Time since fire strongly and variously influences anthophilous insects in a fire-prone landscape

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Abstract.   Drivers of species productivity and ecosystem function are of great ecological significance. In fire-prone ecosystems, dispersion patterns of important pollinator species are driven by the various fire events over space and time. However, different species have varying responses to fire intensity and frequency. Here, we assess how time since last fire influences abundance, composition, and dispersion patterns of flowering plants and anthophiles in a highly fire-prone landscape. We classified study area into age since last fire, which were <1 yr (short-term burned), 2–3 yr (medium-term burned), and 9–10 yr (long-term burned). We collected insect anthophiles using yellow, blue, and white pan traps at sites established in each post-fire class. We also estimated flower abundance at each study site. Overall, anthophile abundance was highest in medium-term burned, while lowest in short-term burned sites. Also, flower abundance was highest at medium-term burned and lowest in long-term burned sites. Species composition of flowering plants and anthophiles, especially bees and flies, differed significantly across post-fire class. Overall, flower abundance had a significant positive effect on bee abundance. Of all the taxa, bees were the only group that showed dispersion patterns reflecting those of flower abundance. Other factors, especially requirements for other resources such as logs, drive the distribution of other anthophile taxa, especially flies. We conclude that fire drives the distribution patterns of bees through its direct effect on flower abundance and composition in a fire-prone landscape. While high frequency of short-term fire may reduce flower abundance, flower-rich areas with moderate time since fire may increase diversity of anthophiles in this fire-prone landscape.

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INTRODUCTION

The maintenance of natural habitat for the persistence of species, especially those responsible for the delivery of ecosystem services, is of great importance (Chandler and King 2011). Flower-visiting insects are critical biotic constituent of terrestrial ecosystems, as some species play crucial ecological roles in the pollination of flowering plants in both natural and agricultural ecosystems (Klein et al. 2007, Potts et al. 2010). Pollination by

insects alone increases crop yields globally by 35% (Klein et al. 2007). However, despite the high level of dependence of human food security and ecosystem functions on pollination services (Vanbergen and Insect Pollinators Initiative 2013), there is an ongoing decrease in the abundance and distribution of insect pollinators (Potts et al. 2010).

Several drivers influence this decline through their impact on flower distribution in natural habitat. Understanding these drivers of species diversity and distribution is pertinent to

designing important conservation strategies in disturbed landscapes. Fire is one of the major factors driving floral diversity in many terrestrial ecosystems (New 2014) and has a positive influence on plant productivity and diversity at various local and landscape scales (Pausas and Ribeiro 2017).

The Greater Cape Floristic Region (GCFR) biodiversity hotspot is the richest floral kingdom in the world (Myers et al. 2000), and its floral maintenance depends in part on fire events. Fire affects plant reproduction and diversity through complex processes, and although this is still not fully understood, a few processes relating to fire cues have been documented. In legumes with hard seeds, fire helps activate germination by breaking the seed coat through heat from the fire (Sabiiti and Wein 1987, Saharjo and Watanabe 1997), allowing water to penetrate into the seed, and enabling germination to begin. Smoke is also a major constituent of fire that also influences germination (Sparg et al. 2005, Kulkarni et al. 2006, Tigabu et al. 2007), as well as the flowering of plants (Keeley 1993) in fire-prone ecosystems (Staden et al. 2000). In a sensitive fynbos ecosystem like the GCFR, where about 6000 plant species are endemic, the scleropyllous fynbos vegetation is highly dependent on smoke for germination cues (Brown 1993). Germination cues from smoke for fynbos plants partly explain the vegetation dynamics (Light et al. 2004).

In addition to direct influence of fire on plant diversity, fire also plays a critical role in the flowering of plants through its influence on other factors mediating plant growth and diversity. Post-fire conditions influencing plant survival are usually different from pre-fire conditions. There is usually a change in soil composition, especially in microorganism composition and soil structure (Certini 2005). Also, fire opens up closed habitats through reduction of canopy cover. This increases understorey access to sunlight, which is important for flowering plants (Quintano et al. 2013). In addition, fire mediated by human activities often influences the survival of target species by eliminating competitors in the ecosystem (Perkins 2015). This may reduce competition among species through the impact of fire.

Fire history is important in shaping biodiversity composition in flower-rich ecosystems. Changes in fire history across time determine habitat suitability and distribution patterns of flowering plants and insects in fire-impacted areas (Brown et al. 2017). Most often, insect activities and distribution vary with time since fire (Potts et al. 2006, Pauw 2007, Geerts et al. 2012), and this is influenced by important environmental factors driving insect diversity in fire-impacted ecosystems. Flowering plants as drivers of anthophilous insect diversity across landscapes have been well documented in relation to fire incidence. For example, while fire drives fynbos communities, short-interval fires may destroy the seed bank and may eventually result in the loss of fynbos species and associated flower visitors (Vlok and Yeaton 2000). On the other hand, habitat modification results from impact of fire, so creating patches of heterogeneous landscape (Perry et al. 2011). Fire history modifies habitat structure, with ground cover often increasing with time since fire. This shapes species distribution based on functional traits influencing nesting requirements. However, while habitat selection is important for the distribution of anthophilous insects, this has received less attention.

