions, including biological characteristics (e.g. species traits; Isaac *et al.*, 2009), landscape components (e.g. connectivity; Tambosi *et al.*, 2014; Myers *et al.*, 2015), and the historical condition of land cover (e.g. adaptation to the

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disturbance; Allison, 2004). These conditions work together to provide ecological resilience, which is the ability of an environment to suffer a disturbance and maintain its functioning and re-establish previous ecosystem functioning – the properties of resistance and recovery, respectively (Walker *et al.*, 2004; Oliver *et al.*, 2015).

Fire has long been recognised as one of the main disturbances of terrestrial ecosystems. These ecosystems can be classified according to their association with fire as ‘independent’, ‘sensitive’, and ‘dependent’ (Shlisky *et al.*, 2007). ‘Fire-independent’ ecosystems are those where fire occurrence is very rare (e.g. deserts). ‘Fire-sensitive’ ecosystems are those in which fire disrupts ecosystem processes and severely affects populations (e.g. rainforests). Lastly, ‘fire-dependent’ ecosystems are those that have evolved in the presence of fires and their ecological processes depend on them (e.g. savannas). In this context, even natural fires represent a severe disturbance to most forests around the world (Barlow & Peres, 2004, 2008; Macias Fauria & Johnson, 2008). On the other hand, fire caused by natural processes (e.g. lightning) is considered a key component in defining the physiognomy and structure of savanna ecosystems (Bond & Keely, 2005; Bond & Parr, 2010; Hoffmann *et al.*, 2012; Parr *et al.*, 2014).

Species-rich faunas are associated with ‘fire-dependent’ ecosystems (including the Cerrado, the Brazilian savanna), although there is a lack of studies regarding how these animals respond to fire or how they evolved in these habitats (but see Vieira *et al.*, 1996; Briani *et al.*, 2004; Vasconcelos *et al.*, 2017; Pausas & Parr, 2018). Unlike plants, many animals exhibit behavioural traits for avoiding death by burning in flammable environments, such as the ability of most animals to move and escape from fire. Most studies have recognised animals that have a diet adapted to fire-resistant vegetation, a flexible diet, or a high capacity to move towards unburned areas, or even below ground, thus reducing the population death rate (Monteiro *et al.*, 2017; Vasconcelos *et al.*, 2017). Additionally, many organisms lost in a fire event can be replaced via metapopulation/metacommunity dynamics from populations/communities in surrounding areas (Brotons *et al.*, 2005). This replacement might result in the recovery of the previous community or, on the other hand, changes in species composition after fires, given that some animal species are opportunistic, or even specialised to post-fire conditions (Pausas & Parr, 2018).

The *campos rupestres* (rupestrian grasslands) ecosystem in the Cerrado is widely known for its severe and intensive fire regime (Figueira *et al.*, 2016; Alvarado *et al.*, 2017). This ecosystem harbours a unique diversity of plants and animals with a high degree of endemism, and which exist under severe environmental stresses (Fernandes, 2016; Silveira *et al.*, 2016). *Campos rupestres* also provide many valuable ecosystem services, such as protection for a significant number of river headwaters that provide freshwater for local human populations and supply many watersheds in Brazil and other South American countries (Resende *et al.*, 2017). In addition, *campos rupestres* greatly enhance tourism and support local craft activities in the regions where they occur (Resende *et al.*, 2017). Despite the enormous economic and environmental importance of the

campo rupestre ecosystem, it has been severely degraded by opencast mining, annual anthropogenic burnings to support the cattle industry, wood extraction, and invasive species, among many others [for further discussion, see Fernandes (2016) and Silveira *et al.* (2016)].

Dung beetles are great focal organisms for evaluating the effects of post-fire conditions on invertebrate fauna. They are widely used as ecological indicators in monitoring studies and conservation strategies (Nichols *et al.*, 2007, 2013), because they are inexpensive to sample and exhibit high sensitivity to anthropogenic and natural changes in environmental conditions (Gardner *et al.*, 2008; Larsen *et al.*, 2008; Nunes *et al.*, 2016; Beiroz *et al.*, 2017). Additionally, dung beetles can be used as good indicators of ecosystem functioning, as they play key roles in many ecological processes related to biodiversity conservation and human benefits, such as nutrient cycling and parasite suppression (Nichols *et al.*, 2008). They are also widely known for their rapid recovery after changes in environmental conditions (Quintero & Roslin, 2005; Beiroz *et al.*, 2017).

