Oecologia
https://doi.org/10.1007/s00442-019-04471-4

CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Wandering spiders recover more slowly than web-building spiders after fire

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Received: 19 December 2018 / Accepted: 18 July 2019

Abstract

Fire is a natural feature of many ecosystems, with some vegetation types highly adapted to fire. However, very little is known about the effect of fire on spiders, especially as fires have become more frequent owing to human activity. We determine whether different spider functional guilds (web builders vs. wanderers) respond differently to fires in the sclerophyllous fynbos. We determine also the effect of rockiness as refuge for these guilds and whether it influences their post-fire recovery. There were three site categories of time-since-last fire: 3 months, 1 year, and 7 years. We found that fire caused a decline in spider richness and abundance, with the 3-month category supporting the lowest. In sites that were burned within 1 year, abundance of wanderers was as high as in sites that had 7 years to recover, whereas species richness and abundance of web builders in sites that were burned 1 year ago were as low as in recently burned sites. However, assemblages of wanderers differed among categories, while no differences were observed for web builders, highlighting that wanderers took longer time to recover than web builders. Species richness and abundance of both guilds were not affected by different levels of rockiness. However, rockiness is important in shaping assemblages of wanderers. The results emphasize that the assemblages of greatest conservation concern with increased fire frequencies are wanderers and are candidate surrogates for monitoring post-fire recovery. These results highlight the need to allow fynbos vegetation to recover fully between fire intervals and draws attention to the dangers of frequent unplanned fires.

Keywords Arachnids · Fire · Rockiness · Fynbos · Greater Cape Floristic Region

Introduction

The fynbos biome is characterized by high plant species richness, leading to high fynbos biodiversity, with many species being endemic to this biome (Braschler et al. 2012; Kraaij et al. 2013). Fynbos plant species richness and composition are driven partly by fire (Braschler et al. 2012; Kraaij et al. 2013; Pryke and Samways 2012a). However, fire can influence arthropod diversity negatively because of the positive association between arthropods and specific plants (Proçhes and Cowling 2006). Fire also can alter plant species composition (Joubert et al. 2014) and, therefore, can affect arthropod species composition (Hugo-Coetzee and Avenant 2011; Parr et al. 2004; Pryke and Samways 2012b; Yekwayo et al. 2018). However, the effect of fire on arthropod diversity varies among different arthropod taxa (Pryke and Samways 2012b; Yekwayo et al. 2018). For example, fire was reported to cause a decline in beetle diversity (Sasal et al. 2015), while it had little effect on ant diversity (Parr et al. 2004).

The effect of fire on insects and other arthropods is likely to affect spiders indirectly. Spiders are predators that feed on a diverse range of arthropods and are adapted to a variety of environmental conditions (Dippenaar-Schoeman et al. 2001; Foord et al. 2011; Moretti 2002; Uetz 1977). Despite all spiders being predators, they have different hunting strategies. Niche occupation by spiders is often species specific, with different species being restricted to specific physical conditions and biological factors (Foord et al. 2016). As a result, habitat preferences and foraging behaviour are used to group spiders into their functional guilds (Dippenaar-Schoeman

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Communicated by Sven Bacher.

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2014; Dippenaar-Schoeman et al. 2005; Foord et al. 2016). There are two broad functional guilds of spiders: the wanderers which include plant and ground wanderers that hunt actively for prey (Dippenaar-Schoeman 2014; Dippenaar-Schoeman et al. 2005; Foord et al. 2016). The second functional guild include the web builders, which can be stratified further into funnel-web, gumfoot-web, orb-web, modified orb-web, retreat-web, sheet-web and space-web builders, all of which wait passively for prey to enter their webs (Dippenaar-Schoeman 2014; Dippenaar-Schoeman et al. 2005; Foord et al. 2016).

Spider diversity is linked strongly to changes in vegetation structure (Brandt and Lubin 1998). The effect of vegetation structure can be indirect, owing to greater plant diversity, which may be linked with greater arthropod abundance (Ebeling et al. 2018), and thus greater availability of prey for spiders. In addition, vegetation structure can be altered by fire or the presence of large herbivorous mammals. For example, destruction of webs by high activity of large herbivorous mammals causes a decline in web builders (Foster et al. 2015). Vegetation also directly influences opportunities for web-building sites as well as ambush options for wanderers (Brandt and Lubin 1998).

Spiders can be influenced by fire through changes in vegetation structure and climatic conditions. For instance, vegetation hunters may increase after fire in response to an increase in abundance of food for potential prey (Podgaiski et al. 2013). However, the increase in the abundance of vegetation hunters is possible if there are potential refuges for spiders to survive during the fire. On the other hand, the immediate destruction of dense vegetation and microhabitats by fire may cause a decline in the abundance of web builders (Podgaiski et al. 2013). Furthermore, physical features, such as rocks, serve as important refuges for spiders to avoid high temperatures (Taucare-Ríos et al. 2017).

