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A burning issue: Fire overrides grazing as a disturbance driver for South African grassland bird and arthropod assemblage structure and diversity

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ABSTRACT

In this study, we investigated the responses of two faunal groups, birds and arthropods, to varying degrees of disturbance caused by fire and grazing in South Africa, eight study sites of varying fire frequency and stocking density were studied over two summer seasons (October–March). Bird assemblages reflected habitat disturbance in a diversity of ways, driven by factors ranging from direct disturbance to changes in habitat structure and functioning, and shifts in food availability. Similarly, arthropod diversity and abundance changed seasonally in response to management practices. Fire frequency drives faunal assemblage structure and abundance and, in most cases, overrides the effects of grazing at all taxonomic levels. In particular, fire frequency strongly influenced grassland-breeding birds because farms are burnt in the territory-forming stage of the breeding cycle. Insectivores and nectarivores were disproportionately impacted by intensive commercial management. Of particular concern in this system is the yellow-breasted pipit (*Anthus chloris*), which is regionally and globally *Vulnerable* because of habitat loss. This species is sensitive to any form of habitat disturbance, highlighting the need for conservation attention in these grasslands. Of the ten arthropod orders present in the study area, only Orthoptera responded positively to burning. However, orthopterans made up on average 78% of arthropod biomass in moist highland grasslands, resulting in high grasshopper biomass on annually burnt farms: this high biomass in turn supports an abundance of insectivores. This reinforces the importance of process-oriented data where a measure of performance, such as reproductive success, is considered in assessing ecosystem condition.

1. Introduction

Human land-use practices cause large-scale degradation of the structure and functioning of natural ecosystems (Furness et al., 1993; Jansen et al., 1999; Darkoh, 2003; Jeanneret et al., 2003; Dale et al., 2005; Driver et al., 2005), with concomitant implications for biodiversity conservation (Bibby, 1999; Hilty and Merenlender, 2000). Of these ecosystems, grasslands are the most utilized and least protected of any terrestrial vegetation type in the world with only about 1.4% under formal protection (Driver et al., 2005). In South Africa, the grassland biome covers approximately 7750 km^2 yet only 2.2% of its total area is formally conserved (Tarboton, 1997) and 60% has been irreversibly degraded (Driver et al., 2005). There are several different grassland types within the greater grassland biome of South Africa, one of which is the highland grassland of which only 1.5% is formally conserved (Mucina and Rutherford, 2006). Grasslands are generally very sensitive to disturbance (Smit et al., 1997; Little et al., 2005) and the cumulative impacts of over-grazing (Tainton, 1981; Hockey et al., 1988; Neke and Du Plessis, 2004), extensive burning (Uys et al., 2004), plantation forestry (Allan et al., 1997; Lipsey and Hockey, 2010) and invasion by alien plants (Le Maitre et al., 1996) has led to grasslands being considered a conservation priority. As of 2004, only about 53% of the highland grassland biome remained in a "semi-pristine" state, contained mostly in livestock farms and rangelands (Neke and Du Plessis, 2004).

Loss of natural habitat is considered to be the greatest single cause of biodiversity loss in terrestrial ecosystems in South Africa (Driver et al., 2005). Therefore, determining the factors leading to current patterns of biodiversity loss in human-degraded landscapes is a necessary prerequisite to designing future conservation strategies (Jeanneret et al., 2003). Anthropogenic land use leads to a disjointed mosaic of fragmented, intact and disturbed habitats, testing the adaptability of its component species to persist (Morrison, 1986; Hockey et al., 1988; Harrison et al., 1994; Allan et al., 1997). The relative success with which different species do

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so will depend on their ability to utilize both intact patches of natural habitat and the surrounding degraded matrix (Wiens, 1994; Ricketts, 2001). The land making up the 'matrix' between conserved habitats will be crucial in both the future conservation of many species and in the context of broader ecosystem functioning (Wiens, 1994; Norton, 2000; Ricketts, 2001; Donald et al., 2002; Hilty and Merenlender, 2003). Changes in habitat structure outside of pristine habitats thus play a critical role in determining species composition, which is influenced both by losses of indigenous species and gains of species not naturally representative of the original system (Liversidge, 1962; Wiens, 1974; Folse, 1982; Erdelen, 1984; Knopf et al., 1988; Martin and Possingham, 2005).

Bird populations are no exception and it is evident that a number of populations have decreased in many parts of the world associated with agricultural practices (Pain and Pienkowski, 1997; Donald et al., 2002; Laiolo, 2005; Azpiroz et al., 2012). As agriculture is the dominant land-use type in many parts of the world, there is mounting concern over the status of biodiversity associated with farmland environments (Zanette et al., 2000; Jobin et al., 2001; Söderström et al., 2001; Vickery et al., 2001; Benton et al., 2002; Lepczyk, 2005; Marshall et al., 2005; Martin et al., 2005; Martin and Possingham, 2005; Haslem and Bennett, 2008; Herzon et al., 2008).

In most cases, extensive transformation of natural landscapes to monoculture, such as exotic plantations or cereal crop systems, may pose more obvious changes to ecosystem structure and function, however, more subtle but as severe changes may not be as obvious in rangeland agriculture where grazing pressures and burning frequency are generally the driving forces. Worldwide, there have been demonstrations that unnaturally high grazing pressure is detrimental to bird species assemblages (Wiens, 1973; Martin and Possingham, 2005; Batáry et al., 2006). In highland grassland ecosystems, livestock grazing often does not simulate the natural herbivory that would have occurred in an area (McNaughton, 1986) but are often compounded with all-year livestock camp management where natural seasonal migration is no longer evident and indigenous grazers have been replaced by commercial agricultural breeds. Furthermore, the potential impacts of commercial livestock grazing are confounded by the presence of fire as a disturbance agent and a farm management tool in the grassland system. These responses to stocking density have not previously been compared in combination with the effects of burning frequency and the resultant impacts on birds and arthropods. Although grassland systems are naturally maintained by winter and spring fires, there is concern over the possible detrimental impacts of unnaturally frequent fires (coupled with increasing anthropogenic fragmentation) on floral and faunal community structures (Baker, 1992; Swengel, 2001; Giliomee, 2003; Valentine et al., 2007).

