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Acta Oecologica 49 (2013) 99–106

Contents lists available at SciVerse ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

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

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ARTICLE INFO

Article history:
Received 26 September 2012
Accepted 15 March 2013
Available online

Keywords:
Fire
Fynbos
Bird life history trait
Secondary succession
Time since fire
Disturbance

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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http://dx.doi.org/10.1016/j.actao.2013.03.008

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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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present in the strata. Cover percentage was estimated with the help of a cover chart representing 1%, 5%, 10%, 20% etc.

2.5. Data analysis

2.5.1. Impact of time since fire on vegetation and bird species abundance

We used generalized additive mixed models, GAMMs (Wood, 2006), to model the change in plant functional composition and bird species abundance with time since fire. Generalized additive models (GAMs) are a nonparametric form of regression modelling that here use local polynomial regression fitting method (LOESS) as a smoothing function to model nonlinear relationships (Wood, 2006). GAMs represented an appropriate method (Zuur et al., 2009) because plant functional groups and bird species would be expected to have nonlinear responses to time since last fire (Watson et al., 2012). We built a model for each of the following response variables: the cover of each plant functional group, bird species richness, bird total abundance and individual bird species abundance. We only considered bird species present in more than 5 sites (14 species). In all models, time since fire was set as the fixed effect and site as random effect to account for the spatial effects in our sampling protocol. To assess the significance of the fixed effect (time since last fire), each model was compared to a simple random effect model including only the random effect (site) using a test of deviance between the two models.

2.5.2. Role of vegetation for bird species composition

We assessed the role of vegetation structure and plant functional composition on bird species composition using Mantel tests (Mantel, 1967). The Mantel procedure circumvents the lack of independence among data values associated with traditional matrix correlations between all pairs of plots (Douglas and Endler, 1982). We calculated the Canberra distance between all pairs of plots for bird species composition (twenty-nine species), vegetation structure (seven variables) and plant functional composition (three variables). First, we used Mantel tests to assess the role of vegetation structure and plant functional composition on bird species composition. As vegetation structure and plant functional composition are likely to overlap, we tested the correlation between them. We then used partial Mantel tests to assess the role of vegetation structure for bird species composition after controlling for plant functional composition, and vice versa. A partial Mantel test measures the linear correlation between two variables after controlling for the linear effect of a third variable.

2.5.3. Influence of life-history traits

Finally, we assessed the role of bird species habitat and diet on their response to vegetation using habitat and diet preferences described in Hockey et al. (2005). Our variable 'habitat' included the primary and secondary habitat (excluding habitats not present in the study area e.g. savannah or desert). Our variable 'diet' included the primary and secondary food source.

We used the RLQ procedure (Dolédec et al., 1996; Dray and Legendre, 2008) to assess the impact of vegetation structure and plant functional composition on the selection of bird life history traits. We tested the role of bird diet in a first analysis (RLQ-diet) and the role of habitat in a second analysis (RLQ-habitat). The RLQ procedure allows the link between table R (Principal Component Analysis (PCA) using vegetation structure and composition variables) and table Q (PCA using diet or habitat preferences) through table L (Correspondence analysis using bird species abundances). We only considered bird species present in more than 5 plots. The significance of the total inertia between the vegetation variables and bird species traits was tested using a one-sided permutation test (Dray and Legendre, 2008) based on 1000 permutations.

All analyses were run using R 2.14 and the associated R-packages ADE-4 1.4-17 (Dray and Dufour, 2007) for the multivariate analyses, mgcv 1.7-21 (Wood, 2004, 2006) for the GAMM models and VEGAN-2.0-2. (Oksanen et al., 2011) for the Mantel analyses.

3. Results

3.1. Impact of time since fire on vegetation and bird species abundance

Restioids were the single dominant group until 6 years after fire and their cover did not vary significantly with time since last fire. Ericoids significantly increased and became co-dominant with Restioids between 6 and 9 years after fire and their cover significantly decreased afterwards. Finally, Proteaceae increased significantly with time since last fire and became dominant around 10 years after fire (Fig. 1a – Table 1).