We assessed the resistance and recovery [resilience; see Oliver *et al.* (2015) for definition] of dung beetles to fire events in *campos rupestres*. We evaluated the effect of fire on dung beetles in an ecosystem that evolved under a frequent fire regime and is mainly constituted of open habitats. Therefore, we hypothesised that dung beetle communities would exhibit high resistance to the occurrence of fire and fast recovery from its consequences. We expected that the dung beetle communities, before and after fire events, would show similar temporal variation to communities at unburned sampling points. Additionally, if dung beetles are indeed resistant to fire, we expected that the time since the last fire and the fire frequency at each sampling point would not affect community diversity.

Materials and methods

Site description

The study was carried out in *Serra do Cipó*, which is located in the southern part of the Serra do Espinhaço mountain range (Brazil, Minas Gerais State, 19°10' and 19°28'S, 43°29' and 43°36'W; Fig. 1). The Espinhaço range is a quartzite mountain range which extends for more than 1200 km, in two Brazilian states (Minas Gerais and Bahia), from southeast to northeast Brazil (Fig. 1). This mountain range represents a natural barrier between the Atlantic Forest (east slope face) and the Cerrado (west slope face) biomes. Our samplings were taken in the Cerrado domain, in a mosaic of *campo rupestre* habitats. The region has a mean annual temperature of 20 °C and a rainy season between November and February (highland tropical Cwb Köppen climate) (Fernandes *et al.*, 2016). The region of *Serra do Cipó* is well known for its high biodiversity and great number of endemic species (e.g. Silveira *et al.*, 2016).

The study region has been historically affected by a severe natural fire regime and the occurrence of criminal fires (Alvarado *et al.*, 2017). There was an extensive fire event in 2014, and the fire event before that was in 2011 (see Alvarado *et al.*, 2017).