Communities within ecosystems are often represented by particular and often specialized species, however, single-taxon approaches to the assessment of disturbance effects on ecological assemblages have been shown to be inadequate, supporting the use of multi-taxon approaches (Milchunas et al., 1998; Söderström et al., 2001). Indeed, the link between the change in a floral community and its influence on invertebrates and higher vertebrates is often lacking in ecological studies where assemblages or groups of assemblages have changed as a result of management practices such as fire frequency and stocking density within grassland ecosystems (Joern and Laws, 2012). Few studies have explored the responses of arthropod communities to fire and grazing in grasslands (Joern and Laws, 2012), but it has been shown that many arthropod groups decrease rapidly in abundance directly after fire, depending on both the intensity and extent of the burn and the mobility of the taxa concerned (Dunwiddie, 1991). Arthropods respond similarly in areas which are heavily grazed because of structural simplification of the habitat and the loss of protective cover (analogous to the effects of fire – Swengel, 2001). These changes in arthropod community structure are likely to have knock-on effects on insectivorous grassland birds (Benton et al., 2002) and even granivorous birds where the floral community has changed substantially.

Various studies have shown that higher taxonomic level richness acts as an adequate surrogate for arthropod biodiversity, decreasing the need for exhaustive expert identification (Prendergast and Eversham, 1997; Duelli and Obrist, 1998; Biaggini et al., 2007; Öster et al., 2008). Most birds, by contrast, are easy to identify to species level and this allows more in depth interpretation of assemblage effects caused by disturbance pressures.

When assessing bird assemblages species richness alone is a poor biodiversity measure, because changes in habitat structure influence species assemblages through losses and gains of different species (Liversidge, 1962; Wiens, 1974; Folse, 1982; Erdelen, 1984; Knopf et al., 1988; Martin and Possingham, 2005). In other words, species richness can remain constant while assemblage composition changes. This suggests that the responses of individual species and assemblage shifts are important when assessing the impacts of disturbance (Batáry et al., 2006).

In some cases the presence of a particular species in a system reflects some measure of the character of the habitat and the species is considered as bio-indicator (McGeoch and Chown, 1998). Such indicator species have the potential to signal the effects of disturbances on other species with similar habitat requirements (Noss, 1989) and can thus potentially be utilized as an early warning system for habitat degradation. These species, once identified, can also be useful for future monitoring of the system. While the use of indicator species is contentious (McGeoch and Chown, 1998; Duelli and Obrist, 2003; Sauberer et al., 2004), the importance of single species and habitat specialists' responses to disturbance should be taken into consideration. The functional responses of faunal assemblages or the mere presence/absence of birds and arthropods can be used as indicators of changes in the structure and functioning of the environment (Morrison, 1986; Martin and Possingham, 2005; Child et al., 2009; Vassiliki et al., 2009). Among birds, functional richness (the diversity of functional guilds within a community) has been shown to be closely correlated with species richness at large spatial scales (Child et al., 2009), but at finer scales species' responses are expected to be more indicative of ecosystem functioning. Birds respond rapidly to habitat change and move in response to anthropogenic habitat alteration (Liversidge, 1962; Folse, 1982; Knopf et al., 1988). These responses, along with shifts in functional guilds, allow ecologists to infer disturbance processes (Moretti and Legg, 2009).

There has yet to be a broad-scale assessment of both the beneficial and detrimental effects of these habitat changes at a multi-taxon and landscape level in South Africa.

This study focuses on the responses of arthropod and bird assemblages to fire and grazing pressure in the moist highland grasslands (MHGs) of South Africa. The study aims to assess the shifts in assemblage structures through the summer growing season and between management types in order to infer the conservation implications of current land-management practices in both conserved areas and the surrounding farmland. We assess the relative disturbance effects of fire and grazing on functional guild and species responses within arthropod and bird taxonomic groups.

2. Study site and methods

The study area falls within the Mesic Highveld Grassland Bioregion and is specifically identified as Lydenberg Montane Grassland (Mucina and Rutherford, 2006). The study sites were all on the plateau around the town of Dullstroom (centered at 25° 25″S, 30°

10″E), and were between 1900 and 2200 m.a.s.l. The soils are mostly derived from shale and quartzite as well as lavas and dolomites of the Transvaal Supergroup (Mucina and Rutherford, 2006): areas dominated by lava and dolomitic soils were avoided as most of the area falls on shale and quartzite soils. The Dullstroom Plateau Grasslands (encompassing this entire study) have been classified as *Endangered* on the basis of very high irreplaceability of species (National List of threatened Ecosystems, Department of Environmental Affairs, notice 1477 of 2009). The topography includes high-altitude plateaus, undulating plains, mountain peaks and slopes, and hills and deep valleys. The predominant vegetation is short grass in the high-lying areas becoming taller on the lower slopes. Grass species diversity is fairly low, but the diversity of forbs is high (Mucina and Rutherford, 2006). Orographic precipitation (660–1180 mm per year – Mucina and Rutherford, 2006) and heavy mists throughout most months of the year have promoted a unique flora, including a rich diversity of mesophytic plants such as the Orchidaceae. Indeed, forb diversity is so high, with over 2260 plant taxa and 51 endemic plant species, that this grassland type has been proposed as a ‘center of plant endemism’ (Mucina and Rutherford, 2006).