Recovery of vegetation post-fire is dependent on the timing of fire events. However, for flower-visiting insects, recolonization may be dependent on the availability of particular flowering plants providing high-quality floral rewards. Often, activity of adult anthophilous insects is dependent on floral resources used by the insects in the previous season (Potts et al. 2003), and this usually brings about differences in time required for restoration of floral and insect assemblages in flower-rich landscapes. This pattern is of great importance for flower-dependent anthophiles, such as bees, as they track flower resources (Winfree et al. 2009). Here, we explore post-fire diversity and composition of different anthophile groups and flowering plants in a fire-prone landscape. We hypothesize that (1) sites with different times since last fire incidence will have varying species composition of flowering plants and anthophiles. This would be due to the period between germination and flowering, which differs among flowering plant species, and which also influences anthophile species with different floral requirements in different post-fire age classes; (2) abundance and diversity of flowering plants and anthophilous insects will be highest at

sites with a history of long-interval fire incidence, since these areas are expected to have undergone recovery of vegetation over a long period since the last fire incidence; (3) we expect insect taxa with high dependence on floral resources (obligate anthophiles) to be most influenced across post-fire age classes, as they are associated with flowering plants which we also expect to vary with post-fire age class; and (4) distribution patterns of anthophiles will track those of flowering plants across habitats with different post-fire ages.

MATERIALS AND METHODS

The study was conducted in the large natural set-aside areas on adjacent wine farms in the Western Cape Province, South Africa, in the GCFR biodiversity hotspot. Bee diversity in the GCFR is exceptionally high, coinciding with that of plants (Kuhlmann 2005). Two contiguous wine estates were selected (Vergelegen: 34.0764° S, 18.8899° E; and Lourensford: 34.0719° S, 18.8886° E). These estates practice biodiversity-friendly agriculture, with extensive areas of the farms devoted to conservation of indigenous biodiversity, where our sites were positioned. The most recent fire in this landscape occurred between December 2016 and February 2017. This mostly occurred on Vergelegen wine estate, leaving a large proportion of Lourensford unburned. This location previously burned in 2014–2015, and the oldest fire in the area was in 2008–2009.

We classified sites based on time since last fire (TSF). Recently burned sites (TSF = <1 yr) were classified as short-term burned. Patches of vegetation left unburned during the fire incidence in the burned landscape (TSF = 2–3 yr) were classified as medium-term burned. Sites located at Lourensford, where the last fire occurred in 2008–2009 (TSF = 9–10 yr), were classified as long-term burned.

We established six study sites, each of 50-m^2 plot per site, in each of the two shorter-term fire classes, but only three sites were available for the long-term burned areas, making a total of 15 study sites (plots) for all three fire classes. Vegetation sampling was also done at every site where we collected insects, and also in additional sites within the landscape where we could not erect pan traps for insect collection. This makes a total of nine sites within each post-fire class for vegetation sampling. Number of open flowers on each plant species was estimated in five replicates of 2-m^2 plot at each site. Furthermore, we classified vegetation into three major classes (annual plants, short-lived and quick-growth perennial plants, and long-lived, slow-growth perennial plants). This was done by accessing ecological information on plant species from the literature.

The recent fire created a mosaic vegetation structure in the burned area, leaving heterogeneous distribution of unburned patches within the burned landscape. Medium-term burned sites were the patches of unburned areas that fit the size of a study site within the short-term burned area (Fig. 1). The minimum distance between a medium-term and short-term burned sites was 150 m, and minimum distance between sites in the same post-fire age class for medium-term and short-term burned was 250 m. The long-term burned sites are natural areas that border the medium-term and short-term burned sites. The minimum distance between sites located in the long-term burned area was 450 m. Long-term burned area was located 3000 m away from short-term burned area. We assessed spatial autocorrelation of abundance and species richness of insects using Moran's I index (Diggle and Ribeiro 2007). We computed the index using insect species richness and abundance data (Mellin et al. 2010), as well as geographical coordinates (longitude and latitude) of study sites. The index computes spatial autocorrelation of species richness and abundance as a function of distance between study sites. Moran's I index (0.135 ± 0.095, $P = 0.031$) showed a weak overall spatial clustering of insect abundance among study sites. However, we observed no spatial autocorrelation of species richness across study sites (Moran's I index = -0.08, $P = 0.934$). While spatial autocorrelation could increase the possibility of Type I error (Diniz-Filho et al. 2003), we distributed study sites here to reduce the cofounding spatial effects that may influence observed pattern especially in short-term and medium-term burned sites. Also, we included study sites as random variable (Mellin et al. 2010) where applicable in our statistical analysis to account for possible site-specific cofounding variables that could mediate observed patterns.
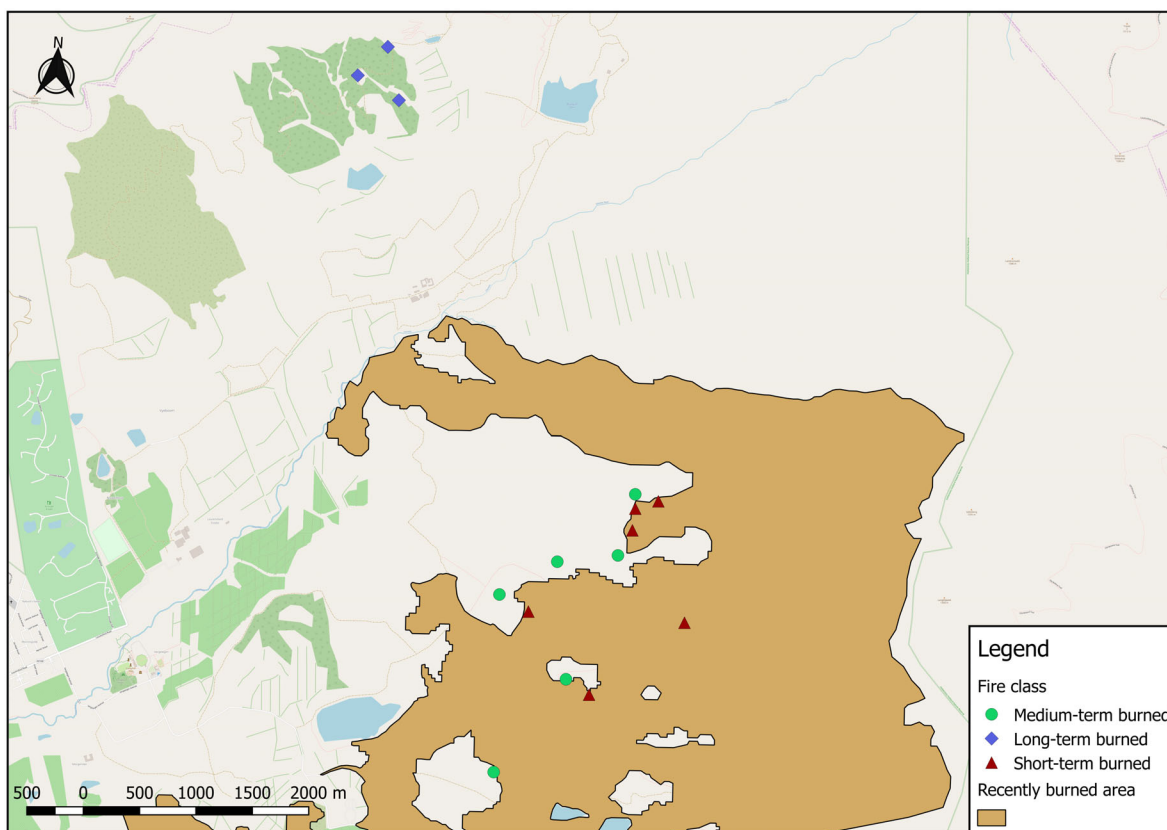
Fig. 1. Study sites at Lourensford and Vergelegen wine estate showing distribution of sites across fire class area.