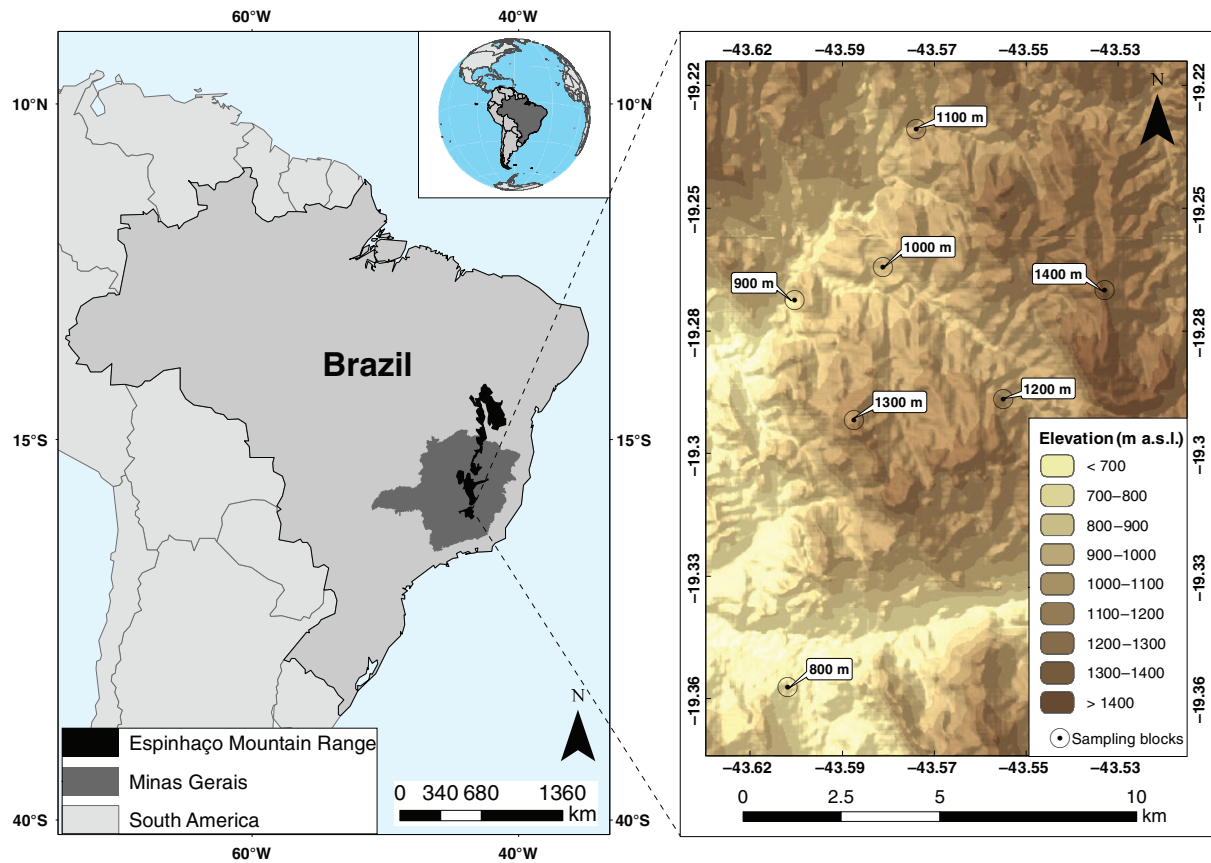


Fig. 1. (a) Location of the Espinhaço mountain range in Brazil. (b) In detail, the distribution of sampling blocks within Serra do Cipó, Minas Gerais State, Brazil. [Colour figure can be viewed at wileyonlinelibrary.com].

Fire assessment and variables

We acquired fire event data from Alvarado *et al.* (2017). These authors mapped burn scars by visual interpretation of false colour composites of each Landsat satellite image from 1984 to 2014 with manual delineation at the fixed visualisation scale of 1:25 000 [see Alvarado *et al.* (2017) for additional details]. We then compared the locations of our sampling sites with the registered fire events to determine which sampling points had been affected by the 2014 fire event, as well as the last local fire event and the frequency of fire occurrence at the sampling points since 1984.

Dung beetle sampling

We established seven sampling blocks that contained nine sampling points each. The blocks were designed to control for the effect of elevation, as we sampled on a mountain ranging from 800 to 1400 m asl (Fig. 1). Thus, the sampling blocks were set at intervals of 100 m asl and separated by more than 2 km (Fig. 1). All nine sampling points in each block had approximately the same elevation and were separated by at least 100 m to ensure spatial independence (da Silva & Hernández, 2015). We therefore considered a sampling

Table 1. Results of linear mixed-effect models with the four response variables of dung beetle communities [abundance, richness, community-weighted mean (CWM) size and composition] against the occurrence of fire in 2014.

| Response variable | χ^2 | P-value |
|----------------------|----------|---------|
| Δ abundance | 1.656 | 0.198 |
| Δ richness | 0.002 | 0.967 |
| Δ CWM size | 1.108 | 0.293 |
| Δ composition | 0.138 | 0.710 |

Δ is the difference between the December 2014 collection and December 2013 collection. Δ composition is β -diversity based on the Bray–Curtis similarity index between pre- and post-fire collection. χ^2 is the value of the χ^2 test between each model and a random model.

point as a sampling unit, for which there were 63 in total (seven blocks with nine points each). Among all 63 sampling points, 28 spread over five blocks had burned during the 2014 fire events, whereas 35 points and two entire blocks had not burned in 2014.

At each sampling point, we set a baited pitfall trap to capture dung beetles. Pitfall traps consisted of plastic containers (depth 9 cm, diameter 15 cm) containing 250 ml of a salt and detergent solution and baited with 25 g of fresh human faeces.

