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Fire-free environments across southern Africa's biomes: distribution and refugial value

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Abstract. It is widely known that southern African forests harbour a variety of organisms absent in several other southern African biomes due to their inability to survive fire. Likewise, biomes where succulent plants are dominant can also provide shelter for some fire-sensitive lineages. There is however little information as to how some other groups that are not adapted to survive veld fires survive in fire-prone biomes, although rocky outcrops and other types of fire-free refugia have been invoked. There is a need for a systematic approach towards understanding the distribution of fire-free refugia in fynbos, grassland, and savanna, and the spatial scales relevant to fire-survival in various groups of organisms, depending on their dispersal abilities and strategies, as well as on seasonal patterns in their life cycle/phenology.

Key words: biodiversity refugia; biomes; Eocene fire minimum; fire ecology; southern Africa.

Introduction

The role of fire in shaping many ecosystems worldwide is well recognised (Bond et al. 2005, Bond 2015). Africa in particular has been the subject of multiple studies looking at how fire influences biomass accumulation, how fire and herbivores compete in consuming biomass, how humans and climate have influenced fire frequency across the continent, and how they may do so in the future (Burgoyne et al. 2005, Archibald et al. 2012). On a finer scale, there are also numerous accounts of how African, and especially southern African, biota are adapted to surviving and in fact thriving in fire-driven environments. Indeed, entire biomes – primarily fynbos, grassland, and savanna, are dominated by fire-adapted plants and animals (van Wilgen et al. 1992, Cardoso et al. 2008, Kirkman et al. 2014).

The effects of fire on plant and animal populations are manifold. Direct impact may include mortality (for both plants and animals), smoke- or temperature-stimulated germination in the case of plants (Pierce et al. 1995, Brits et al. 2014), and active dispersal in the case of those animal lineages that are thus equipped. A whole array of indirect effects, such as population increases and decreases (even to the point of extirpation) are related to the performance of various species in the post-fire environment, and can often be represented in a succession perspective. Our understanding of direct effects is quite good in the case of plants, but most animal studies are in fact focusing on indirect effects (Parr & Chown 2003, Lindenmayer et al. 2008; Polchaninova 2015). The little available literature on the direct effects of fire across multiple southern African animal taxa is largely conjectural (Frost 1984), and elsewhere the need for this type of information as relevant to fire management has been decried (Clarke 2008). In a more theoretical perspective, it would be particularly interesting to understand to what extent the importance of fire in driving endemism patterns, as revealed in plants (Ellis et al. 2014), is even partly paralleled in animal taxa.

This brief study proposes to take a different approach, by asking: what about plant, and especially animal lineages that are not fire-adapted? How is it possible for them to survive in a region dominated by fire-prone vegetation, and where are they most likely to occur? Indeed, some of the lineages involved may be of particular relevance to conservation in a phylogenetic perspective. During the late Eocene, identified as a period critical for southern African endemic lineages (Padayachee & Procheş 2016), the region was less prone to fire than during the Cretaceous and even earlier periods (Bond 2015). Subsequently, as fire frequency increased, it is likely that plant and animal lineages dominant at the time would have had to either adapt to a fire-prone environment, become restricted in their distribution to vegetation types or azonal microrefugia where fire is less likely to affect them – failing which they have become extinct. Indeed, globally, plant phylogenetic diversity appears to be higher (less phylogenetic clustering) in systems that are not fire-driven, such as the Albany thicket in South Africa (Procheş et al.

2006) and the cerrado of Brazil (Silva & Batalha 2010) – and this is likely the case with animals too.

The paper, restricted to southern Africa in its narrowest sense (South Africa, Lesotho and Swaziland) thus sets two goals: (i) to map the broad vegetation types where fire-sensitive lineages are likely to survive in the long run, and (ii) to discuss, providing examples, possible mechanisms of survival for such lineages in other, fire-prone, vegetation types.

Methods

The two comprehensive treatments of the vegetation of southern Africa (Cowling et al. 1997, Mucina & Rutherford 2006), together with a variety of materials relevant to endemism patterns (see below) were consulted to understand the fire dynamics and endemism levels specific to each biome, bioregion, and vegetation type, and the GIS files provided in the latter publication were used to map these units as classified into four categories: (a) largely fire free, endemic-rich; (b) largely fire-free, endemic-poor; (c) largely fire-prone, but endemic-rich and rich in fine-scale fire-free refugia; and (d) fire-prone, and either endemic-poor, or poor in fire-free refugia. This classification was started at biome level, but insofar as one biome showed substantial variability in the details relevant here, it was taken to finer levels (while being aware that the delimitation of vegetation types changes over time; cf. Low & Rebelo 1996 with Mucina & Rutherford 2006 – for which reason the specifics of narrowly-defined vegetation types are not at the core of the presentation below).