Although the impact of fire on spiders has been investigated, the focus has been on spiders in forests (Moretti 2002), web builders in eucalypt forests (Foster et al. 2015), and spiders in grassland (Hore and Uniyal 2008). Here, we aim to investigate the extent to which different spider functional guilds (wanderers and web builders) respond to fire in the sclerophyllous fynbos vegetation of the Greater Cape Floristic Region, South Africa. In addition, we aim to determine how rockiness of the landscape interacts with the fire to create refuges for spiders during fire events, and so potentially allowing more rapid post-fire recovery. Fynbos fires have been shown not to affect spider diversity in terms of the whole assemblage (Pryke and Samways 2012b). However, here we expect that the two functional guilds will have differential responses to fire, as they are not equally reliant on the recovery of the vegetation structure (Podgaiski et al. 2013). Also we expect the rocky sites to support greater spider diversity than non-rocky sites and to facilitate post-fire recovery through the provision of refuges from high temperatures.

Materials and methods

Study sites

The study was carried out in the Cape Winelands Biosphere Reserve (CWBR) (33°56′46.57″S, 19°7′50.16″E) and Kogelberg Biosphere Reserve (KBR) (34°15′02.1″S, 019°07′52.9″E), Western Cape, South Africa (Fig. 1). The two biosphere reserves are characterized by high mountains with steep slopes and scrubby fynbos vegetation (Mucina and Rutherford 2011). These reserves experience a summer season that is warm and dry, while winter is cool and rainy. Natural fynbos vegetation in CWBR and KBR grows on sandy soils. Fire is an important component in shaping plant species composition in the fynbos biome (Cowling 1992). However, fynbos vegetation in CWBR and KBR has been experiencing increased frequency of fires because of arson, runaway control burns, and discarded cigarettes. As a result of these anthropogenic activities, the recommended burn cycle of 12–15 years (Richardson and Van Wilgen 1992) is no longer maintained. As such, the oldest fynbos in our study sites was approximately 7 years since the last fire.

A total of 90 study sites ranging between 236 and 598 m asl were selected. The 90 sites were divided further into three categories based on the last time since they were burned and these categories were called collectively “time-since-fire”. The first category was called “3-month category”, sampling took place at approximately 3 months since fire in the area. The second category was called “1-year category”; sampling was conducted after a year since fire in the area. The last category was called “7-year category” and were burned more than 7 years ago. We were unable to find sites that were burned greater than 7 years previously, due to the high frequency of unplanned fires in the area. As a result, sites in the 7-year category were used as reference even though they were recovering still. All three categories were different in terms of vegetation structure (Fig. 2). In the 3-month category, the vegetation cover was lost completely in most of the sites. However, in some of the 3-month category sites, there were a few stands of plants and tree stems, particularly of a *Protea* sp. that were burned but not entirely (Fig. 2a). Furthermore, some of the sites in the 3-month category had started to recover, with vegetation, especially, fern seedlings starting to cover the soil surface. Unlike in the 3-month category, there was an increase in the vegetation cover in the 1-year category (Fig. 2b). However, the structure in the 1-year category was simple still, with the soil surface being exposed because the vegetation was not dense (Fig. 2b). Contrary to the other two categories, the

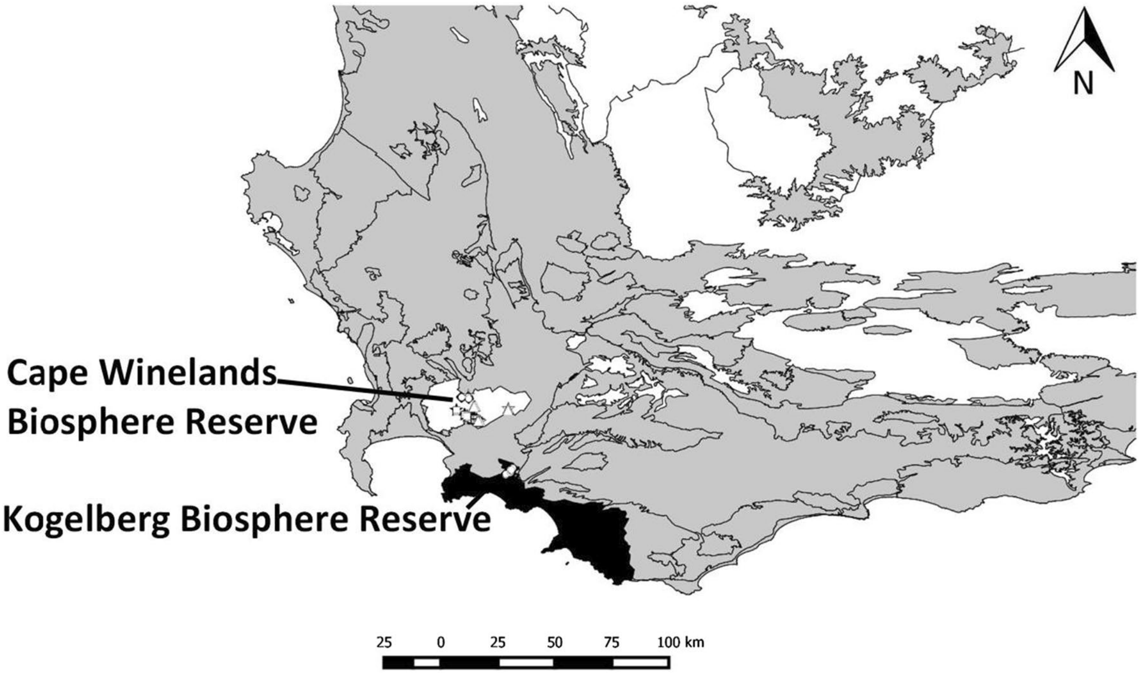

Fig. 1 Map indicating the study sites. Fynbos biome (grey), Cape Winelands Biosphere Reserve (clear), Kogelberg Biosphere Reserve black)

7-year category was very dense in terms of plant biomass, with the soil surface covered completely (Fig. 2c).