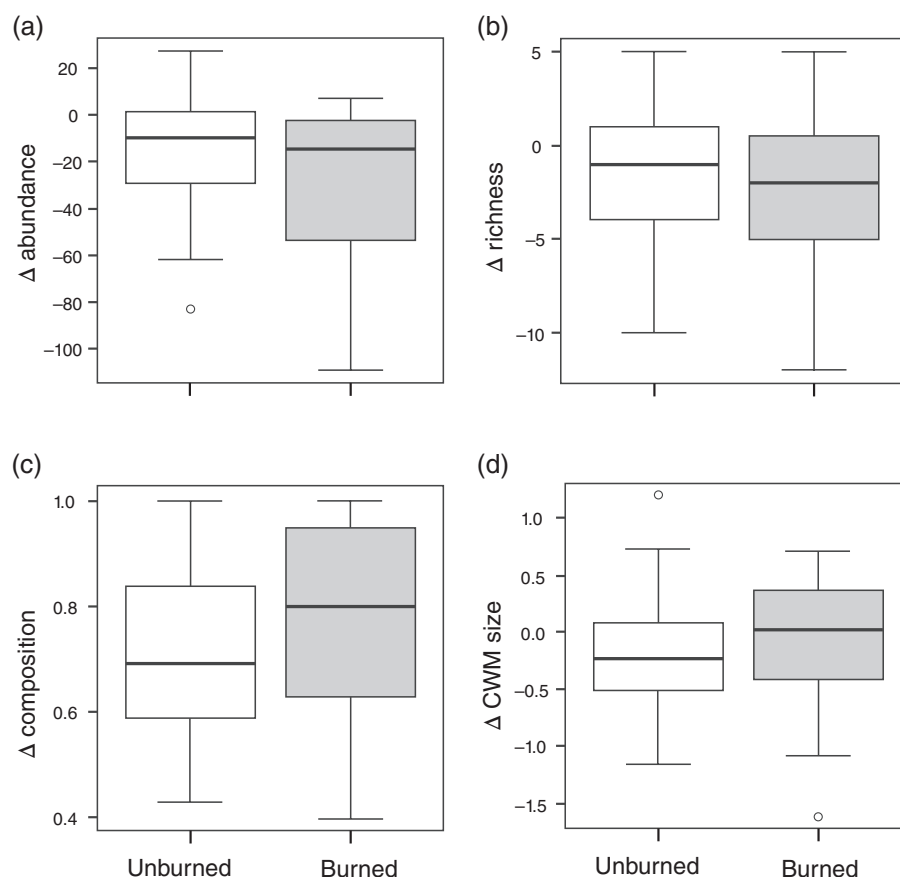


Fig. 2. Dung beetle recovery from fire disturbance at Serra do Cipó, Minas Gerais, Brazil: (a) Δ abundance, (b) Δ richness, (c) Δ composition and (d) Δ community-weighted mean (CWM) biomass. Δ is the difference between the pre and post-fire collections. Δ composition is β -diversity based on the Bray–Curtis similarity index. None of these response variables were influenced by the fire events of 2014.

We left traps in the field for 48 h, after which the beetles were collected, preserved, and transported to the laboratory. All individuals were counted and identified to the lowest taxonomic level possible. We used the dichotomous key of Vaz-de-Mello *et al.* (2011) to identify genera and comparisons with voucher specimens to identify species. We measured all individuals from the clipeous to the pygidium to obtain their size. We also dried out all individuals in an oven for 48 h at 40 °C and then weighed them on a 0.001-g precision balance to obtain their body mass. As both individual and mean size are highly correlated to their respective body mass values (see Supporting information, Fig. S1), we decided to consider only size for analysis, because body mass exhibits variation due to uncontrolled conditions (e.g. daily variation in air humidity during weighing). Some of the individual specimens were deposited in the Scarabaeinae collection of Universidade Federal de Mato Grosso, and the remainder were sent to the Ecologia Evolutiva e Biodiversidade laboratory at the Universidade Federal de Minas Gerais, Brazil.

We collected dung beetles twice at each sampling point following the same methods. The first collection was carried out in December 2013, approximately 9 months before the 2014 fire events. The second collection was made 1 year later, about

2 months after the 2014 fire events, in December 2014, to control (or minimise) effects of seasonal variation.

Data analysis

To evaluate the recovery of dung beetles from the 2014 fire event, we used pre-fire dung beetle community metrics as a temporal control to examine post-fire consequences, in both burned and unburned sampling points. Thus, we calculated variation in the number of individuals, species richness and the community-weighted mean size (hereafter called Δ abundance, Δ richness and Δ CWM size, respectively) for each sampling point. We also determined variation in community composition (considering species abundance) based on pairwise Bray–Curtis dissimilarity distance between communities before and after the 2014 fire event (hereafter Δ composition). We built linear mixed-effect models (LMMs) using sampling block as a random effect, variation in community metrics as response variables, and categorical data regarding the 2014 fire event as an explanatory variable. These models were compared with their respective null models, to evaluate the statistical significance

