



Original article

Effects of time since fire on birds in a plant diversity hotspot

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ABSTRACT

Global changes are influencing fire regimes in many parts of the world. In the Fynbos plant diversity hotspot (Cape Floristic Region, South Africa), fire frequency has increased in protected areas where the mean fire interval went from 12–19 to 6–9 years between 1970 and 2000. Fire is one of the main drivers of plant diversity in the Cape Floristic Region. Too frequent fires threaten the persistence of slow-maturing plant species, and such insights have led to the adoption of fire management principles based on plant responses. The effects of fire on Fynbos fauna are much more poorly understood, and have not generally been considered in depth in Fynbos conservation policies, planning or management. We assessed the response of bird communities to long-term fire-induced vegetation changes using space-for-time substitution. We studied bird communities, vegetation structure and plant functional composition in 84 Fynbos plots burnt between two and 18 years before. Ten of the 14 bird species analysed showed a significant change in their abundance with time since fire. We observed a significant species turnover along the post-fire succession due to changes both in vegetation structure and plant functional composition, with a characteristic shift from non-Fynbos specialists and granivorous species to Fynbos specialists and nectarivorous species.

If current trends of increasing fire frequency continue, Fynbos endemic birds such as nectarivores may become vulnerable. Conservation management should thus aim more carefully to maintain mosaics of Fynbos patches of different ages. Future research needs to estimate the proportion of vegetation of different ages and patch sizes needed to support dependent fauna, particularly endemics.

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1. Introduction

Fire plays an essential role in maintaining the distribution and ecological properties of numerous ecosystems, such as grasslands, savannas, Mediterranean shrublands and boreal forests (Bond et al., 2005). There have been dramatic changes in fire regimes of most of these fire-prone ecosystems, both in terms of frequency and spatial extent of fires due to land use changes, and in recent decades,

seemingly also due to climate change (Westerling et al., 2006; Wilson et al., 2010). In parallel, escalating risks of uncontrolled fires for the increasing human population have resulted in the development of fire management strategies (Gill and Stephens, 2009). This has contributed to a growing concern about the ecological impacts of changes in fire regimes, in particular for biodiversity (e.g. Bradstock, 2002). Understanding the role of fire for the different components of these ecosystems is therefore necessary to assess their vulnerability to changes in fire frequencies and to provide scientific support for fire management (Driscoll et al., 2010).

Fire management strategies that consider biodiversity conservation often focus on plant communities (e.g. Laughlin et al., 2004). This is due to the fact that the vegetation of fire-prone ecosystems is adapted to recurring fires, i.e. resilient and able to regenerate relatively quickly after fire. Some plant species in these systems depend on fire to activate flowering, seed dispersal or germination (Le Maitre and Midgley, 1992; Lamont and Downes, 2011). Nevertheless, fire

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also impacts animals, directly through mortality and indirectly through abrupt modification of habitat. For highly mobile species such as birds, direct impacts are low (Lawrence, 1966). However, changes in vegetation structure are well known to have a strong impact on birds (MacArthur and MacArthur, 1961). As a result, fire has been shown to have major impacts on birds through vegetation structure modifications (Brotons et al., 2004). Yet other studies have also highlighted the importance of vegetation composition rather than structure for bird communities (Fleishman et al., 2003). It is thus possible that fire also has indirect impacts on bird species by modifying vegetation composition, as well as structure.

The impact of fire on bird communities in Mediterranean-climate ecosystems has been well studied in the Mediterranean Basin (Herrando et al., 2002; Pons and Prodon, 1996), in Australia (Watson et al., 2012) and in California (Lawrence, 1966; Purcell and Stephens, 2005). In Fynbos, research on fire impacts has mainly focused on plant communities (Cowling, 1992) because of their high diversity (Myers et al., 2000; Rebelo, 2006). Despite the presence of several endemic animal species, there are only a few studies on the impacts of fire on Fynbos fauna (Willan and Bigalke, 1982; Parr and Chown, 2003), including birds (but see Fraser, 1990). Moreover, most studies focus on short-term responses of the avifauna to fire (e.g. Fraser, 1989; De Swardt, 1993), neglecting longer-term responses (Watson et al., 2012) essential for effective fire management (Driscoll et al., 2010). Characteristics of Fynbos such as high compositional turnover rates, high plant diversity and a lack of trees suggest that fire may influence bird communities differently in Fynbos compared to other Mediterranean systems. First, the transition period between early post-fire vegetation (sparse restioid tussocks, similar to grass tussocks) and a dense Proteaceae shrubland is likely to be most diverse in terms of both vegetation structure and composition (Van Wilgen, 1982). As a result, we expect bird species richness to be highest in the open shrubland stage. Second, since Fynbos is characterized by low structural complexity and high plant species diversity, we expect Fynbos bird communities to be affected both by vegetation composition and structure. Third, with some Fynbos birds dependent on a specific resource, such as nectar for sugarbirds and sunbirds, we expect species turnover along the post-fire succession to be strongly influenced by life-history traits, in particular diet.