In each category, there were 30 sites and sites in the 3-month category were found in both CWBR and KBR, while sites in the 1-year and 7-year categories were found in CWBR only. For each category, the 30 sites were stratified further into 15 rocky and 15 non-rocky sites. However, in the 7-year category, a total of 15 non-rocky sites were unavailable. As a result, for the 7-year category we selected seven non-rocky sites and 23 rocky sites. The minimum distance between rocky and non-rocky sites within the same category was 100 m. The study sites within the same treatment were ≥ 300 m apart. Each study site was 10 × 10 m.

Sampling was conducted during a warm summer to autumn period (March to April 2016), because spiders are active mostly when temperatures are high (Cera and Spuņģis 2011; Chai and Wilgers 2015). This period also has the first major rainfall events since November and is likely the reason for high species richness of arthropods in late summer (Pryke and Samways 2010). Pitfall trapping, active searching, and suction sampling were used to sample spiders. The three techniques were used to increase the number of spiders caught, and to target different functional guilds. Data from the three techniques were pooled to form a single sample per sites. There were a total of 16 pitfall traps per site, with four traps placed in a square at each corner of the 10 × 10 m site. Each of the four pitfall traps were 2 m apart. Data from the 16 traps per site were pooled to form a single pitfall trap sample. 50% ethylene glycol solution was used as a preservative in the pitfall traps. Pitfall traps were plastic jars, 6 cm in diameter and 9 cm in height. Traps were left open in the field for 7 days.

Furthermore, within a 10 × 10 m site, we searched actively for spiders for a period of 30 min. In addition, suction sampling, using a Stihl SH 86 leaf blower set in reverse, with a 15 cm diameter nozzle and a bag of fine mesh, was used for aerial sampling from vegetation (Stewart and Wright 1995). Suction sampling was recommended by Swart et al. (2017) as an effective technique to sample arthropods in the fynbos. Spiders, along with other arthropods, were sucked from low fynbos plants using 60 insertions per 10 × 10 m site. Samples were stored in bags and frozen, for later sorting in the laboratory.

All collected specimens were preserved in 70% ethyl alcohol. From suction samples and pitfall traps, we extracted spiders. Spiders were sorted to morphospecies and identified to family and genus level where possible. Spider morphospecies were later assigned to a broader functional guild, a wanderer or web builder, following Dippenaar-Schoeman (2014) and Dippenaar-Schoeman and Leroy (2003). Assignment of spiders to a specific functional guild was based on the type of habitat and predatory method a species prefers (Dippenaar-Schoeman 2014; Dippenaar-Schoeman and Leroy 2003).