The study sites all comprised undulating hills ranging from ca 1900–2200 m.a.s.l. Eight study sites subject to differing management regimes were sampled over two summer seasons. These included an annually burnt farm (AF); communally grazed lands (Com); a biennially burnt farm that was burnt (BF) or was not burnt (BFu) in the study year; a nature reserve site (Verloren Valei Nature Reserve) with a high density of indigenous grazing ungulates that was burnt (NRH) or was not burnt (NRHu) in the study year; and a nature reserve site with a low density of indigenous grazing ungulates that was burnt (NRL) or was not burnt (NRLu) in the study year, the high stocking density part of the reserve was fenced off from the rest of the reserve. The nature reserve sites were both burnt biennially while the communal grazed lands were not burnt in planned burns due to low fuel loads as a result of intensive mixed grazing. Burning season is governed by provincial regulations and occurs after the first rains, usually in September.

Within each site, four replicates were chosen such that one was orientated in each of the four cardinal compass directions. Each of the four 25 ha replicates were marked out with at least 500 m between replicates, the largest territory of any of the grassland passerine species in this study is no more than 100 m in diameter (Hockey et al., 2005). Sampling sites were selected with sufficient distance between sites to avoid pseudo-replication (Hurlbert, 1984), but were sufficiently close together to standardize as far as possible for extrinsic factors including soil type, rainfall, aspect, slope and temperature.

Field work was conducted during the birds’ breeding season (October–March) in 2007–2008 and 2008–2009. Based on data from the local weather station neither temperature, rainfall nor wind speed showed significant differences between years, months or days between the field seasons, these also showed no significant difference to 50 year averages (Students *t*-test for dependent samples). Grazing stocking densities were collected by interviewing farmers or managers of the study sites and were augmented/validated with animal counts (Table 1).

Relative stocking density was recorded as the number of hectares of grazing land available per large animal unit (ha LAU^{-1}). One LAU was defined as being equivalent to one cow or five sheep, and represented the metabolic equivalent of a 454 kg cow (Meissner et al., 1983; Tainton, 1999).

Table 1

Average stocking density in the eight study sites (ha LAU^{-1}). Livestock farms all stocked domestic cattle, commercial grazing lands stocked a mixture of cattle, sheep, goats, pigs and horses while the reserve are had a mixture of wild game including Blesbok *Damaliscus dorcas*, Black Wildebeest *Connochaetus gnou* and Zebra *Equus quagga* along with other small antelope species. Young animals born in the study year were treated as 0.5 LAUs.

ha LAU^{-1}	
NRLu	63.671
NRL	46.714
NRHu	13.613
NRH	14.408
BFu	2.092
BF	1.963
AF	1.251
Com	1.071

2.1. Vegetation structural sampling

Vegetation structure was sampled monthly throughout the sampling season using two techniques. The first sampling method was modified from Wiens and Rotenberry (1981). Three 500 m transects were established within each of the four replicates per study site. Along each of these, at 50 m intervals, a 10 m tape was laid out perpendicular to the transect line. Vegetation was sampled at 1 m intervals along the tape yielding 100 point samples per transect (in total, 1200 samples per site per month). At each sampling point a 6 mm diameter rod was positioned vertically through the vegetation to the ground. This rod was marked at height intervals 0–49 mm, 50–99 mm, 100–199 mm, 200–299 mm, 300–399 mm, 400–499 mm, 500–599 mm and 600–1000 mm. At each sampling point two variables were recorded (a) the number of vegetation contacts with the rod per height interval, and (b) whether the contact was a grass or a forb. Open ground (in the case of no contact with vegetation) and overall maximum height of vegetation were also recorded. From these data three sets of vegetation structural indices were recorded.

Cover – Percent grass cover (%grass), percent forb cover (%forb) and percent total plant cover in the form of grass and forb combined (%veg), calculated as the percent of points recording each of these parameters.

Structural measures – Average maximum height of vegetation (AveMaxHt) and horizontal density (AvHorDen), derived from the mean number of contacts with the rod in the 0–100 mm interval, and vertical density (AvVerDen) derived from the mean number of contacts over the entire length of the rod.

Heterogeneity measures – canopy heterogeneity (HorHetHt) given by the coefficient of variation of the maximum height contacts, and overall heterogeneity (HorHetTo) given by the coefficient of variation of the mean total number of contacts over the entire rod and a patchiness index (Patchine) which groups the 10 samples per 50 m and then calculates landscape patchiness according to the equation of Wiens and Rotenberry (1981).

$$Patchiness = \Sigma(Max - Min)/\Sigma x$$

where *Max* = maximum number of contacts recorded in each sample group, *Min* = minimum number of contacts recorded in each sample group, and x = the mean number of contacts recorded in each sample group.

The second technique quantifies vegetation biomass. The quantity of herbage available to herbivores is a function of phytomass (O’Reagain and Turner, 1992; Smith, 2006). Measurement of standing crop is essential for determining herbage production and stocking rates in the management of herbivores (Ganguli et al., 2000).

Phytomass was sampled using a Disc Pasture Meter (DPM – Bransby and Tainton, 1977; Danckwerts and Trollope, 1980; Trollope and Potgieter, 1986). The DPM is made up of a 1.5 kg, 457 mm diameter disk mounted onto a central rod with a measuring scale in 5 mm increments. The disk was dropped vertically from 0.6 m above ground onto the grass sward; the settling height of the disk was then recorded. Vegetation was sampled every 5 m along the three 500 m transects, yielding 100 DPM samples per transect and a total of 1200 samples per site per month.

The DPM is calibrated for a specific vegetation type to convert the DPM reading into biomass estimates (kg ha^{-1}). Although DPM calibrations were available for a number of vegetation types in South Africa and some outside of South Africa (Bransby and Tainton, 1977; Danckwerts and Trollope, 1980; Trollope, 1983; Trollope and Potgieter, 1986), MHG had not been calibrated. Data collected by Colin Everson in the late 1970s were used to calibrate the DPM. The best fit calibration was the linear regression, $y = 358.768\times-746.352$ ($r = 0.95$, $r^2 = 0.91$, $p < 0.0001$).