Unlike the earlier treatment of the vegetation of southern Africa (Cowling et al. 1997), which included a full chapter dedicated to fire ecology (Bond 1997), the more recent one (Mucina & Rutherford 2006) only has sections on fire ecology in the chapters on patently fire-prone biomes (fynbos, grassland and savanna). Consequently, the map produced here started off as based of Bond (1997), while using further information from Mucina & Rutherford (2006) to point out the likely occurrence other fire-free refugia in vegetation types with high rock cover (cf. Bradstock et al. 2005, Robinson et al. 2013) or high tree cover, as linked with moisture availability (cf. Mackey et al. 2012, Leonard et al. 2014). Levels of endemism reflect the information in de Klerk et al. (2002), Minter et al. (2004) and Linder (2014), while adding the characteristic vegetation of arid koppjes, newly described in Mucina & Rutherford (2006). These geological formations are not particularly rich in plant or vertebrate endemics, but are likely remarkable in terms of ground-level insect endemism (Haaf 1957; Louw 1986), and this pattern would be consistent with their higher topographic heterogeneity, although this will need to be confirmed across a broader spectrum of taxa. A broad survey of the southern African ecological and taxonomic literature was also conducted in an attempt to extract generalities relevant to fire survival strategies across lineages.

Results

A locally discontinuous belt of fire-free environments stretches from the extreme west to the eastern-most parts of the region, although vegetation physiognomy is dramatically different from one extreme to the other. This endemic-rich and largely fire-free belt is comprised of three biomes: (1) the arid, low-cover, Succulent Karoo occurring along the west coast and patchily along the southern interior, where it grades into (2) taller but still largely succulent Albany Thicket, reaching top diversity and cover in the south-east. This in turn grades along the southern portion of the east coast into (3) Afromontane to subtropical forest. This occurs patchily along the south coast and in the eastern interior, quite often in gullies and on steep slopes (Afromontane temperate forest), and along the east coast itself (subtropical coastal forest). This belt is mapped in Figure 1, and illustrated in Figure 2. Endemism patterns also peak along this belt, while also including fire-prone fynbos in the south and sub-Escarpment grassland in the east. The characteristic vegetation types in this fire-free belt accumulate substantial amounts of water in stems or leaves, and in some cases (primarily forest) are also located in more humid meso-scale climate patches. Also largely fire-free – either by their own water content or simply by virtue of the non-flammable nature of surrounding vegetation (succulent or too sparse) – are a variety of shrubby assemblages occurring along the coast, but also in the central interior. A fourth mostly fire-free biome, the Nama Karoo, is endemic-poor at least in

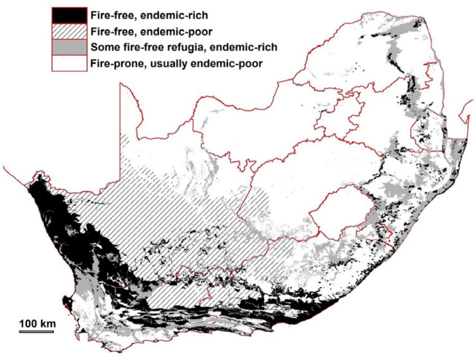

Figure 1. Southern Africa (narrow sense: South Africa, Lesotho and Swaziland) indicating the relictual value of natural vegetation in terms of preserving fire-sensitive endemic lineages. Vegetation boundaries based on Mucina & Rutherford (2006). Red lines indicate province boundaries.