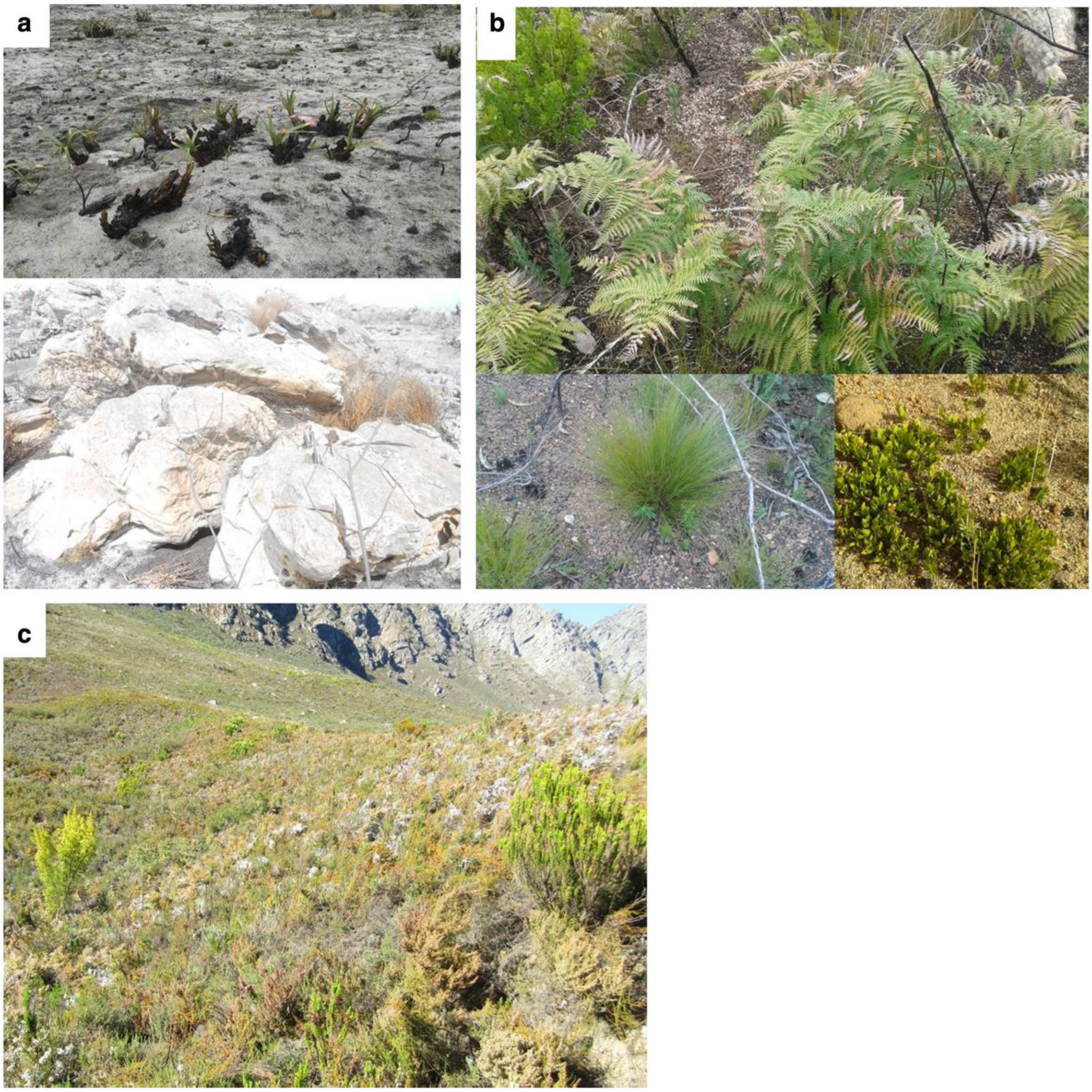

Fig. 2 Vegetation structure among different time-since-fire categories. **a** 3-month category, **b** 1-year category, **c** 7-year category

Data analyses

The *lme4* package in R (Bates 2005) was used to create generalized linear mixed models (GLMMs) to test the effect of time-since-fire, rockiness, and the interaction between these factors on species richness and abundance of wanderers and web builders. Two models were created for each guild. In the first model, time-since-fire and rockiness were fixed factors, while the sampling area and elevation were random factors. To create the second model, we added a third fixed factor (interaction between time-since-fire and rockiness). From the second model, we reported interaction results only. Laplace approximation was used to calculate GLMMs and for both guilds, species richness data fitted to a Poisson distribution and abundance data fitted to a negative binomial distribution (Bolker et al. 2009). For all the tested factors, χ^2 and p values were calculated. The *multicomp* package in R (Hothorn et al. 2008) was used to perform Tukey post hoc tests on significant factors.

Permutational multivariate analysis of variance (PERMANOVA) in PRIMER 7 was used to test the effect of time-since-fire, rockiness, and the interaction between these factors on species composition. Analyses were performed for each functional guild. Time-since-fire, rockiness and the interaction between rockiness and time-since-fire were used as fixed factors while elevation and sampling area were random factors. Similarly with GLMMs, there were two models that were created: one included all three fixed factors, while the other one excluded the interaction effect. Data were square-root transformed to reduce the weight of common species, and Bray–Curtis similarity measures were used to perform the analyses (Anderson 2001). *F*- and *p* values were calculated using 9999 permutations (Anderson 2006) for all the tested factors. Canonical analyses of principal coordinates in PRIMER (Anderson and Willis 2003) were used to detect trends of dissimilarities in species composition among time-since-fire categories graphically. In addition, similarities of assemblages between categories were determined also using the Jaccard index of similarity. The number of species unique to each category and those shared between categories were presented using Venn diagrams. The *indicspecies* package in R (de Cáceres and Legendre 2009) was used to calculate indicator values (IndVal) to identify species that were unique indicators to each category and those shared between categories. IndVal provided the χ^2 and *p* values for significant indicator species ($p < 0.05$).

Results

In total, 1455 specimens of spiders were collected, with 1228 individuals belonging to wanderers, while 227 individuals were web builders. We sampled 123 species of wanderers and half of these species were singletons and doubletons. For web builders, singletons and doubletons contributed 52% of the 27 species that we collected. Time-since-fire influenced both species richness and abundance of wanderers (Table 1). Species richness of wanderers was higher in the 7-year category, which had the highest number of unique species than the 3-month and 1-year categories (Table 1; Figs. 3a, 4a). Although species richness of wanderers in the 1-year category was slightly higher than that in the 3-month category, there were no significant differences between these two categories (Fig. 3a). Abundance of wanderers did not differ between the 1-year and 7-year categories (Fig. 3b). However, the 3-month category had the lowest abundance of wanderers compared to the other categories (Fig. 3b). Species richness and abundance of wanderers and web builders were not affected by rockiness or the interaction between time-since-fire and rockiness (Table 1). There were no differences in species richness and abundance of web builders between the 3-month and 1-year categories (Fig. 3c, d). However, the 7-year category supported greater species richness and abundance of web builders than other categories (Fig. 3c, d). There were two species of web builders that were unique to the 3-month and 1-year categories, while the 7-year category had 14 unique species (Fig. 4a).