2.2. Arthropod sampling

Arthropod abundance was sampled monthly along the same transects where birds were censused (see below), using a circular sweep net with a diameter of 450 mm. Samples were collected in the beginning of each month on a selected warm, windless day. These samples consisted of 200 sweeps (a sweep is made with each long stride) per transect (600 sweeps per treatment) per month. Sweep nets are effective in catching most of the prey groups eaten by the Motacillidae (insectivorous wagtails – Brodmann and Reyer, 1999). Arthropods samples were immediately placed in a sealed container with ethyl acetate. The arthropods were separated from vegetation matter and preserved in ethanol for later identification to order level, this being sufficient resolution to detect taxonomic responses to land use at local scales (Prendergast and Eversham, 1997; Duelli and Obrist, 1998; Zanette et al., 2000; Vickery et al., 2001; Biaggini et al., 2007; Dennis et al., 2008; Öster et al., 2008; Champlin et al., 2009). Samples were then dried and weighed for biomass assessment (Cressa, 1999; Zanette et al., 2000; Boulton et al., 2008). Pitfall trapping was attempted, but controlling for catch success between sites was not possible (even with raised covers) because of erratic rainfall patterns and the need for traps to stay out for at least 3 days, this results in some of the replicate samples being destroyed due to flooding and hence no comparable samples.

2.3. Bird sampling

In order to quantify presence/absence and abundance of bird species, censuses were undertaken that encompassed all taxa present.

A 50 m weighted rope was dragged along 500 m long line transects. This is a modification of the fixed-strip or belt transect method (Kendeigh, 1944) and is the most appropriate census method in large, open areas (where it is more accurate than point counts – Bibby et al., 1992). Rope drags also obviate problems of having to correct for effective transect width and prevent birds from hiding in taller grass clumps and swards (Krook et al., 2007). Birds not utilizing the habitat directly, i.e. flying over, were not included in the analyses.

For each of the four replicates per management type, three 500 m parallel transects were walked perpendicular to a plot boundary: each 500 m transect covered an area of 7.5 ha. Censusing began when breeding territories were established in early October and were conducted monthly throughout the breeding season. These were divided into sampling periods in the morning (06h00–10h00) and in the afternoon (14h00–18h00). Census sessions were spread between the two observation periods in rotation according to a randomly selected schedule (MacNally and Horricks, 2002).

2.4. Statistical analysis

The Software packages PC-ORD 5.10 (McCune and Mefford, 2006) and STATISTICA 9.0 (StatSoft Inc., 2009) were used to analyse these data.

To assess differences in bird assemblages based on management type, as a function of early to late summer season and in response to burning, we averaged the counts per transect and used these averaged values as the monthly count per replicate. We then used a one-way, pairwise, Permutation-based Non-parametric MANOVA or PerManova with a Sørenson (Bray–Curtis) distance measure and 5000 iterations (Anderson, 2001) and a pairwise Multi-Response Permutation Procedure (MRPP) using a Sørenson distance measure and a natural weighting (Mielke, 1984). MRPP is a non-parametric test of differences between groups (species assemblages), designed for multivariate analysis of terrestrial communities. The A-statistic (chance–corrected, within-group agreement) describes effect size: when $A = 0$, groups are no more or less different than expected by chance; when $A = 1$, sample units within groups are identical (McCune and Mefford, 2006). Sørenson distance measures were selected as these are recommended for abundance data and give robust outputs with zero-dominated data sets (McCune and Grace, 2002). Both PerManova and MRPP results are reported as MRPP is considered more robust while PerManova has been more extensively published (McCune and Grace, 2002).

To assess the relative influences of grazing type (areas with domestic stock vs areas with indigenous animals) and burning (burnt vs unburnt), on bird species richness and abundance (calculated as average abundance from the three transects per replicate, sampled monthly for 6 months, October to March), Wilcoxon Matched-Pairs tests were performed. To assess the difference in bird species richness and arthropod biomass between management types as a function of season (from early to late summer) and in response to burning, Analyses of Variance (ANOVA) with *post hoc* Tukey Tests were performed. Data were log transformed where necessary in order to meet assumptions of normality.

To assess species' as well as functional guild responses to management type and month, we ran an Indicator Species Analysis (McCune and Mefford, 2006) using a Monte Carlo Test of significance with 5000 permutations (Dufrêne and Legendre, 1997). This method combines species' abundances and occurrence: a 'perfect indicator' should be present in all replicates within a site and not present in any other sites, this would have an indicator value of 100.

To determine which vegetation structural indices play the most important role in predicting bird species richness and arthropod diversity, we used a Backwards Stepwise Multiple Regression with a partial correlation analysis. The *beta* coefficient compares the relative contribution of each independent variable in the prediction of the dependent variable. The tolerance of a variable is defined as 1 min the squared multiple correlation of this variable with all other independent variables in the regression equation. Therefore, the closer to zero the tolerance of a variable, the more redundant is its contribution to the regression.

Non-metric Multidimensional Scaling Ordinations (Kruskal, 1964; Mather, 1976) were run using a Sørenson distance measure with 250 runs of the real data and 500 iterations in order to separate out replicate sites in bird species space and monthly samples in arthropod biomass space. DPM data were secondarily overlaid over the ordination with vegetation structural indices as a biplot. Orthopteran abundance data were secondarily overlaid onto the ordination and illustrated as a biplot.

To assess grassland bird assemblage site preference a Two-way Cluster Dendrogram (McCune and Mefford, 2006) with a Sørenson distance measure and group-average linking method without relativisation was run.