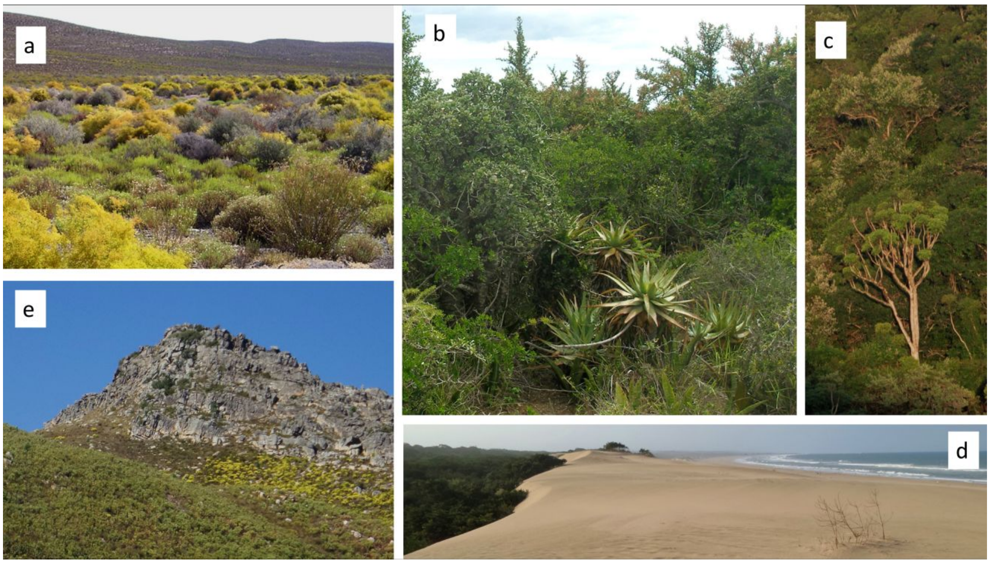

Figure 2. Vegetation with fire-refugial value in southern Africa: a) Succulent Karoo near Sutherland (Northern Cape); b) Albany Thicket in Port Elizabeth (Eastern Cape); c) Afromontane forest in Magoebaskloof (Limpopo); d) coastal forest near Mtunzini (KwaZulu-Natal); e) rocky outcrops in the middle of fire-prone fynbos near Villiersdorp (Western Cape). Photos: the author.

the case of plants, essentially due to low present day rainfall predictability, but also to past climatic change. Several sub-biome units in otherwise fire-driven biomes (fynbos, grassland and savanna) are characterised by substantial percentages of patchy rock cover, likely to act as fire breaks, or, even in the event of a fire burning all surrounding areas, to provide some refugial value, at least in the case of low-intensity fires. Such rocky outcrops are documented – across several of the vegetation units considered here – to harbour tree clumps otherwise uncharacteristic of the matrix vegetation, which could act as refugia for additional taxa. These fire-prone, but patchily fire-protected units somewhat strengthen the fire-free belt represented by the first three biomes enumerated here, but also occur elsewhere in archipelago-like patterns likely to promote endemism (Figure 1). The taxon-specific literature survey revealed that the information is too scattered and inconsistently presented to produce cross-lineage analyses. However, a number of exciting examples were retrieved that can provide an important starting point in understanding geographic and ecological patterns of fire-sensitive lineage survival in fire-prone landscapes.

Discussion

While the belt of fire-free vegetation stretching across the region is in a sense surprisingly continuous given the diverse physiognomy of the biomes involved, it is nevertheless broken by fire-prone sections. Especially in the eastern section of the region, forest and rocky outcrops are only patchily distributed, and only the rocky ridges of the Great Escarpment (Clark et al. 2011) present a certain level of continuity. Their width is probably insufficient in places to provide fire-free corridors functional for a broad array of taxa. It is quite likely that, through the vegetation changes of the Holocene, not to mention earlier eras, even larger sections of this belt would have been flammable at one time or another. In this context, although the distinction between areas that burn and those that do not is still important over short time scales, many of the lineages of interest here would be long extinct if they were to rely on entirely unburnt habitat. Thus, key to their survival may be more subtle, continuous variables, as commonly considered in studies of animal survival in fire-prone environments (Kerby et al. 2007). These are related to the fires (frequency, intensity), aspects of the pre-fire environment (percentage rock cover, percentage tree cover, as well as patterns and scale in the patchiness of these), but also intrinsic to the organisms themselves (the existence of dormant life stages, the coincidence thereof with the fire season, reproductive abilities as needed to replace fire kill before the next fire event).