Non-rocky and rocky sites supported different assemblages of wanderers (Table 1). Assemblage composition of wanderers differed significantly among all categories (Table 1; Fig. 5). However, the Jaccard index of similarity revealed overlap of assemblages of wanderers between all categories (Fig. 4a). Interaction between time-since-fire and rockiness did not influence the assemblage composition of wanderers (Table 1). Assemblages of web builders were not affected by time-since-fire, rockiness, or the interaction between these factors (Table 1; Fig. 4b).

The 7-year category had five indicator species of wanderers (four species of Salticidae and a single species of Gnaphosidae) (Table 2). Indicator species of wanderers for the 1-year category were *Oponaea spinose*, Salticidae sp., Cyrtaucheniidae sp., Philodromidae sp. and two species of Gnaphosidae (Table 2). Despite the fact that no indicator species of wanderers was identified for the 3-month

Table 1 Effect of time-since-fire, rockiness, and the interaction between these factors on species richness, abundance and species composition of wandering and web-building spiders

	Wanderers			Web builders		
	df	χ^2	*p*	*df*	χ^2	*p*
Species richness						
Time-since-fire (TSF)	6	25.42	< 0.001	5	34.44	< 0.001
Rockiness	6	0.01	0.91	5	2.57	0.11
TSF*rockiness	8	2.33	0.31	8	0.62	0.73
Abundance						
Time-since-fire (TSF)	7	7.69	0.02	7	37.70	< 0.001
Rockiness	7	0.01	0.93	7	2.06	0.15
TSF*rockiness	9	0.05	0.97	9	2.07	0.36
	df	Pseudo-F	*p*	*df*	Pseudo-F	*p*
Species composition						
Time-since-fire (TSF)	1	2.34	< 0.001	1	1.03	0.43
Rockiness	1	1.73	0.03	1	1.23	0.24
TSF*rockiness	2	1.09	0.31	2	1.47	0.07

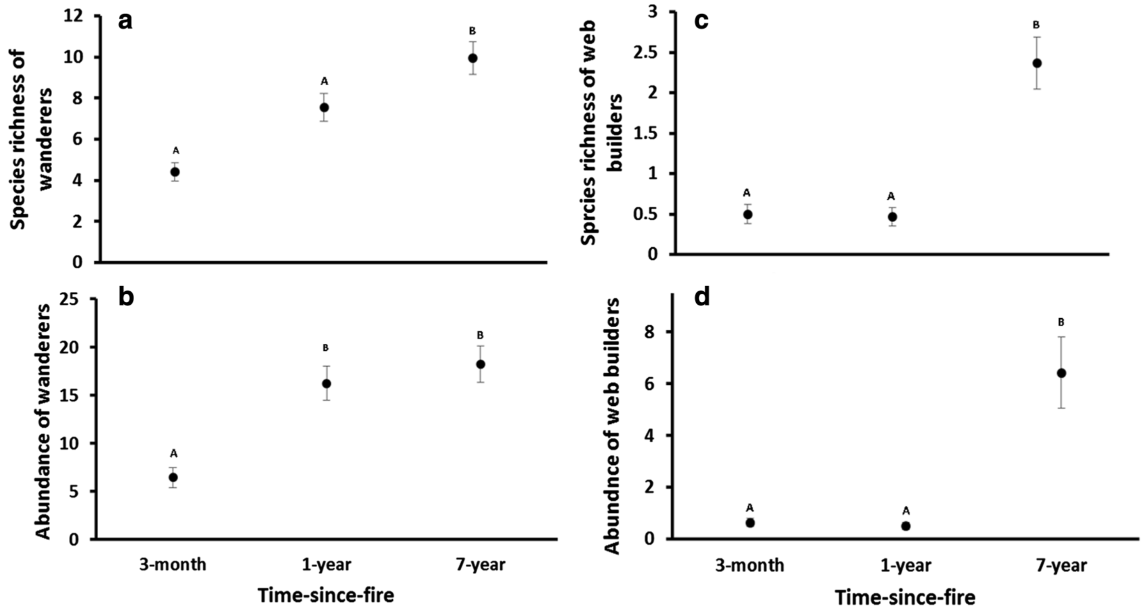

Fig. 3 Effect of time-since-fire on species richness and abundance of wandering spiders, species richness and abundance of web-building spiders. Different letters above standard errors indicate different significances, $p < 0.05$. Analyses were performed in R using generalized linear mixed models (GLMMs). Species richness of wanderers was greater in the 7-month category than other categories, while abundance was higher in both 1-year and 7-year categories. The 7-year category had the highest species richness and abundance of web builders

category, *Scytodes* sp. was shared between the 3-month and 7-year category (Table 2). Furthermore, the 1-year and 7-year categories shared six indicator species of wanderers (*Pellenes cingulatus*, *Oxyopes* sp., *Coryssiphus* sp., *Tibellus* sp., *Hewittia* sp. and a Gnaphosidae sp.) (Table 2). For web dwellers, indicator species (*Tybaertiella* sp., *Oecobius* sp. and *Ursa* sp.) were detected for the 7-year category only (Table 2).