3. Results

3.1. Arthropods

Of the 32 159 arthropods collected, Coleoptera accounted for 36.6%, Orthoptera 33.5%, Hemiptera 8.5%, Diptera 7.9%, Hymenoptera (excluding ants) 3.5%, Araneae 3.3%, Caterpillars 2.8% and ants 2.1%. Isoptera, Thysonaptera, Psocoptera, Mantodea, Phasmatodea, Lepidoptera, Blattodea, Ixodida, Trichoptera, Odonata and Dermaptera collectively accounted for the remaining 1.6% (Fig. 1a).

Overall biomass was dominated by Orthoptera (Fig. 1a), which, at any one site, reached highest biomass in the year in which that site had been burnt (Wilcoxon Matched-Pairs Test, $p < 0.001$ – Fig. 1b). When compared between management practices, there were marked differences in orthopteran biomass between all burnt vs all unburnt sites combined (ANOVA, *post hoc* Tukey Test, $p < 0.01$, df = 79), indicating that burning strongly influences orthopteran biomass.

In areas burnt in that year (in the month before sampling started), Orthopteran biomass increased towards the end of the summer with significant differences between both October/November and January (ANOVA, *post hoc* Tukey Test, $p < 0.05$), and between October/November and February (ANOVA, *post hoc* Tukey Test, $p < 0.001$ – Fig. 1b). Total arthropod biomass mirrored the patterns of orthopteran biomass, highlighting the overriding contribution of Orthoptera to overall arthropod biomass in this system (Fig. 1b and c). This is confirmed by the significant relationship between Orthoptera biomass and total arthropod biomass (Mantel Test, $t = 2.92$, $p < 0.005$).

Vegetation structural indices were explored as possible explanations as to why arthropod ordinal diversity changes across time and according to management (Fig. 2). Both forb cover (%) and vegetation biomass (kg ha^{-1}) seemed to influence arthropod assemblages structure at the ordinal level, but this was not convincing given the low r^2 values (Table 2).

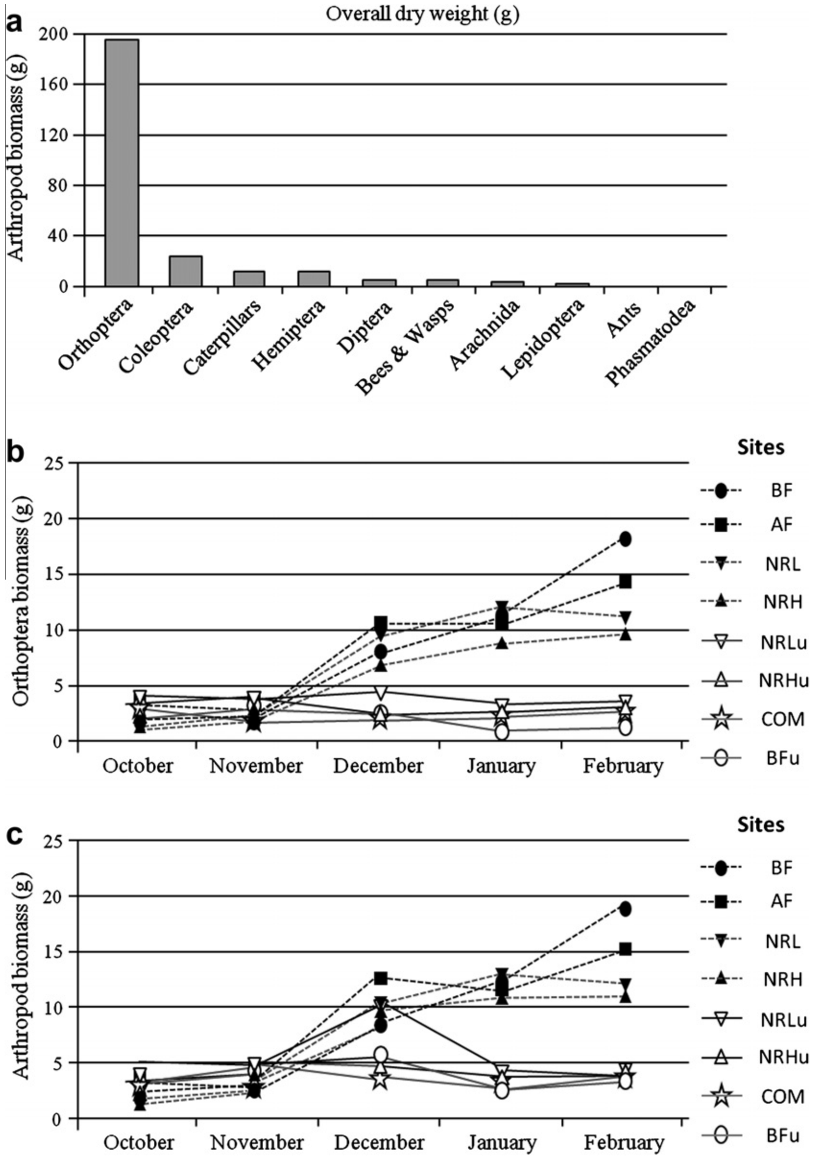

Fig. 1. (a) Relative biomass of each arthropod order in MHGs, this pattern was similar in all management types; (b) monthly trends in orthopteran biomass (dry weight in grams per 25 ha) through the summer season; and (c) biomass of all arthropods from all sites and all sampling months.