Table 2. Results of linear mixed-effect models with four response variables of dung beetle communities [abundance, richness, Simpson's diversity index (1-D) and community-weighted mean (CWM) size] against time since last fire, fire frequency and the interaction between these two explanatory variables.

| Response variable | Explanatory variable | χ^2 | P-value |
|-------------------|----------------------|----------|---------|
| Abundance | Time since last fire | 0.141 | 0.707 |
| | Fire frequency | 0.016 | 0.899 |
| | Interaction | 0.443 | 0.506 |
| Richness | Time since last fire | 1.007 | 0.316 |
| | Fire frequency | 0.660 | 0.416 |
| | Interaction | 0.255 | 0.613 |
| Simpson's index | Time since last fire | 0.001 | 0.978 |
| | Fire frequency | 0.249 | 0.618 |
| | Interaction | 0.028 | 0.866 |
| CWM size | Time since last fire | 0.748 | 0.387 |
| | Fire frequency | 0.037 | 0.849 |
| | Interaction | 0.013 | 0.909 |

Dung beetle community attributes were calculated from the December 2014 collection. χ^2 is the value of the χ^2 test between each model and a random model.

of the response variable, using the Wald χ^2 test in the *car* package (Fox & Weisberg, 2011).

To evaluate dung beetle resistance to fire disturbance, we used post-fire (communities sampled in December 2014) abundance, species richness, Simpson's diversity index (1-D) and CWM size as response variables, and time since last fire and fire frequency as explanatory variables. We also performed LMMs to test our hypothesis that dung beetle communities would be resistant to fire, using sampling blocks as a random effect. We then ran multiple regressions for each response variable, with time since last fire, fire frequency and the interaction between these two variables as explanatory variables. We used the *lme4* package to build LMM and ran all analyses in R (Bates *et al.*, 2013; R Core Team, 2013).

Results

We collected a total of 2900 individual dung beetles (pre-fire, 2107; post-fire, 793) of 50 species (pre-fire, 44; post-fire, 42). The list of species and their abundance per sampling point on the two collection dates are presented in Table S1.

Dung beetle abundance, richness, CWM size, and composition were not affected by the fire events of 2014 in Serra do Cipó (Table 1; Fig. 2). Similarly, dung beetle abundance, richness, CWM biomass, and diversity (Simpson's diversity index) were not explained by time since last fire, fire frequency or the interaction between these two explanatory variables (Table 2; Fig. 3).

Discussion

Dung beetles of *campos rupestres* showed high resilience to the consequences of fire. As we expected, dung beetle communities from burned areas before and after fire events showed temporal variation similar to that of unburned areas. This indicates that