We used 30 pan traps (10 each of blue, yellow, and white bowls) to collect flower-visiting insects at each site. Colored bowls were half-filled with water, and few drops of liquid detergent were added to reduce water surface tension. Colored bowls were raised to the immediate vegetation height and were openly active for 24 h. Insects were collected twice at each study site within the period of late August to mid-September, and also within the first 2 weeks of October of 2018 (i.e., early–late spring). Insects acquired in each pan trap were rinsed and kept in 75% ethanol until sorting and identification. The insect groups sampled were bees, beetles, flies, and wasps. Insect families included in our analyses are those with roles established as flower visitors in literature.

Statistical analyses

Data collected in the two sampling rounds were pooled, and overall abundance for all insect taxa and flowering plants was used in the analysis. To account for sampling adequacy, we estimated species rarefaction curves for flowering plants and anthophile species richness across study sites using the rarefy function in vegan R package (Oksanen et al. 2006). We assessed the difference in flower and pollinator abundance across post-fire age class using a generalized linear model (GLM) in R version 3.4.1 (R Core Team 2017) and fitting a Poisson distribution. We also used GLM to assess how flower abundance differs among vegetation types (annual plants, short-lived and quick-growth perennial plants, and long-lived, slow-growth perennial plants) in different fire classes fitting Poisson distribution. Similarly, differences in anthophile abundance among taxonomic groups in each fire class were assessed using GLM. Anthophile abundance or flower abundance was specified as the dependent variable, with insect taxa or vegetation

types as the explanatory variable in the different models. Furthermore, z-values for pairwise comparison between treatments in simplified models were recorded where overall significance was observed.

The effect of flower abundance on each anthophile taxonomic group (bees, beetles, flies, or wasps) was computed using a generalized linear mixed model fitting a Poisson distribution. We specified the abundance of each anthophile taxon as the dependent variable; flower abundance, post-fire age class, and their interaction were specified as the explanatory variables. We used backward elimination to highlight the influence of explanatory variables and their interactions. We computed diagnostic checks for possible influential data in our model. For bees, which are the most obligate anthophile/pollinator taxon here, we assessed how bee families responded to differences across post-fire age classes using the glmer function specifying Poisson distribution.

We computed Simpson and Shannon diversity indices for species richness and diversity, respectively, for flowering plants and anthophiles. We also assessed species evenness using the Pielou evenness index (Mulder et al. 2004). Differences in diversity metrics for anthophiles and flowering plants across post-fire age were assessed. To do this, we used simple ANOVA. Shapiro–Wilk's test was computed to assess data normality. We also performed Bartlett's test for homogeneity of variance before data were subjected to ANOVA. Tukey's honestly significant difference post hoc test was computed to analyze differences between groups. To understand how frequency of distribution for each anthophile taxon differs across post-fire age, we included evenness index for each taxon as dependent variable in different models and post-fire age class was specified as fixed factor.

Finally, we assessed pollinator and flowering plant species composition across post-fire age class using canonical analysis of principal coordinates. We then analyzed differences in species composition across post-fire age class using PERMANOVA. The PERMANOVA was performed using the Bray–Curtis similarity index obtained from the square-root transformation of abundance data and selecting Type III SS (sum of square) to account for unbalanced design

(Anderson et al. 2008). Data were permuted 999 times for the analysis. To understand the similarity in the pattern of distribution of flowering plants and anthophile species across post-fire age class, we used the RELATE function in Primer 6 software (Clarke and Gorley 2006) to compare species composition for each anthophile taxa with flowering plant composition.

Results

A total of 9492 insect individuals, belonging to four taxa (bees, beetles, flies, and wasps) and 113 morphospecies, were collected over the sampling period (Appendix S1: Table S1). Anthophile species estimator indices for all post-fire classes were as follows: Chao = 349.25 ± 94.27 and Jackknife2 = 233.75. Sixty-one species were recorded in short-term burned sites with species estimator scores of Chao = 132.30 ± 35.45 and Jackknife2 = 112.23. We found 63 insect species in medium-term burned sites with species estimator score of Chao = 126.38 ± 30.72 and Jackknife2 = 113.70. Long-term burned sites had 50 species with estimator score of Chao = 101.04 ± 25.97 and Jackknife2 = 83.67. Overall, the rarefaction curve for flowering plants across all sites reached an asymptote (Appendix S1: Fig. S1). However, the asymptotic level for the insect curve was less pronounced (Appendix S1: Fig. S2), because of the occurrence of many rare species in our samples. However, this richness did not differ across post-fire age class.