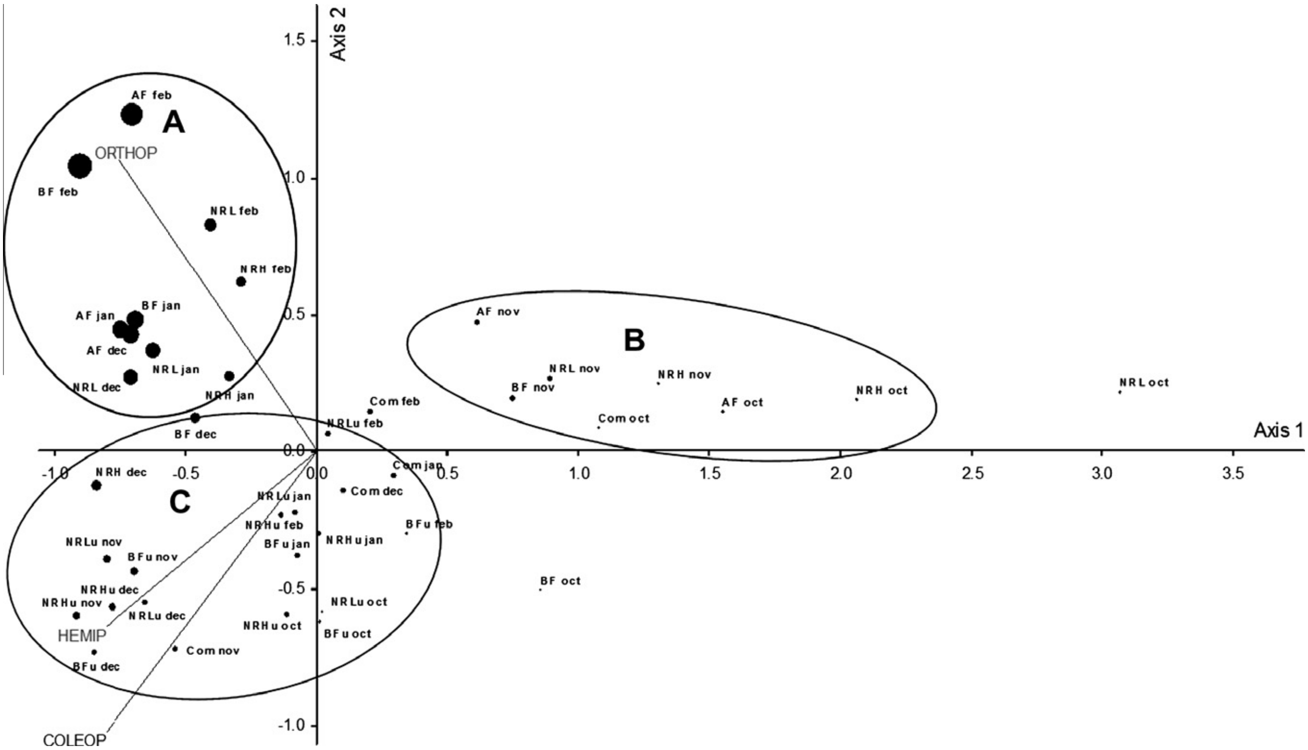

Fig. 2. Non-metric Multidimensional Scaling ordination of arthropod biomass per site per month. Orthopteran biomass per site per month is overlaid and indicated by the size of the black circles. Arthropod ordinal biomass is illustrated as a biplot (lines extending from the center of the graphic): the length and direction of the lines illustrate the biomass and in which sites these orders were more abundant. Group A was characterized by high Orthoptera (Orthop) biomass while group C was characterized by high Hemiptera (Hemip) and Coleoptera (Coleop) biomass. Axes one and two respectively explained 30.05% and 24.83% of the variance in the original distance matrix.

Table 2
Partial correlation analysis illustrating the two vegetation structural indices which play the most important role in predicting arthropod ordinal diversity (measured using the Shannon Index). Overall regression results: $r^2 = 0.52$, $F_{3,145} = 25.75$, $p < 0.001$.

	Beta	Tolerance	r^2	t (145)	p
%Forb	−0.292	0.978	0.011	−4.065	0.001
DPM	0.453	0.989	0.021	6.315	0.000

Arthropod biomass varied according to time of year and land management. This variation in biomass was similar for all arthropod orders except for orthopterans which showed high biomass in late summer in burnt sites. This variation in arthropod diversity per site per month can be illustrated in 2-dimensional space (Fig. 2), making it possible to identify sites that have similar arthropod biomass. Group B includes sites that had very recently been burnt and supported the lowest arthropod biomass. Group C were unburnt sites with relatively high biomass of non-orthopteran arthropods (mainly Hemiptera and Coleoptera). Group A comprised sites that were sampled in late summer and were burnt in that year: these had high overall arthropod biomass dominated by Orthoptera.

With the exception of orthopterans, arthropods in general showed a preference for unburnt areas, illustrating a sensitivity to this form of disturbance. However, the dominance of orthopterans in the system resulted in burnt areas having higher overall arthropod biomass in the latter part of the season than unburnt areas.

3.2. Birds

Bird species assemblages responded strongly to management (PerManova, $p < 0.001$; MRPP, $A = 0.59$, $p < 0.005$). There was an observed decrease in both overall bird abundance and the number of specialist grassland species with increasing frequency of burning and intensity of grazing: this response was significant across all management types (PerManova, $p < 0.05$; MRPP, $A > 0.21$, $p < 0.05$) except NRH vs Com, BFu vs Com and BF vs AF.

Bird species assemblages also changed as the breeding season progressed (PerManova, $p < 0.001$; MRPP, $A = 0.14$, $p < 0.0001$), with abundance decreasing through the season (Fig. 3). Bird abundance in October was significantly greater than in both January (PerManova, $p < 0.05$; MRPP, $A = 0.12$, $p < 0.01$) and February (PerManova, $p < 0.05$; MRPP, $A = 0.11$, $p < 0.05$). Abundance in November was also significantly greater than in both January (PerManova, $p < 0.01$; MRPP, $A = 0.15$, $p < 0.005$) and February (PerManova, $p < 0.005$; MRPP, $A = 0.18$, $p < 0.005$). There was a general shift from assemblages being dominated by specialist grassland insectivores (such as yellow-breasted pipits and wing-snapping cisticolas) early in the season to dominance by nomadic granivores (such as southern red bishop and cape canary) in the latter part of the season, after most of these insectivorous species had completed breeding and grass seeds become abundant. Finally, bird species assemblages were affected by whether or not an area was burnt in the year of sampling, regardless of grazing pressure (PerManova, $p < 0.05$; MRPP, $A = 0.24$, $p < 0.05$), with overall abundance and the abundance of grassland specialist species being lower if an area was burnt in that year. Overall, the influence of burning over-rode that of grazing in terms of both species richness (Wilcoxon Matched-Pairs Test, $Z = 2.97$, $p < 0.005$) and abundance (Wilcoxon Matched-Pairs Test, $Z = 3.10$, $p < 0.005$), both of which decreased with annual burning. While grazing is rotational on these livestock farms they are grazed all year round but not even in the heavily grazed areas does vegetation biomass get reduced to the extent that burning does and these areas still show vegetation structural growth with grass flowering in late summer. Stocking density plays a role when all four farm sites (high grazing pressure) are compared with all four reserve sites (low grazing