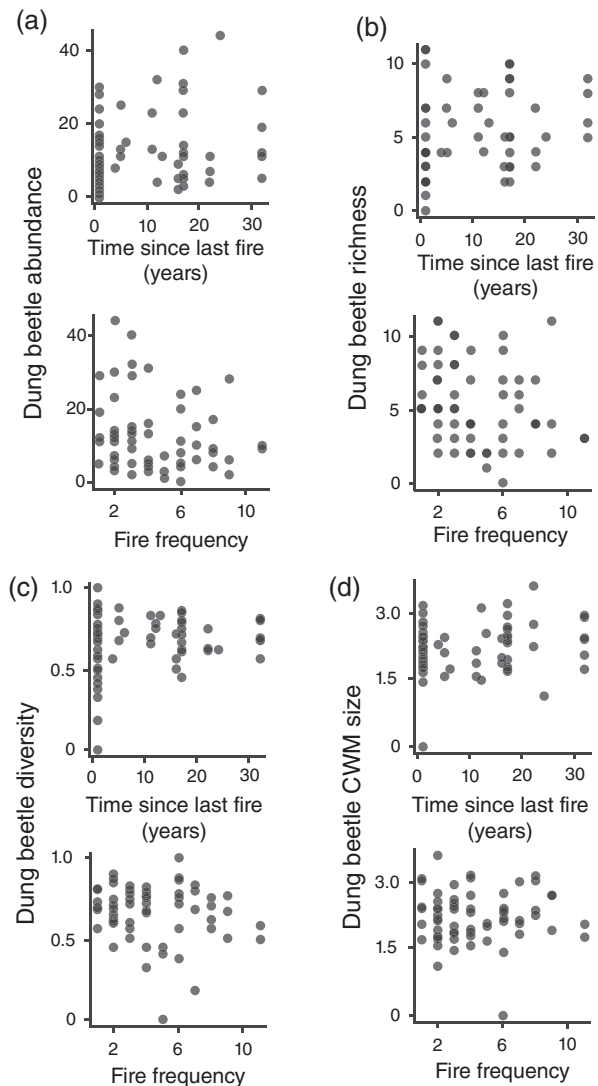


Fig. 3. Dung beetle resistance to fire disturbance in Serra do Cipó, Minas Gerais, Brazil: (a) abundance, (b) richness, (c) diversity (Simpson index; 1-D) and (d) community-weighted mean (CWM) biomass. All response variables were calculated from the December 2014 collection. None of these response variables were influenced by time since last fire (years) or by fire frequency.

dung beetle communities during the studied interval could readily return to undisturbed conditions or even that they do not change in response to fire. Additionally, dung beetle communities were not affected by time since last fire and fire frequency, indicating that changes in these communities are independent of the time since last fire or after several fire events.

Some non-mutually exclusive mechanisms promoting the resistance and recovery of dung beetles in *campos rupestres* could be acting in synergy. One of these potential mechanisms is the mismatched seasonality between fire events and dung beetle occurrence (Fig. 4a). Natural and anthropogenic fires in the Cerrado occur mainly during the dry season or at the beginning of rainy season, when climatic conditions and fuel accumulation

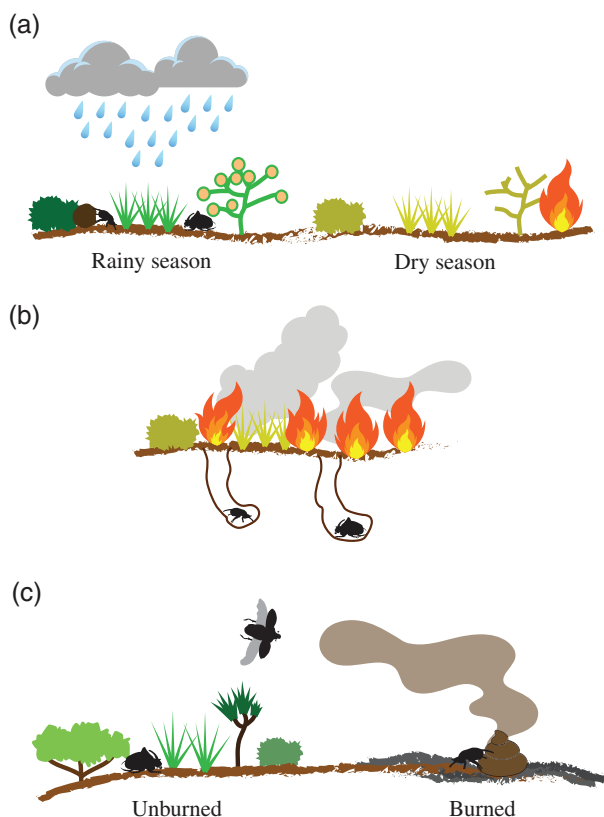


Fig. 4. Potential non-mutually exclusive mechanisms that promote resistance and recovery of dung beetles to fire. (a) Mismatch in seasonality between fire events and dung beetle occurrence: dung beetles are present in the rainy season, whereas fires occur during the dry season; (b) dung beetles remain buried during the dry season diapause, a behaviour that could protect individuals from being burned during fire events; (c) replacement of species in burned areas by the movement of individuals from unburned areas, attracted by resources and/or by metacommunity dynamics. [Colour figure can be viewed at wileyonlinelibrary.com].

make the vegetation more prone to ignition (Pivello *et al.*, 2010; INPE, 2018). On the other hand, dung beetle communities possess highly marked seasonality and are much more abundant and diverse during the rainy season (Andresen, 2005; Fig. S2). Thus, when conditions are less favourable for fire events, dung beetles are more active. This mismatch of occurrence of fire and dung beetles could be acting as a mechanism of resilience to fire for the communities. Thus, dung beetle communities might not respond to fire simply because most of the individuals and species are not active during fire events.