A whole variety of animal lineages that are either entirely endemic to southern Africa, or reach their maximum diversity and endemism here, are known from published records to be fire-sensitive. Some of these are virtually entirely fire-intolerant by virtue of simply being extremely sensitive to humidity variations, and most often almost entirely forest specialists, as is the case with the southern African lineage of velvet worms (Peripatopsidae; Daniels et al. 2009). Most other lineages, however, do exhibit a range of fire adaptations, while remaining essentially fire-sensitive (Figure 3). The most popular and well-studied of these

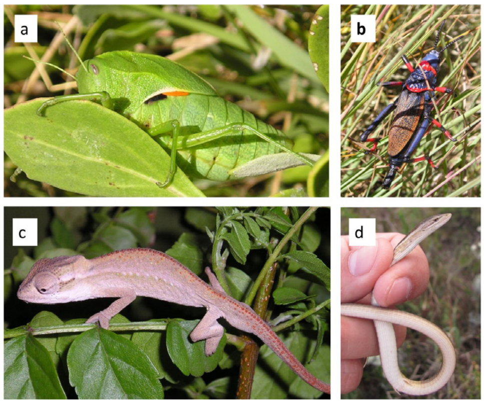

Figure 3. Representatives of selected fire-sensitive animal lineages either endemic to, or reaching maximum diversity, in southern Africa: a) Pneumoridae (bladder grasshoppers); b) Pyrgomorphidae (gaudy grasshoppers); c) *Bradypodion* (dwarf chameleons); d) *Chamaesaura* (grass lizards). Photos: the author.

may be the dwarf chameleons (genus *Bradypodion*), the distribution of which is to a large extent represented by forests, with one species in various types of karoo and thicket in the south, and a couple in succulent karoo in the west (Tolley et al. 2008). The genus does include several species known to occur in fire-prone fynbos, but only one (*B. pumilum*) of these has a broad range that is fynbos-centred. It does appear however that even this species avoids areas entirely lacking fire refugia. Furthermore, this species has different strategies as regards reproduction and other intraspecific interactions, putatively linked to an increased ability of recolonising burnt areas (Rebelo 2014). Another lizard lineage, the grass lizards (*Chamaesaura*, Cordylidae), is not as well equipped for seeking refuge under rocks as most lizards are, and is consequently known to suffer high fire mortality, although almost entirely restricted to fire-prone environments (Boycott 2015). Among invertebrates, a whole series of orthopteran families and genera, often similar in body size to the aforementioned reptiles, are also exposed to similar risks from fire events. These include bladder grasshoppers (Pneumoridae), with a distribution that almost perfectly reflects the fire-free belt illustrated in Figure 1 (see Dirsch 1965), but also gaudy grasshoppers (Pyrgomorphidae), many of which are in fact important herbivores in fire-prone habitats, and have been shown (in Australia) to be impacted by fire frequencies (Barrow 2009), but remain very little studied in South Africa. Elsewhere, the discovery of exciting new orthopteran species is often associated with fire-free refugia in a fire-prone matrix (e.g. Deyrup 1996). The importance of fire-free refugia has also been highlighted in other insect groups (e.g. Swengel & Swengel 2007).

In the context of the pyrodiversity-biodiversity debate (does or does not a diverse array of burning regimes at the landscape scale promote biodiversity across larger scales; Parr & Andersen 2006) these observations might suggest that, insofar as a pyrodiversity approach is indeed followed, this needs to comprise a heavy no-burning end of the scale. While unburned patches are indeed in existence across most southern African biomes, these are often in urban or peri-urban settings, where there may be other threats to lineage persistence. The existence of such patches is more than compensated for by increased fire frequencies elsewhere (Archibald et al. 2012). The effects of such fire frequency alterations on biodiversity are manifold, and primarily detrimental. In southern Africa, cradle of humankind, such fires may have occurred over time scales relevant to evolutionary processes. Given the ways in which fire adaptations can promote rapid speciation (Bond et al. 1995), we cannot write off the possibility that a fraction of the plant diversity of the Cape Floral Kingdom – or the southern African grasslands – is in fact the result of fire adaptations developed in conjunction with anthropogenic fire. But even if this is the case, the putative gain in young species, or rescuing them by bringing back fire to former anthopogenic fire exclusion areas (e.g. Gibbs 2014) is minor in a phylogenetic perspective. Such gains, while remarkable for the here and now, would without a doubt be more than outweighed by any losses in more ancient lineages (Padayachee & Procheş 2016). Some such lineages, found nowhere outside southern Africa, may be hanging on the brink of extinction due to the increased extent and frequency of fires. Anthropogenic changes in fire frequency that have occurred in Australia over millennia, have resulted in dramatic extinctions (Flannery 1994, White 1994) – and, while Africa has so far proved to be more resilient, future fire management should ideally consider the points made here. The obvious start would be building a better understanding of fire survival strategies across taxa, and of the distribution and persistence of fire-free refugia across temporal and spatial scales.

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