Discussion

Effect of time-since-fire on wanderers

Wanderers include both plant and ground dwellers (Dippenaar-Schoeman 2014; Lapinski and Tschapka 2013). The lowest species richness and abundance of wanderers recorded in the 3-month category may be due to two possibilities, spiders being killed directly by the fire or spiders finding refuges (possibly unburned plant patches or under rocks). For example, plant dwellers might have been killed by the fire while hunting actively among plants, whereas ground dwellers might have been killed due to increased heat on the ground. In addition, some ground dwellers hunt for prey within the leaf litter (Lapinski and Tschapka 2013), and the destruction of leaf litter by fire in the 3-month category in our study was apparent; thus, the recorded low species richness and abundance. Pryke and Samways (2012a) attributed similarities in spider richness and abundance between burned and unburned fynbos to the use of refuges, such as under rocks and plant patches left by fire. Furthermore, related taxa, such as ants, were reported to escape fire by migrating to their nests below ground and a depth deeper than 10 cm into the soil is safe from fire (New 2014).

In addition, low species richness and abundance in the 3-month category may have been due to the severely reduced plant biomass. Plant biomass is associated positively with increased vegetation structure, which may affect microclimatic conditions. The reduction of plant biomass in the 3-month category after fire led to an open and simplified vegetation structure, with many of our study sites lacking vegetation completely. Furthermore, previous work has shown that an increase in fynbos vegetation cover tends to be visible within 9 months after fire (Van der Merwe and Van Rooyen 2011). This was true for the 1-year category in our study, which had increased vegetation cover, even though there were still areas of bare ground. Increased vegetation cover contributes towards increased ecological niches for a variety of arthropods (Ebeling et al. 2018). Arthropods, such as herbivores, feed and live on plants, while detritivores live and feed on leaf litter, with a decline in the abundance of detritivores through a decrease in the leaf litter layer (Kwon et al. 2013). Therefore, an increase in the diversity of these arthropods may cause an increase in species richness and abundance of wanderers because of abundance of prey. We show that the impact of fire on species richness of wanderers

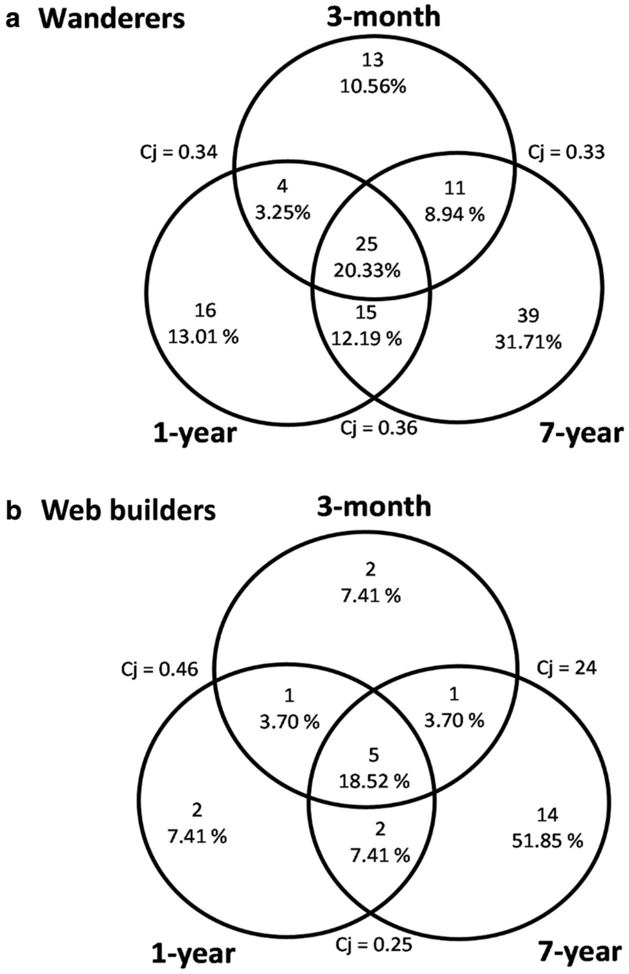

Fig. 4 Venn diagrams indicating the number of species unique to each category and those shared between and among categories. Cj: the Jaccard index of similarity showing similarities between categories. The Jaccard index of similarity showed overlap of assemblages between categories