Ten of the 14 bird species for which models could be constructed showed a significant response to time since fire (Fig. 2, Table 1).

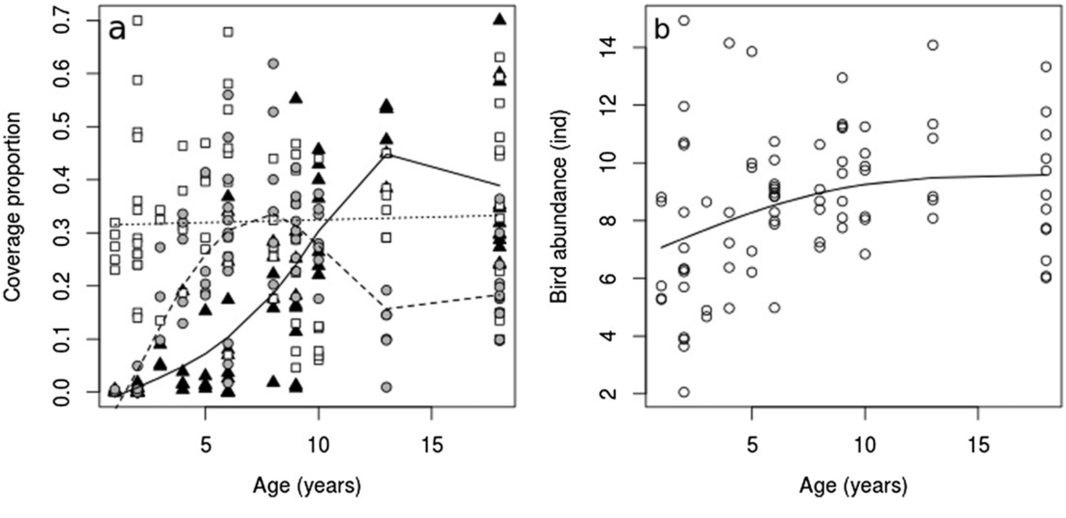

Fig. 1. a – Cover percentage of the different plant functional groups: Proteoid (black triangles and solid line), Ericoid (grey circles and dashed line) and Restioid (white squares and dotted line). b – Relationship between bird abundance (number of individuals per plot) and time since fire. Dots represent the empirical values and lines represent the associated GAMM model. In b, empirical values were slightly noised to avoid their overlap in the graph.

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Table 1
Results of the GAMM models. The first column refers to the estimation of the degree of freedom of the GAM modelling. The other columns refers to the parameters of the test of deviance between the GAMM model and the associated null model with only the random effect (Site).

Response variable	Estimated degree of freedom of the gamm model	Test of deviance with the random effect model		
		Difference in degree of freedom	Log likelihood ratio	*p*-Value
Vegetation functional group				
Ericoid	4.26	2	52.7	<0.0001
Proteoid	3.82	2	78.3	<0.0001
Restioid	1.00	2	0.094	0.95
Bird community variables				
Bird abundance	1.67	2	7.68	0.02
Bird richness	1	2	1.15	0.56
Individual bird species				
A. similis	3.13	2	23.8	<0.0001
A. violacea	2.10	2	56.5	<0.0001
C. caffra	1.64	2	12.27	0.0022
C. familiaris	1.00	2	8.76	0.012
C. fulvicapilla	1.00	2	0.00865	0.99
C. subruficapilla	1.00	2	7.48	0.024
C. totta	1.00	2	0.872	0.65
E. capensis	1.00	2	3.82	0.15
N. famosa	1.00	2	6.32	0.042
P. cafer	5.67	2	43.3	<0.0001
P. maculosa	2.24	2	10.5	0.0053
S. afer	2.89	2	0.103	0.95
S. canicollis	1.00	2	7.62	0.02
S. torquatus	1.00	2	0.700	0.70

Four species showed a decreasing response, either progressive (*Cercomela familiaris*, *Cisticola subrificapilla*, *Serinus canicollis*) or irruptive (*Anthus similis* – seldom detected beyond 2 years after the last fire). Five species showed an increasing response. *Anthobaphes violacea* increased progressively from one year after the last fire whereas *Nectarinia famosa* and *Cossypha caffra* appeared only four and six years respectively after the last fire (Fig. 2, Table 1). *Promerops cafer* increased and became most abundant after 10 years after the last fire while *Prinia maculosa* was most abundant around 9 years after the last fire. Finally, five species did not show any significant relationship with time since last fire (*Cisticola fulvicapilla*, *Crithagra totta*, *Emberiza capensis*, *Sphenoeacus afer*, *Saxicola torquatus*; Fig. 2, Table 1).