Besides the mismatch between dung beetle activity and fire occurrence (Fig. S2), a behavioural trait could be helping to keep dung beetles safe from being burned. These insects remain buried for most of their lifetime, including during nesting, feeding and the dry season diapause (Halffter & Edmonds, 1982; Hanski & Cambefort, 1991). When fire occurs, the air temperature becomes very high and burns almost everything above the ground. However, a few centimetres of soil are enough to buffer the heat, and at a depth of 20–30 cm, the soil

temperature is similar between areas under the effect of fire and those that are not (Coutinho, 1982; Bradstock & Auld, 1995; Pivello *et al.*, 2010). Therefore, individual dung beetles can keep themselves protected from fire inside their tunnels, which can be as deep as 50 cm (Halffter & Edmonds, 1982; Sowig, 1996; Gregory *et al.*, 2015), or survive fire events by staying sheltered under a soil layer during the dry season diapause (Fig. 4b).

The lack of effects of fire on dung beetle communities may be due not only to sheltering from fire, but also to the rapid replacement of species in burned communities. The promptness with which dung beetles find and trace feeding resources from far distances is well known, as they usually feed on mammal faeces or decomposing animals and fruits, which are ephemeral resources in the environment (Riffell *et al.*, 2008; Tribe & Burger, 2011). As *campos rupestres* are open habitats where the odour of a resource can spread greater distances than in closed habitats (Riffell *et al.*, 2008), exposed resources in burned areas could attract beetles from unburned areas, leading them to colonise the disturbed portion of the habitat (Fig. 4c). This dispersion to burned areas can also explain the lack of response to immediate and historical fire events, or to fire frequency. This movement of individuals would provide a seeming resistance and recovery, as this process would occur independently in each fire event.

The recolonisation of burned areas should be expected due to metacommunity dynamics; surrounding populations from unburned areas could provide individuals that recolonise the burned areas over time (Brotons *et al.*, 2005). Although this replacement could cause changes in species composition after fires (Pausas & Parr, 2018), we did not observe this trend, as communities before and after fire were similar in composition. It seems that dung beetle dispersal is not a constraint to colonisation of post-fire areas, as almost all species that occur in an area before fire were present after the disturbance. Dung beetles are, indeed, insects that generally have great dispersal capabilities (Hanski & Cambefort, 1991; da Silva & Hernández, 2015). For instance, individuals of *Oxysternon* and *Onthophagus*, both common genera in *campos rupestres*, were recaptured 1 km and 700 m away 2 days after release (Peck & Forsyth, 1982). Therefore, dung beetles could move rapidly into a burned habitat from an undisturbed area (Quintero & Roslin, 2005).

Our study showed that dung beetle communities were highly resilient (high resistance and fast recovery) to fire. However, we focused our questions on the communities and their structure and did not evaluate immediate, physiological, or behavioural effects on dung beetles. It would be interesting to perform experiments where researchers control fires in the habitat to test their immediate effects on dung beetles and their subsequent colonisation after fire. Additionally, one could investigate whether the olfactory capability of dung beetles is affected by smoke produced by fire, and whether it confuses them when searching for food resources. Furthermore, there may be sublethal effects on dung beetles, such as changes in body fat accumulation, as happens with logging in tropical forests (França *et al.*, 2016).

Although we generally consider fire as an important disturbance that could drive community assembly, we found that dung beetle communities in *campos rupestres* did not change due to fire. We argue that in this 'fire-dependent' ecosystem, fire does not drive dung beetle community assembly as it might

do in forested habitats. Due to natural selection of life-history traits that are adapted to fire, plant and animal communities of 'fire-dependent' ecosystems (i.e. savannas) are not as negatively affected by fire as are communities of 'fire-sensitive' ecosystems (i.e. rainforests) (Bond & Parr, 2010; Parr *et al.*, 2014). Dung beetle communities of open ecosystems seem not to be structured by fire, but by environmental factors such as vegetation (Louzada *et al.*, 2010), soil properties (Davis, 2002), elevation (Nunes *et al.*, 2016), and factors associated with land-use changes (Almeida *et al.*, 2011; Correa *et al.*, 2016).

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Author contributions

Project design: CAN, WB, PGdS, FSN. Data collection: CAN, RFB. Data analysis: CAN, WB. Writing of the manuscript: CAN, WB, PGdS, RFB, GWF, FSN.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. List of collected species, their abundances and explanatory variables per sampling point.

Figure S1. Correlation between dung beetle size and weight.

Figure S2. Seasonal occurrence of fires and dung beetles.

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