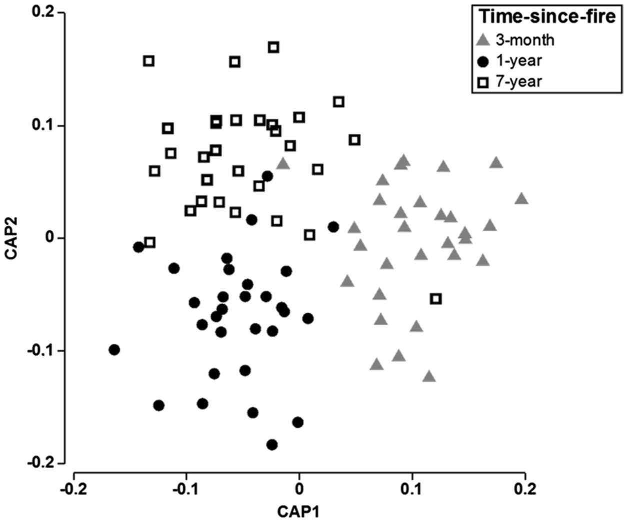

Fig. 5 Canonical analyses of principal coordinates showing assemblages of wandering spiders across different time-since-fire categories. Data were analysed using permutational multivariate analysis of variance, with elevation and sampling area as random factors. All three categories supported different assemblages of wanderers

becomes evident even after a year of recovery, which was evident in the low species richness that we recorded in the 1-year category compared to the 7-year category.

Dissimilarities in species composition of wanderers among different time-since-fire categories were expected because of the differences in vegetation structure and climatic conditions. The 3-month category was characterized by bare ground with little and/or no vegetation cover, while, in turn, the 1-year category had less amount of vegetation compared to the 7-year category, which had greater plant cover. In addition to the effect of fire on vegetation cover, fire reduces soil moisture, while increasing soil temperature (Hore and Uniyal 2008). Such dissimilarities in moisture levels can lead the 3-month category to support different assemblages from the other two categories, which has had time to recover after fire. However, it is important to note that both the Jaccard index of similarity and the indicator value (IndVal) analyses revealed overlap of assemblages between categories, especially between the 1 and 7-year category. All species that were shared between the 1 and 7-year categories are plant dwellers, which inhabit both shrubs and flowers (Dippenaar-Schoeman 2014). However, IndVal showed that not all species are exterminated by fire. For example, a *Scytodes* sp., which was a shared indicator between the 3-month and 7-year categories, may have survived fire by being able to live under stones and below the soil surface (Dippenaar-Schoeman 2014).

Although it is evident from our results that fire alters assemblages of wanderers, we show also that there are some individual species that benefit from fire and, thus, the observed dissimilarities in assemblages among categories. We recorded 13 species that were sampled in the 3-month category only and these species belonged to eight families, which included both ground and plant wanderers. These species that were recorded in the 3-month category were represented by a single or two individuals, with the exception of a species from family Nemesiidae. It is possible that these species that are unique to the 3-month category may have occupied burned sites immediately after fire, because all these species are adapted to a variety of habitats (Dippenaar-Schoeman 2014) and are not dependent directly on the plants and can have alternative habitats in the absence of plants. For example, philodromids may use rock crevices in the absence of leaves, while caponiids may live under stones in the absence of leaf litter (Dippenaar-Schoeman 2014). In addition, some philodromids, such as *Thanatus* species,

Table 2 Indicator species across time-since-fire categories

	3-month category	1-year category	7-year category
Wanderers			
Opopaea spinose		0.49***	
Asemesthes sp. 1		0.68***	
Gnaphosidae sp. 1		0.47*	
Salticidae sp. 1		0.56**	
Cyrtaucheniidae sp. 1		0.52**	
Philodromidae sp. 1		0.43*	
Salticidae sp. 2			0.51***
Salticidae sp. 3			0.51***
Salticidae sp. 4			0.48***
Salticidae sp. 5			0.41*
Gnaphosidae sp. 2			0.40*
Scytodes sp. 1	0.51*		0.51*
Pellenes cingulatus		0.62***	0.62***
Oxyopes sp. 1		0.61**	0.61**
Coryssiphus sp.1		0.58*	0.51*
Tibellus sp. 1		0.45*	0.45*
Hewittia sp.1		0.43*	0.43*
Gnaphosidae sp. 3		0.45*	0.45*
Web builders			
Tybaertiella sp. 1			0.63*
Oecobius sp. 1			0.52*
Ursa sp. 1			0.52*

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

prefer bare ground and/or open habitats with little vegetation cover (Dippenaar-Schoeman 2014).

Effect of time-since-fire on web builders

Our results are similar to another study, which reported a negative impact of fire on web builders (Foster et al. 2015). Greater species richness and abundance of web builders in the 7-year category were expected due to the vegetation structure that is complex. The low species richness and abundance in the 3-month and 1-year categories are associated with the negative effect of fire on the vegetation (Foster et al. 2015). Although vegetation in the 1-year category had started recover, it was not as dense as that in the 7-year category, which meant that there were not many potential sites for web attachment. There is a correlation between the construction of webs and dense vegetation, which allows web attachment and improves the ability to capture prey (Fasola and Mogavero 1995; Foord et al. 2016). For example, sheet webs are built in low vegetation, while orb webs are built between vegetation (Dippenaar-Schoeman 2014). Both the sheet and orb web builders were abundant in the 7-year category, while they were either absent or represented by a single or two individuals in the 3-month and 1-year categories. Our results are in agreement with Hore and Uniyal (2008) who found a decline in the abundance of orb weavers in burned sites. However, in our study there was an exception of a *Hahnia* species, which was sampled in the 3-month category only, and a single Agelenidae species that occurred in the 3-month and 1-year categories only. The Hahniidae and Agelenidae build their sheet webs near the soil surface (Dippenaar-Schoeman 2014), and so are able to occupy sites with little and/or no vegetation. Furthermore, forest web builders have been reported to build their webs in leaf litter and low vegetation (Melliger et al. 2018). In our study, the 3-month category had no leaf litter and little and/no vegetation, hence the low species richness and abundance recorded, unlike the 7-year category, which supported greater number of unique species. The 7-year category was structurally complex with many potential sites for web attachment.