Bird species richness did not vary with time since last fire (Table 1), with an average of 5.6 bird species per plot. Total bird abundance increased significantly with time since last fire, especially during the first ten years (Fig. 1b, Table 1).

3.2. *Role of vegetation for bird species composition*

Differences in bird species composition between plots were significantly explained by both vegetation structure and plant functional composition (Table 2). There was a significant correlation between vegetation structure and plant functional composition. Nevertheless, the correlation between bird species composition and plant functional composition remained significant after controlling for the effect of vegetation structure (Table 2). Similarly, the effect of vegetation structure on bird species composition remained significant after controlling for the effect of plant functional composition.

3.3. *Influence of life-history traits*

RLQ axes were similarly associated with vegetation variables in RLQ-diet and RLQ-habitat. Proteoid cover, vegetation cover for the highest layers (30–50 cm; 50–100 cm; >100 cm), vegetation maximal height and maximal height at which vegetation cover exceeded 25% had positive scores along the first axes of both RLQ-diet and RLQ-habitat, while rock cover had negative scores for both RLQ analysis. The first axes of both RLQ-diet and RLQ-habitat were significantly and positively correlated with time since last fire (RLQ-diet: $r^2 = 0.863$, $df = 82$, $p < 0.001$; RLQ-habitat: $r^2 = 0.859$, $df = 82$, $p < 0.001$). The first axes represented a high proportion of the total variance (98% for RLQ-diet and 95% for RLQ-habitat) highlighting that both RLQ-diet and RLQ-habitat were mainly structured by the post-fire succession of the vegetation. The second axes of RLQ-diet and RLQ-habitat were strongly associated with the cover of the first stratum (0–30 cm), restioid and ericoid cover, but only accounted for a minor part of the variance in species diet (3.9%) and species habitat (4.9%).

There was a significant change in bird diet ($p < 0.001$) and bird habitat ($p < 0.001$) along each first axis, with a segregation of 95.6% for diet and 93.8% for habitat. Granivorous species were associated with younger Fynbos (negative values on the first axis of RLQ-diet) whereas nectarivorous and insectivorous species were associated with older Fynbos (positive values on the first axis of RLQ-diet; Fig. 3).

Species with a preference for Fynbos or Thicket were associated with older Fynbos patches (positive values on the first axis in RLQ-habitat) whereas species with a preference for other habitats were associated with younger Fynbos patches (negative values on the first axis in RLQ-habitat; Fig. 3).

4. Discussion

4.1. *Rapid post-fire vegetation succession*

Plant functional composition showed a significant and rapid change between one and 18 years after fire. Our results suggest a recovery time of the vegetation around 10 years after the last fire, during which time the Proteoid functional group typical of mature Fynbos becomes more abundant than the two other groups (Fig. 1a). However, most changes in plant functional composition happened during the first 5–6 years (Fig. 1a). The recovery process observed in our study is thus overall comparable with other studies (e.g. Hope et al., 2012), with a recovery time slightly longer than the average recovery time of seven years estimated by Hope et al. (2012) from NDVI in five Fynbos vegetation stands in the CFR. Our study highlights the temporal dynamics of the different functional plant groups important for different bird guilds during the Fynbos post-fire succession. The successive dominance of the Restioid, Ericoid and Proteoid groups (Fig. 1a) is consistent with differences in their maturation rates. Restionaceae and Ericaceae need as little as two years to reach reproductive maturity, whereas Proteaceae need four years or more to reach maturity (Le Maitre and Midgley, 1992).