The aim of this study was to assess the long-term impact of fire on bird communities in Fynbos using 84 plots of different fire ages, last burnt in different years between 1991 and 2007. We asked the following questions: (i) How does time since last fire affect Fynbos plant functional groups and subsequently bird species richness and abundance? (ii) How do vegetation structure and plant functional composition influence bird species community composition? (iii) Do life-history traits influence bird species turnover during post-fire succession?

2. Material and methods

2.1. Study area

The study was conducted in the Cape Floristic Region (CFR), South Africa (S 34.15, E 18.95), an area dominated by nutrient-poor sandstone mountains. It is characterized by a Mediterranean climate and frequent fires (every 6–9 years in the Cederberg, Hottentots-Holland and Outeniqua reserves; Southey, 2009; every 13.5 years in the Table Mountain reserves, Forsyth and van Wilgen, 2008). This area is part of the highly diverse Fynbos biome, mostly composed of Restionaceae, Ericaceae, Proteaceae and Asteraceae. There are significant spatial variations in species composition and vegetation dynamics across the CFR, driven mainly by abiotic factors like soil type, altitude and hydrology (Campbell, 1986). To

control somewhat for potential impacts of these spatial variations on bird communities in our space-for-time substitution, we restricted our study to “Sandstone Fynbos” (Rebelo, 2006), formerly known as “Mountain Fynbos” (Campbell, 1986). Within this category, we restricted the study to the Proteoid Fynbos, i.e. Fynbos stands whose local environmental characteristics (rainfall and soil depth) permit the growth of Proteaceae species (Campbell, 1986).

2.2. Census-plot selection

We selected 84 plots in seven sites (Table S1; Fig. S1). Plots were located in 17 patches burnt in different years between 1991 and 2007 (i.e. 1–18 years after fire). We calculated time since fire for each plot based on the data provided by the conservation agencies CapeNature (De Klerk et al., 2007) and Table Mountain National Park. Since most fires occur during the austral summer (November–March), a ‘fire year’ is defined as the period July–June. Time since fire refers to the number of years since the ‘fire year’. For example, in April–May 2009 (our sampling period), a three-year-old plot was last burnt during the “fire year” July 2005–June 2006. Plots were located along existing paths for accessibility reasons and separated by at least 300 m to prevent double counting during bird surveys and minimize spatial autocorrelation in our dataset.

2.3. Bird surveys

Bird communities were sampled in April–May 2009 using the point-count method (Bibby et al., 1992). Birds heard or seen within a 100 m radius of the observer were recorded during a 10-min session. Each plot was visited twice, one month apart, in particular to minimize the bias due to lower bird detection probabilities in open habitat (Gonzalo-Turpin et al., 2008). Point-counts were conducted during the period of peak vocal activity, i.e. in the three first hours after sunrise, and during good weather conditions, without rainfall or strong wind. Raptors, aerial feeders (swallows, swifts and bee-eaters) and crepuscular species were excluded from the analysis, as this method is not appropriate to assess their abundance (Bibby et al., 1992). Individuals flying above and across the plot without any interaction with the vegetation were also excluded from the study. For each plot, we calculated species abundance per plot as the maximum number of individuals detected during one of the two visits. Total bird abundance per plot was the sum of species abundance values. Bird species richness per plot was the total number of species detected over the two visits.

2.4. Vegetation surveys

Vegetation structure and plant functional composition were estimated in each plot within a 50 m radius of the observer using the visual estimation technique widely used in avian studies described by Prodon and Lebreton (1981). We used seven structure variables: rock cover, vegetation cover for different layers (0–30 cm; 30–50 cm; 50–100 cm; >100 cm), vegetation maximal height and maximal height at which vegetation cover exceeded 25% (below referred as vegetation main height). These variables have been proved useful to assess the relationship between vegetation structure and bird communities in other Mediterranean ecosystems (e.g. Herrando and Brotons, 2002). We recorded the percentage cover of three plant functional groups: Proteaceae, ‘Ericoids’ (non-Proteaceae dicots, mainly Ericaceae) and ‘Restioids’ (monocot species, mainly Restionaceae) (classification adapted from Van Wilgen, 1982). In each stratum and for each functional group, the observer estimated the percentage of plot area that would be covered by the shadow cast on the ground by the foliage

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