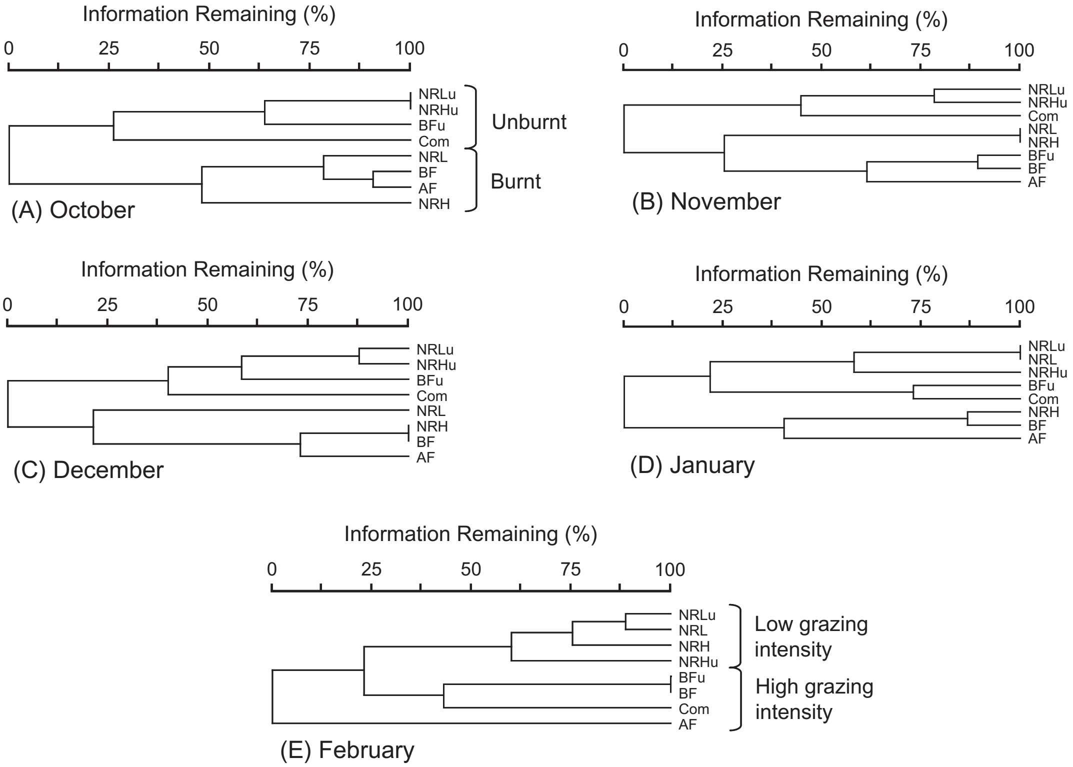

Fig. 3. Cluster analyses showing shifts in the main drivers of bird assemblage structure through the breeding season.

pressure). Birds were almost twice as abundant in the nature reserve as they were on farms (Wilcoxon Matched-Pairs Test, $Z = 3.75$, $p < 0.001$).

Burning drives bird assemblage structure early in the breeding season while stocking density drives late-season assemblage structure (Fig. 3). Early season (October) assemblages were strongly influenced by whether or not a site was burnt. As the season progressed, however, and burnt areas recovered, recovery of the vegetation structure promoted a within-season shift in bird assemblage structure until, in the late part of the growing season (February), differences in bird species assemblages were driven by disturbance through grazing.

Bird species assemblages and species abundances were significantly different between burnt and unburnt sites for all months of the breeding season (MRPP, $A = 0.22$, $p < 0.005$). Thus, if a site was burnt at the beginning of a breeding season (prior to the first bird surveys), this had an overriding influence on bird species assemblage structure for the remainder of that season (Fig. 3).

When burnt and unburnt sites were combined, and grazing management strategies were separated into four levels of stocking density (NRL, NRH, BF, and AF combined with Com) a seasonal structuring of bird species assemblages was evident. In October, all four levels of grazing were significantly different from one another (MRPP $A > 0.09$, $p < 0.05$). By November and December only NRL was significantly different from all other sites (MRPP, $A > 0.14$, $p < 0.05$). By January, NRH and AF + Com were also significantly different from the other sites (MRPP, $A > 0.08$, $p < 0.05$). By the end of February all treatments had differing species assemblages (MRPP, $A > 0.15$, $p < 0.005$). In this month the reserve treatments grouped together, separate from the livestock farms, suggesting that with increasing time since burning, the grazing regime (pressure and possibly the type of grazers) plays an increasingly important role in determining both bird species diversity and community composition (Fig. 4).

Bird species richness on the other hand showed a marked difference only between the seasonal extremes (October vs February – ANOVA, *post hoc* Tukey Test, $p < 0.05$). There were marked differences in overall species richness between NRL and all other sites except Com (ANOVA, *post hoc* Tukey Test, $p < 0.01$), as well as between AF and all reserve sites (ANOVA, *post hoc* Tukey Test, $p < 0.005$).