There was a significant difference in flower abundance across post-fire age classes. Highest flower abundance was recorded at the medium-term burned sites, which was significantly different from flower abundance recorded at long-term ($z = -33.16$, $P < 0.0001$) and short-term burned sites ($z = -38.32$, $P < 0.00001$). In addition, there was a significant difference in flower abundance among vegetation types in different fire classes. In short-term burned sites, short-lived perennials had the highest flower abundance with lowest flower abundance recorded for annual plants ($z = -16.467$, $P < 0.0001$, Fig. 2A). Similarly, short-lived perennials had the highest flower abundance in medium-term burned sites, and this was significantly different from lowest flower abundance recorded
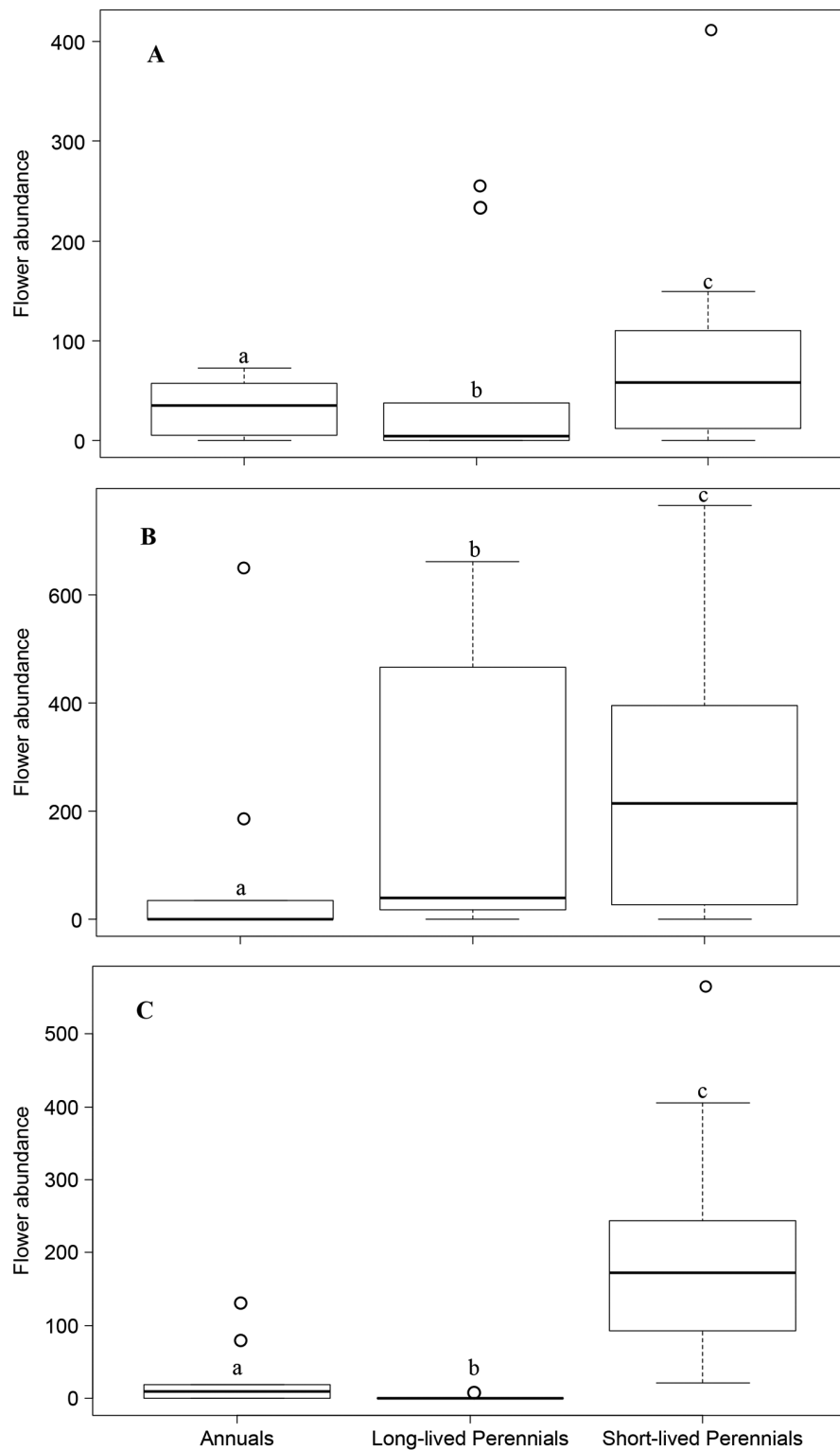
Fig. 2. Flower abundance among vegetation classes in (A) short-term burned sites, (B) medium-term burned sites, and (C) long-term burned sites. Median with common lettering is not significantly different at $P > 0.05$.

for annual plants ($z = -22.924$, $P < 0.0001$, Fig. 2B). However, in long-term burned sites, while short-lived perennials had the highest flower abundance, long-term perennials had the lowest flower abundance ($z = -9.649$, $P < 0.0001$, Fig. 2C).

There was a significant difference in anthophile abundance across post-fire age class. Highest anthophile abundance was recorded at the medium-term burned sites, and this was significantly different from anthophile abundance recorded at the long-term burned sites ($z = -2.83$, $P = 0.02$). In addition, there was a significant difference in anthophile abundance among taxonomic groups in each fire class. Beetles and flies were the most abundant group in short-term fire class with the lowest abundance recorded for wasps ($z = -11.061$, $P < 0.001$, Fig. 3A). Flies were the most abundant in medium-term burned sites, and the lowest abundance here was also recorded for wasps ($z = -21.37$, $P < 0.0001$, Fig. 3B). However, in long-term burned sites, beetles had the highest abundance, followed by bees and flies, and least for wasps ($z = -11.78$, $P < 0.0001$, Fig. 3C).