The low species richness and abundance of web builders in the 1-year category could be associated with the correlation between post-fire flushes in vegetation and large herbivore activity (Foster et al. 2015). Greater activity of large herbivores in burned sites may lead to greater destruction of webs, which inevitably affects spiders. In addition to web builders being influenced by the vegetation, they can be influenced also by prey abundance, predators, competition and substrates for web attachment (Fasola and Mogavero 1995). For example, 3 months post-fire in the studied area supports low abundance of ants and species richness of mites (Yekwayo et al. 2018) and these arthropods are an important food source for spiders. In addition, reduction of prey in burned sites can lead to competition among web builders.

Although fire reduced abundance and species richness of web builders, we show that all three time-since-fire categories support similar assemblages. These similarities in assemblages indicate that there are potential refuges that were used by a few individual species that survived the fire. The refuges could be due to the uneven burning of fire that left stands/clusters of vegetation not burned completely. Although, all three categories in our study have been burned, the 7-year category has had greatest time to recover. Here, we sampled web builder spiders in low numbers (27 species), with higher species richness and abundances in the 7-year post-fire sites, although showed no difference in assemblage composition. This finding is similar to those of Moretti (2002) who reported a decline in spider abundance in burned areas but similarities in assemblages between burned and unburned sites. In contrast, Foster et al. (2015) found dissimilarities in species composition of web builders between burned and unburned sites. As such, our results need to be interpreted with caution and we encourage more comprehensive studies to disentangle these effects.

Effect of rockiness on wanderers and web builders

Small-scale landscape features, such as rocky areas, play a vital role in the conservation of arthropods in the landscape (Crous et al. 2013; Hunter 2005). In a South African grassland, Crous et al. (2013) found that grassland sites with greater rockiness supported higher species richness of butterflies and grasshoppers. Contrary to our expectations, species richness and abundance of both functional guilds did not differ between rocky and non-rocky sites. The greater dispersal ability of some wanderers, such as Thomisidae (Foord et al. 2011), might have contributed to the observed similarities in diversity and perhaps could have traversed the ≥ 100 m distance between rocky and non-rocky sites. Furthermore, some spiders are generalist predators that can occupy a variety of habitats, and environmental conditions, dissimilarities between rocky and non-rocky sites possibly mattered little to them. However, assemblage composition of wanderers differed between rocky and non-rocky sites, highlighting the site specificity among some of the spider species. Differences in assemblage composition emphasized the importance of rocky areas in the fynbos landscape for increased spider heterogeneity, but do not appear to play a role in providing fire refuges. Furthermore, we expected rocks to provide refuges during fire, with rocky sites in the 3-month category supporting greater species richness and abundance of spiders than the 3-month that is non-rocky sites. However, our results show that rocks do not influence the recovery time after fire.

Conclusion

In these systems, a true unburned control is unrealistic, as fire is a natural phenomenon that prevents succession to forest and maintains fynbos. Even so the fynbos vegetation in our study area has recently had a much greater frequency of fires that the natural background rate. As such our study lacked true unburned control sites (all sites were younger than the recommended 15 year reset period), yet our results showed that the impact of fire on species richness and abundance of spiders is apparent even within these shortened time since fire categories. For both functional guilds, the 3-month category supported the lowest species richness and abundance, highlighting the immediate impact of fire on spiders. Our results show that the time it takes for spiders to recover after fire depends on the functional guild. Dissimilarities in species richness, abundance and composition of wanderers among the time-since-fire categories revealed that it takes a long time for wanderers to recover after fire unlike web builders. This suggests that monitoring wanderers for post-fire recovery would capture much of the response of arthropods to fire frequency. The long-term effect of high fire frequencies and how spiders survive fire in this area are not yet explored, and so we recommend that precautions are to be taken to reduce fire frequency, and where possible, old fynbos remnants should be retained nearby for recolonization after a fire.

Acknowledgements We thank Rustenburg, Boschendal, and Montagne farms for access, and D. Ngadze, P. Tshililo, Z. Tyeku, F. Becker, B. Dlamini, M. Mukundamago, S. Mensah, R. Agrela, L. Sikhutshwa, M. Pheme, S. Adu-Acheampong, and A. Katumanyane for field assistance. Funding was from the National Research Foundation (freestanding postdoctoral fellowship—SFP150722129143), and the work was carried out under Cape Nature collection permit no. AAA007-00196-0056.

Author contribution statement IY, JSP, RG and MJS conceived and designed the project, IY investigated and curated data, IY and JSP analysed data, IY, JSP and MJS acquired funding, IY administered the project, IY and JSP acquired resources, IY validated and visualized the project, IY wrote the original draft of the manuscript, JSP, RG and MJS edited and reviewed the manuscript.

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