4.2. *Winners and losers*

The abundance of most bird species showed significant changes between one and 18 years after fire, with most changes occurring during the first 10 years. Almost half of the species associated with a significant change in abundance decreased with time after fire, whereas the rest showed an increase. As a result of the equal number of “decreasing species” and “increasing species”, we did not observe any significant change in bird species richness with time since last fire. However, we observed a significant increase in the total abundance of birds, suggesting that the abundance increase of “increasing species” more than offsets the abundance decrease of “decreasing species”. This pattern is consistent with the increase of available resources occurring when vegetation complexity increases, in particular for insects (Procheş and Cowling, 2006). Our study also suggests that species can be

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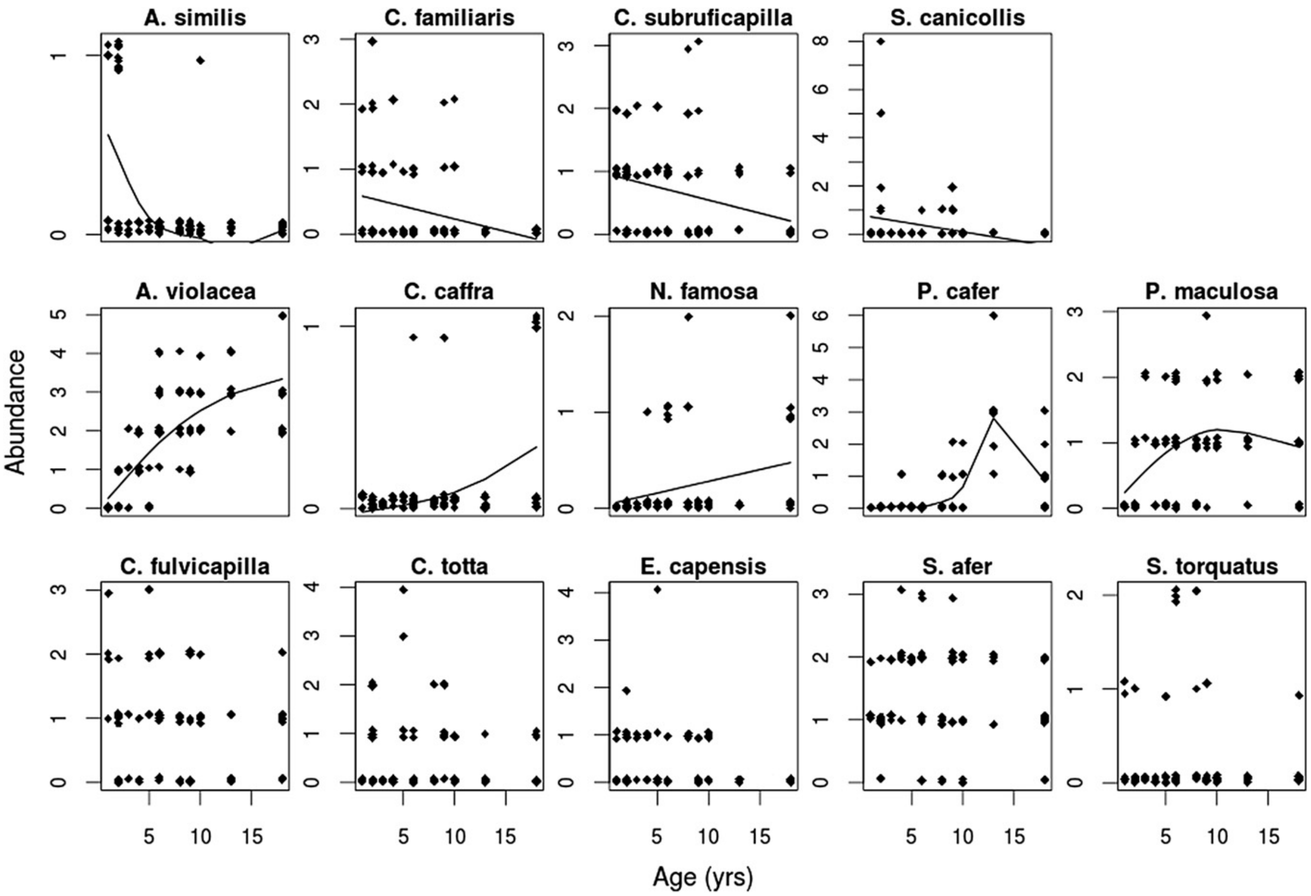