Effect of flower abundance on insect taxon across post-fire age class

Flower abundance was significantly associated with the abundance of bees ($\chi^2 = 10.496$, $P = 0.01479$, df = 3). There was no significant effect of post-fire age class on bee abundance ($\chi^2 = 8.567$, $P = 0.089$, df = 4). Although the slope of bee–flower abundance relationship was higher at medium-term burned and lower at short-term burned, where a negative relationship was also observed ($z = -2.104$, $P = 0.0354$), there was no overall significant interaction effect of flower abundance and post-fire age class on bee abundance ($\chi^2 = 4.524$, $P = 0.104$, df = 2).

There was no significant effect of flower abundance on the abundance of beetles ($\chi^2 = 1.580$, $P = 0.664$, df = 3), flies ($\chi^2 = 2.119$, $P = 0.548$), and wasps ($\chi^2 = 6.454$, $P = 0.091$, df = 3). In addition, there was no significant effect of post-fire age class on the abundance of beetles ($\chi^2 = 3.354$, $P = 0.500$, df = 4), flies ($\chi^2 = 1.149$, $P = 0.886$, df = 4), and wasps ($\chi^2 = 4.180$, $P = 0.382$, df = 4). In addition, there was no interaction effect of post-fire age class and flower abundance on the abundance of beetles

($\chi^2 = 0.728$, $P = 0.695$, df = 2), flies ($\chi^2 = 1.081$, $P = 0.582$, df = 2), and wasps ($\chi^2 = 1.578$, $P = 0.454$, df = 2).

Bee family distribution across post-fire class

There was a significant difference in bee abundance among families represented. Megachilidae was the most abundant family, which differed significantly from least abundant Andrenidae ($z = 5.375$, $P < 0.00001$). Also, there was a significant interaction effect between bee family and fire class on bee abundance ($\chi^2 = 111.12$, df = 6, $P < 0.00001$). While megachilid bees were highest in medium- and short-term burned sites, Halictidae and Apidae were highest in long-term burned, yet with low abundance of Megachilidae.

Species composition

There was a significant difference in species composition of anthophiles across post-fire age classes (Pseudo-$F = 1.9214$, $P = 0.036$, Fig. 4A). Species composition at the medium-term burned ($t = 1.7403$, $P = 0.014$) and short-term burned sites ($t = 1.4668$, $P = 0.049$) was significantly different from species composition at the long-term burned sites. Similarly, there was a significant difference in species composition of flowering plant species sampled across the post-fire age classes (Pseudo-$F = 1.8907$, $P = 0.002$, Fig. 4B). Species composition of flowering plants at the medium-term burned ($t = 1.4175$, $P = 0.012$) and short-term burned sites ($t = 1.5615$, $P = 0.002$) was significantly different from species composition at the long-term burned sites. There was no significant difference in species composition of flowering plants between medium-term and short-term burned sites ($t = 1.135$, $P = 0.118$). The RELATE function showed no significant relationship between the overall composition of anthophile and flowering plants across post-fire age class ($\rho = 0.081$, $P = 0.235$).

Taxon response to post-fire classes

There was no significant difference in bee species composition across post-fire age classes (Pseudo-$F = 1.275$, $P = 0.113$). There was a significant difference in the species composition of flies across the post-fire age classes (Pseudo-$F = 3.2298$, $P = 0.008$, Fig. 5). Between-pairs
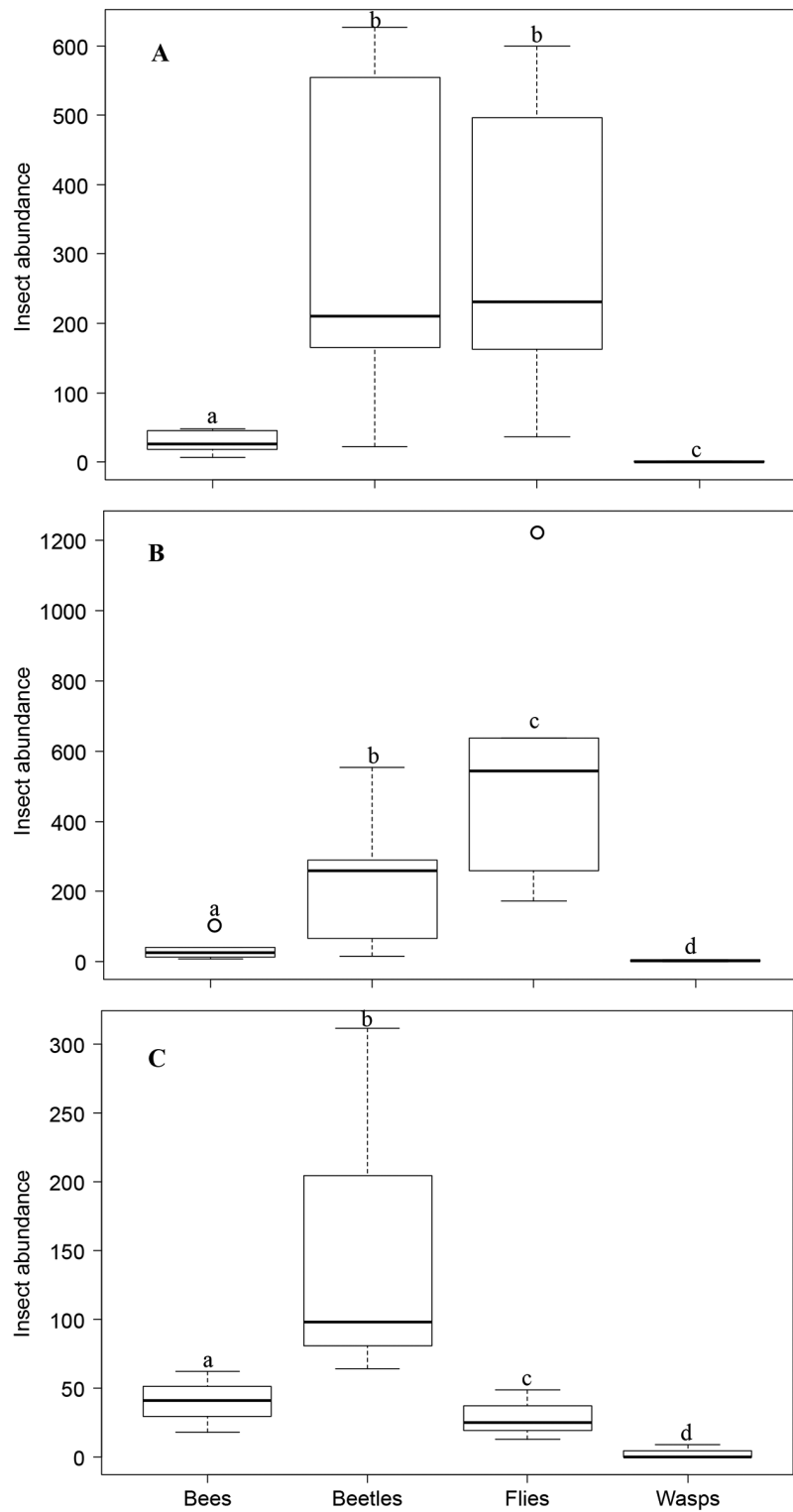
Fig. 3. Anthophilous insect abundance among taxonomic groups in (A) short-term burned sites, (B) medium-term burned sites, and (C) long-term burned sites. Median with common lettering is not significantly different at $P > 0.05$.
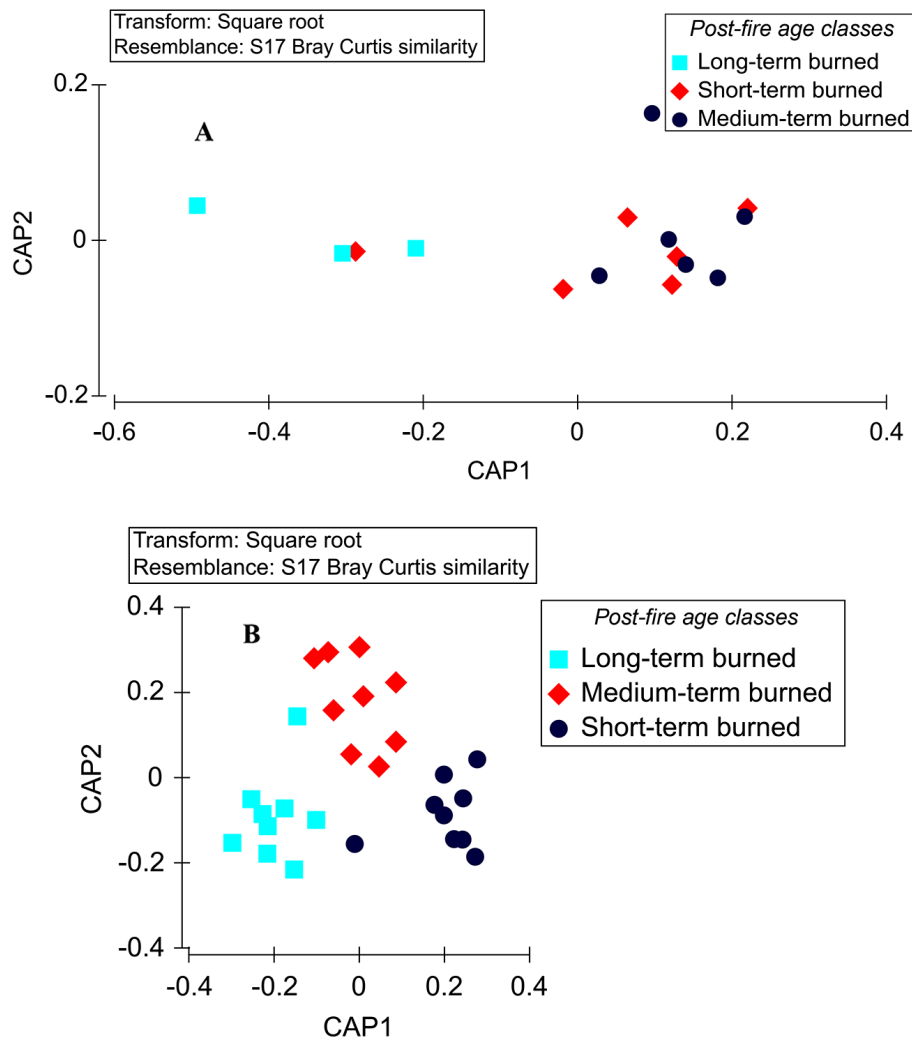
Fig. 4. Canonical analysis of principal coordinates showing differences in the composition of (A) insect anthophiles and (B) flowering plants across sites in different post-fire age classes.

comparisons showed a significant difference in fly composition between short-term burned and long-term burned sites ($t = 1.7037$, $P = 0.037$), and also between medium-term burned and long-term burned sites ($t = 2.2289$, $P = 0.008$). There was no significant difference between short-term burned and medium-term burned sites ($t = 1.1929$, $P = 0.202$). There was no significant difference in species composition of beetles across the post-fire age classes (Pseudo-$F = 0.78794$, $P = 0.651$). Similarly, there was no significant difference in species composition of wasps across the post-fire age classes (Pseudo-$F = 0.99508$, $P = 0.539$).