Fig. 2. Relationships between individual bird species abundances (number of individuals per plot) and time since last fire based on the generalized additive mixed models (see Methods for details). Only species occurring in at least 5 sites were analysed. Dots represent the empirical values and lines represent the associated local polynomial regression. Empirical values were slightly noised to avoid their overlap in the graph. Table 2 contains the associated test statistics.

segregated in three groups: bird species associated with early Fynbos whose abundance declines when the vegetation becomes older; bird species associated with mature Fynbos whose abundance increases; and generalist species whose abundance remains constant regardless of time since last fire. Our study thus highlights the absence of bird species associated with intermediate stages of Fynbos. This may suggest that post-fire succession of Fynbos vegetation is too rapid for intermediate stages to represent a niche stable enough for bird species to specialise in this stage.

4.3. *Role of plant functional composition*

Bird species composition was influenced significantly both by vegetation structure and plant functional composition. This result is consistent with our initial hypothesis about the important role of plant species composition for bird communities in a biome characterized by high plant diversity and low vertical complexity. However, this contrasts with other Mediterranean vegetation systems, where vegetation gradients usually go from homogeneous grassland to complex forests, and vegetation structure seems to be the dominant factor influencing bird communities (e.g. Herrando et al., 2002). The important role of plant functional composition for bird communities is likely to be explained by the strong relationship between plant species composition and specific resources for birds, such as seeds, insects and nectar. It is thus very likely that a more detailed description of plant species composition, rather than the plant functional composition emphasized in our study, would provide a better understanding of the relationship between plant species composition and bird species composition. In particular, this would allow disentangling the relative roles of Asteraceae and Ericaceae, as well those of bird-pollinated Proteaceae compared to other Proteaceae.

Table 2
Results of the Mantel and partial Mantel (with covariate) tests (Z represents the Mantel statistic). The Mantel statistics were tested with 999 permutations.

Variable 1	Variable 2	Covariate	Z	*p*-Value
Bird	Structure		0.44	<0.001
Bird	Functional composition		0.39	<0.001
Structure	Functional composition		0.70	<0.001
Bird	Structure	Functional composition	0.26	<0.001
Bird	Functional composition	Structure	0.13	0.005

4.4. *Influence of life-history traits*

Bird species turnover along the post-fire gradient was significantly influenced both by species habitat preference and diet. Indeed, the first RLQ analysis showed that recently burnt Fynbos hosted species primarily associated with other habitats than Fynbos. For example, *A. similis* and *C. familiaris* are associated primarily with grassland and rocky areas respectively. Inversely, older stands of Fynbos hosted bird species endemic to the Fynbos biome, e.g. *P. cafer* and *A. violacea*. We therefore observed a shift of the bird