Diversity among post-fire classes

There was no significant difference in overall Simpson ($F_{2,12} = 0.167$, $P = 0.848$) and Shannon ($F_{2,12} = 1.997$, $P = 0.178$) diversity of anthophiles across post-fire age. Similarly, there was no significant difference in Simpson ($F_{2,24} = 0.600$, $P = 0.557$) and Shannon ($F_{2,24} = 2.712$, $P = 0.086$) diversity indices for flowering plant across post-fire age. Also, there was no significant difference in overall evenness diversity index for flowering plants ($F_{2,24} = 1.37$, $P = 0.273$) and anthophiles ($F_{2,12} = 2.721$, $P = 0.106$) across post-fire age. However, overall average species evenness for anthophiles (0.467) and for flowering plants
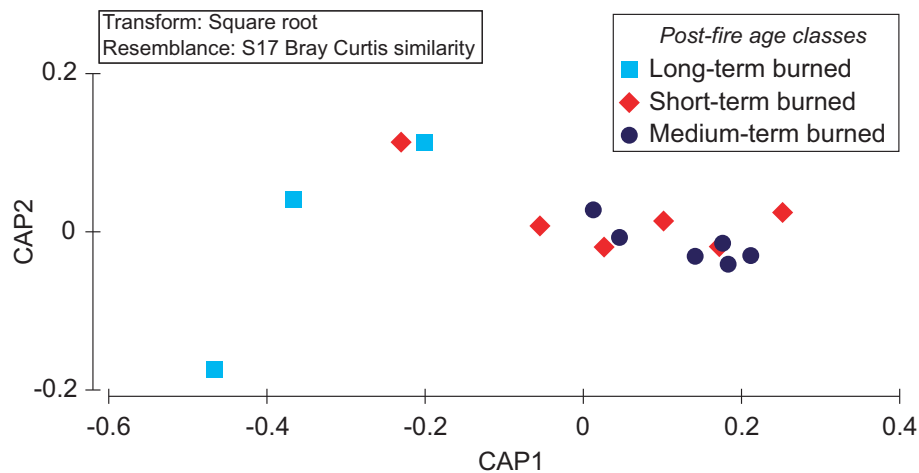
Fig. 5. Canonical analysis of principal coordinates showing differences in the composition of flies across sites in different post-fire age classes.

(0.706) was moderately high. This showed that assemblages were fairly even in frequency of different species.

Evenness among post-fire classes

Overall mean species evenness for anthophiles was highest for bees (0.721 ± 0.039), followed by beetles (0.566 ± 0.045), wasps (0.289 ± 0.112), and flies (0.244 ± 0.063). Flies were the only taxon that showed a significant difference in species evenness across the post-fire age classes ($F_{2,12} = 5.011$, $P = 0.0262$). Highest evenness was recorded at long-term burned sites and least at medium-term burned sites. There was no significant difference in the evenness diversity index of bees ($F_{2,12} = 0.423$, $P = 0.666$), beetles ($F_{2,12} = 1.292$, $P = 0.31$), or wasps ($F_{2,12} = 0.45$, $P = 0.648$) across post-fire age classes.

Discussion

Fire influences the distribution patterns in terms of diversity and composition of flowering plants and the various anthophile taxonomic groups. Varying responses of different ecological communities in fire-impacted areas are often associated with uneven spread of fire across a heterogeneous landscape (Suding and Gross 2006, Pausas and Verdú 2008, Myers and Harms 2011, Myers et al. 2015). Overall, short-lived perennial plants were highly successful in terms

of flower abundance compared to other groups. Most of the perennial plants, such as *Phylica buxifolia*, *Protea laurifolia*, *Oesteospermum* sp., and *Lobostemon dorothea*, are important flowering plants in the GCFR and provide quality floral reward for endemic insect anthophiles and birds (Anderson et al. 2014). Some of these plants take flowering cues from smoke and then resprout during the next flowering season after fire (Staden et al. 2000). However, for slow-growing, long-lived perennials, such as *P. laurifolia*, the germination from seed to first flowering after fire takes an average of seven years (Notten 2009). This explains why flower abundance was low for slow-growing, long-lived perennial plants. In areas prone to fire, while short-lived perennials and annuals could recover within a short time, longer period of recovery of long-lived perennials may influence the low flower abundance of these plants, especially in areas with high fire frequency.

Similar to flower abundance across post-fire age classes, anthophile abundance was also highest at medium-term burned sites. However, while flower abundance was lowest at short-term burned sites, lowest abundance of anthophiles was recorded at long-term burned sites. This illustrates that flower distribution does not entirely track anthophile distribution across the post-fire age classes. Contrary to our hypothesis, other factors may be responsible for the

distribution of anthophiles across post-fire age classes. One possible explanation is habitat selection on the part of different anthophile taxa. Flies dominated anthophile abundance in our study. Furthermore, fly composition was different between long-term burned and short-term burned sites. Flies were most abundant in medium-term burned and short-term burned sites, and lowest at long-term burned sites. This was contrary to the abundance of flowers among the post-fire age classes. Although flies can be important pollinators of flowering plants (Larson et al. 2001), in comparison with other anthophiles, most flies are also carrion feeders and may be driven by factors apart from flower availability. *Drosophila* spp. made up about 40% of the entire fly samples, and these flies breed in decaying logs and plant branches (Offenberger and Klarenberg 1992). In our study, they are predominantly associated with short-term burned and medium-term burned sites, with poor representation at long-term burned sites. The entire short-term burned landscape has heterogeneous distribution of decaying burned logs and twigs, which may be the major factor driving their dispersion patterns in this region compared to the great reduction of flies at the long-term burned sites.