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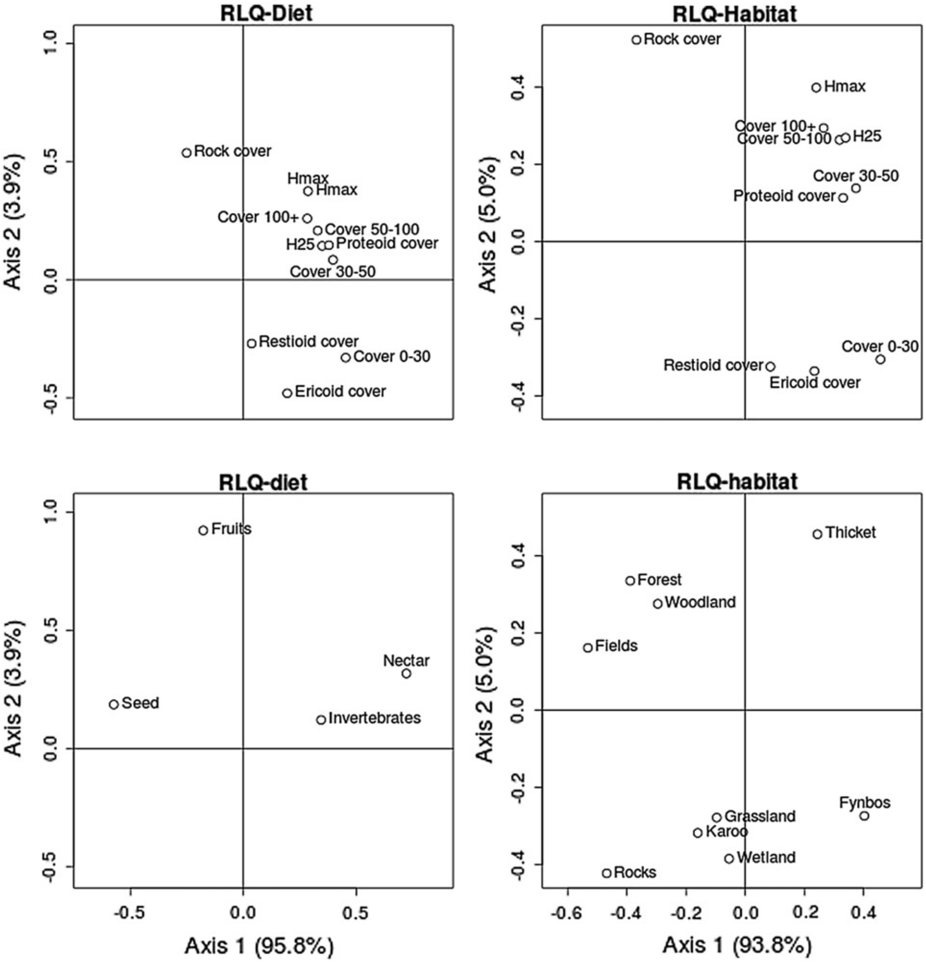

Fig. 3. Results of the RLQ-diet analyses on vegetation variables (top left) and diet (bottom left) and results of the RLQ-habitat on vegetation variables (top right) and habitat preferences (bottom right). For both RLQ-diet and RLQ-habitat, the explained variance of each axis is reported on the axis labels as the fraction of the total explained variance.

community along the post-fire succession from habitat generalists (characterized by multiple habitat preferences) to Fynbos specialists. This result suggests that Fynbos specialists favour Fynbos burnt infrequently. Similarly, the second RLQ analysis showed that recently burnt Fynbos was associated with granivorous bird species. This result is consistent with other observations of avian granivores (*C. totta*, *Pternistis capensis*, *S. canicollis*, *Scleroptila africanus*) foraging on recently burnt Fynbos stands (Dean, 1989; Fraser, 1989; Kruger and Bigalke, 1984). Moreover, species such as *S. canicollis* and *C. totta* are known to move in large flocks across recently burnt areas to extract seeds from Proteaceae cones (Fraser, 1989; L. Chalmandrier and P. Barnard, personal observations). This dominance of granivorous bird species in the earlier stages of the post-fire succession can be explained by the reproductive ecology of Fynbos plants. Indeed, a high proportion of Sandstone Fynbos plants species are serotinous, in particular within the Proteaceae (Le Maitre and Midgley, 1992). As a result, a high volume of seeds is immediately available after a fire. This is a common feature across Mediterranean ecosystems where granivores are dominant in early stages of the succession, e.g. in the Mediterranean Basin (Jacquet and Prodon, 2009). As Fynbos matures and vegetation becomes taller, the bird community becomes dominated by insectivorous and then nectarivorous bird species. In our study, the abundance of nectarivorous species was highest in older Fynbos (*A. violacea*, *N. famosa* and *P. cafer*) whereas insectivorous species were present throughout the succession (e.g. C. *fulvicapilla* and *S. afer* were remarkably ubiquitous and abundant; Fig. 2). The high dependence of the nectarivore guild on mature Fynbos is consistent with the negative impact of frequent fire on this guild already described by Geerts et al. (2012). There are however variations among nectarivorous species. *A. violacea* appeared early in the succession (from two years after a fire; Fig. 2), consistent with the fact that it is feeding on *Erica* species (Rebelo et al., 1984) already present in young Fynbos (Fig. 1a). *N. famosa* and *P. cafer* only became abundant in Fynbos older than five and seven years respectively, as they feed preferentially on resources maturing in patches of intermediate and older fire ages.