Bees were very different from flies. They tracked flower abundance across post-fire age classes, with their highest abundance at long-term burned and medium-term burned sites, while lowest at short-term burned sites. In short, bees followed flowering plant distribution patterns. This could be a mass movement of bees into the medium-term burned and long-term burned sites during the fire events, with the presence of more flowers here providing quality nectar rewards, which may drive this pattern (Wojcik 2011). The presence of important nectar- and pollen-rewarding flowering plants here may drive the distribution of bees in the absence of other cofounding environmental variables. However, in response to natural fire, flower abundance across post-fire age class seems to be an important influence for bee abundance across sites with different times since fire.

Unlike other taxonomic groups, where other ecological roles, such as parasitism and predation, have been discussed, several studies have shown pollination as the major functional role of bees in most ecosystems through their dependence on floral rewards. This also explains the differences in bee composition, with distinct segregation of bee species among post-fire age classes. According to Van Nuland et al. (2013), flower abundance is the mechanism by which fire indirectly influences anthophile visitation. Overall, this implies that over a period of succession in a heterogeneous fire mosaic landscape, the quality and abundance of flowering plants providing floral resources for anthophiles, especially bees, and the flower distribution patterns play a major role also in the distribution patterns of insect anthophiles.

Bees also differed significantly in response to time since fire among families. Overall, megachilid bees are highest in abundance. However, this pattern was not observed across all post-fire age classes. While Megachilidae was highest in abundance in medium- and short-term burned sites, our results also showed highest abundance for Apidae and Halictidae in long-term burned sites. This shows that species-specific factors may be driving the distribution of bee in different families across post-fire age classes. This could be due to dietary requirements, habitat selection, body size, specialization habit, and tongue length, among other factors.

Several studies have shown how bee functional groups may influence their distribution across landscape (Winfree et al. 2007, Hoehn et al. 2008, Munyuli 2012). However, studies showing how bee functional groups respond to time since fire are few. Fire regime, most especially fire frequency, filters biotic assemblage composition and abundance through its direct impact (Keeley et al. 2011). While we show here how habitat modification in terms of fire influences the distribution of bees, future studies should address how species-specific requirements among families influence bee distribution across post-fire age classes.

Evenness and diversity

Simpson and Shannon diversity indices here showed no significant pattern in species diversity across fire classes or among insect groups and flowering plants. However, we found some differences in species evenness, especially among insect groups. Species evenness and diversity do not necessarily show similar response patterns, as these two indices may be influenced by different

ecological processes (Wilsey and Stirling 2007). Overall, flowering plant and anthophile evenness indices are moderately high, suggesting that the frequency of distribution is moderately even among species, especially for flowering plants (Smith and Wilson 1996). While this pattern of distribution may be as a result of fire incidence in our study area, this region is a biodiversity hotspot, with several endemic species, some of which are adapted to the local fire regimes.

Species diversity response to disturbance is complex. However, a decline in species richness may lead to an offset in the distribution of different species and components of biodiversity in disturbed landscapes. Yeboah et al. (2016) showed a complex response by species diversity and evenness in a tree stand relative to TSF. Our results show that annual plants such as *Oxalis* spp. and a few perennial Asteraceae regrew quickly after fire and dominated the entire landscape. However, we recorded very low flower abundance of bushy *Protea* spp. and *Leucadendron* spp., which are important for anthophile foraging, as are a few other long-lived perennials. The implication of this is that the full complement of anthophiles depends largely on plants with very low frequency of flowering. These long-lived fynbos plants are an important source of nectar for insect anthophiles, as well as for certain birds. Anthophilous insects, especially the specialized group, may compete for the low resources of a few rich nectar-rewarding plants available across our post-fire age classes. This may, over time, lead to temporal loss of these insect groups that are unable to find a replacement for the limited rich nectar flower across our study area.

Bees showed the highest species evenness, followed by beetles. However, for flies and wasps, evenness was moderately low, illustrating species dominance and differences in frequency of occurrence of species of these two groups. Here, as *Drosophila* spp. constituted almost 40% of all the flies collected, they created a major imbalance in the frequency of occurrence of flies. Wasps, on the other hand, displayed very low abundance, with many rarely captured species. Across post-fire age classes, flies showed significant differences in species evenness. Highest evenness was recorded at long-term burned sites and lowest at short-term burned and medium-term burned sites. One possible explanation for this is the mosaic nature of the burned landscape, with medium-term burned areas acting as refuge patches across areas impacted by fire. As mentioned above, flies may also be driven by decayed burned logs at our sites. However, these logs were in patches and not evenly distributed across the landscape. This may explain a varying frequency of occurrence of fly species among sites across the heterogeneous burned landscape.

CONCLUSIONS

The effect of fire on the abundance of bees was influenced by flower abundance. In addition, other species-specific factors appeared to be influencing the distribution among families, especially for bees and flies. Overall flower abundance declined in association with a short-interval fire frequency, and this was especially pronounced among long-lived perennial plants. While other anthophile taxonomic groups, aside from bees, may not be influenced much by the fire regimes, bees are mostly obligate flower visitors and are highly associated with flower distribution pattern. Thus, flower-rich area with moderate time since fire incidence may increase the diversity of bees in fire-prone areas.

Limitation of study design

Like most fire ecology studies, the inference here may be limited by other site-specific conditions other than fire itself. For instance, variation in other abiotic features such as soil structure, and microclimate may influence observations here. While the distribution of medium-term and short-term burned sites reduces variation in other confounding spatial structures, the block design of the long-term burned area may have been influenced by different spatial factors not associated with medium-term and short-term burned areas. To reduce the effect of other confounding environmental variables, sites in all fire classes should be distributed evenly across the landscape. This may be possible in a controlled burning experiment. However, the situation here reflects how natural fire creates uneven patches of vegetation distribution across burned area. While including study sites as a random variable in our model may reduce the influence of confounding spatial factors, in a natural fire distribution experiment, caution is needed when drawing conclusion about the effect of post-fire

age on anthophile and flowering plant distributions across landscapes.

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