4.5. Implications for conservation

In three reserves of the CFR (Cederberg; Hottentots-Holland and Outeniqua reserves), the mean fire return interval appears to have decreased from 12–19 years in 1970 to 6–9 years in 2000, probably due to increasing human populations and climatic changes (Southey, 2009). Areas more densely populated such as Table Mountain are also intensively burned, with some areas having an average fire frequency of under 7.5 years over the last 38 years (Forsyth and van Wilgen, 2008). Although these changes in fire frequency are not evenly applicable to the entire CFR, fire frequency has been identified as a major concern (e.g. Van Wilgen, 1982) likely to become problematic under future climatic conditions (Southey, 2009).

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As nectarivorous Fynbos endemic birds are associated with older vegetation, increased fire frequency represents a potential threat for the persistence of species such as *A. violacea* and *P. cafer*. None of the Fynbos endemics are currently considered threatened in the regional Red Data List (Barnes, 2000), though their status has been carefully reconsidered in the current revision (Taylor, in press), based on an initial assessment of recent range change using atlas data (Lee and Barnard, 2012). Moreover, abundance of all three nectarivores significantly increased with time since fire (*A. violacea*, *N. famosa* and *P. cafer*). These three nectarivores are the primary pollinators of 320 plants species of the CFR (Pauw and Louw, 2012). This is particularly true for *N. famosa* which plays an irreplaceable role as the exclusive pollinator of plant species with long nectar tubes (Geerts and Pauw, 2009). If the trend towards increasing fire frequency continues, the critical ecosystem services provided by these three bird species to the iconic Fynbos vegetation may be jeopardized. This potential threat is even more worrying when taking into account that urbanization also reduces the functional diversity of this nectarivore guild (Pauw and Louw, 2012) and that future climate change scenarios predict an overall decrease in Proteaceae abundance (Keith et al., 2008).

If the trend towards increasing fire frequencies continues, and potential decreases of pollinating bird species are to be mitigated, a mosaic of young and old Fynbos patches needs to be maintained and the ecological requirements of bird species need to be much more explicitly included in conservation planning. This would imply a shift in fire management objectives, from one mainly based on fuel reduction and maintenance of plant diversity (Van Wilgen, 1982), to one explicitly including bird diversity. It needs to be determined to what extent other animal groups, such as small mammals (Willan and Bigalke, 1982) and insects, (Procheş and Cowling, 2006) would also benefit from this strategy of landscape-scale mosaic planning, but maintaining mosaics of different vegetation ages should increase the connectivity between suitable patches, increase survival during fire events, and favour recolonization processes after fire (Brotons et al., 2005). This new fire management strategy should thus include animal taxa as much as possible while remaining compatible with plant conservation objectives, as the CFR flora remains for now the most threatened component of this biodiversity hotspot. In the long term, maintaining a mosaic of different aged Fynbos vegetation, with particular focus on maintaining sufficient areas of vegetation older than ten years, is likely to benefit both the Fynbos fauna and flora and improve the resilience of the CFR biodiversity hotspot to global changes.

Acknowledgement

We thank SANParks and CapeNature for granting us the permits (to P. Barnard, L. Chalmandrier and C. Sirami) to conduct the surveys and supportive fieldwork. We thank the Western Cape Nature Conservation Board (Scientific Services) for the fire database in the CapeNature Reserves and SANParks for the fire database in Silvermine and Cape of Good Hope Nature Reserves within the Table Mountain National Park. Support from EU FP-7 GA 243888 is acknowledged.

Appendix A. Supplementary material

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.actao.2013.03.008.

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