When considering species-specific responses to disturbance, abundances did not appear to respond strongly to the presence or absence of fire (Fig. 4). Most species showed a preference for the conserved area with a low density of native ungulates (NRL), while a small proportion of species show a preference for disturbed areas (Table 3). Included within the species assemblage that prefers the conserved area are the grassland specialist species.

When a similar analysis was run for functional feeding guilds, habitat preferences were also evident with most guilds showing a preference for the conserved area (NRL) and relatively few favouring disturbed areas. Only six of the 15 functional feeding guilds showed significant responses to disturbance (Table 4).

Grassland birds rely on the structure of the vegetation for foraging, nesting and predator avoidance, but it is uncertain what indices can be derived to provide a rapid assessment of grassland bird species richness and what specific vegetation structural aspects are most important for sustaining a diversity of bird species. Bird species richness increased with increasing vegetation cover and biomass, and decreased with increasing average horizontal vegetation density (Table 5).

To investigate the effect of management treatments on bird species abundance, bird count data were plotted in 2-dimensional ordination space (Fig. 5). On axis 1, sites separated out according to whether or not they were burnt in that year (groups B and C vs groups D and E). On axis 2, the nature reserve areas (A and B) separate out from farmlands (especially C and D, with group E being intermediate between the nature reserve and other farmed sites). Axes 1 and 2 respectively explained 33.42% and 18.90% of the variance in the original distance matrix (total 52.32%).

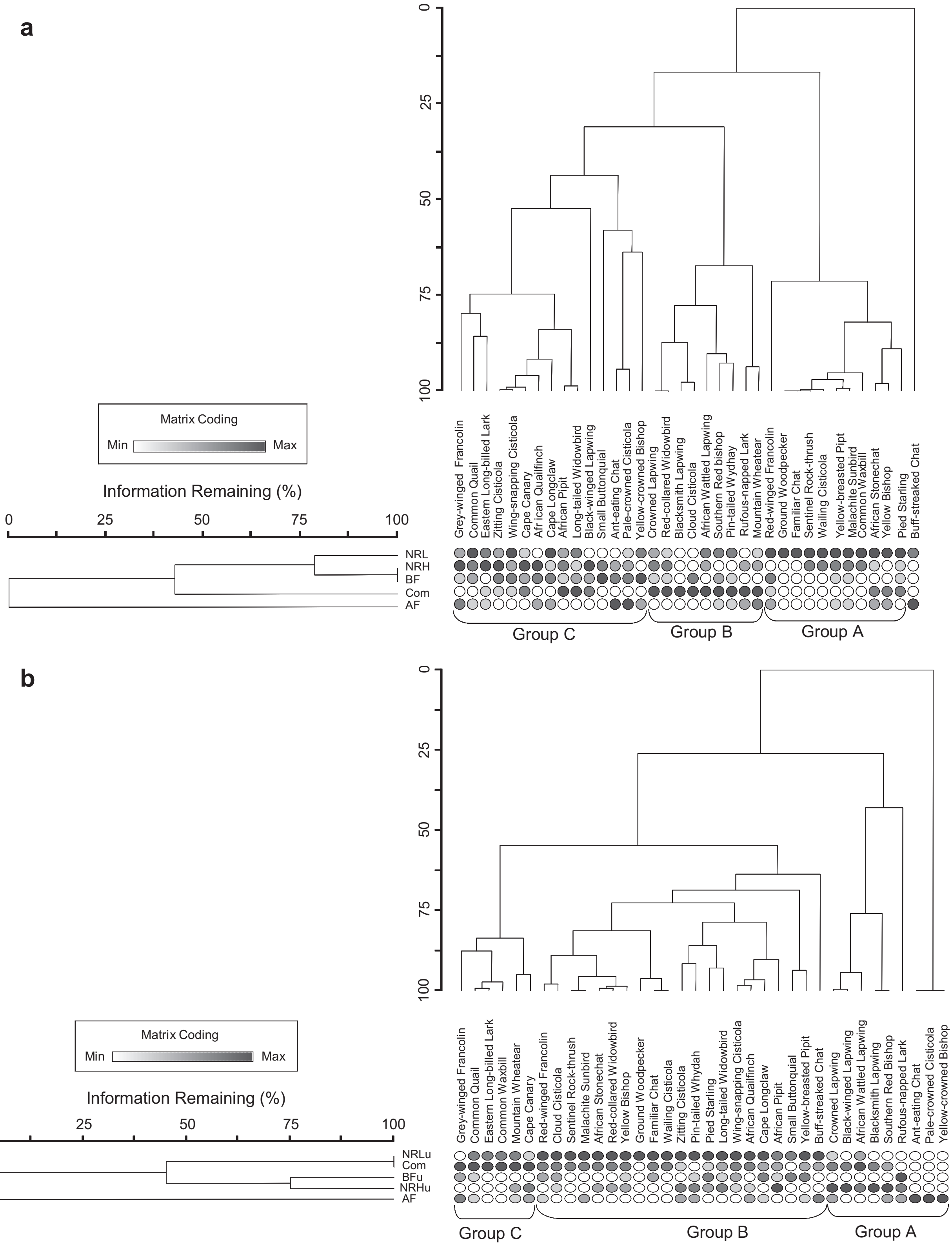

Fig. 4. Bird species assemblages (based on abundance) as a function of whether or not a site was burnt in the focal year: (a) includes only abundance measures from sites that were burnt in that season, while (b) includes only abundance measures from sites that were not burnt in that year. Communal lands and the annually burnt farm were included in both (a) and (b) for comparative purposes (they are both managed in the same way in all years). Groups A, B and C refer to bird species assemblages that show similar abundance in a specific site or group of sites.

4. Discussion

Multiple factors influence the composition of bird assemblages, including disturbance, changes in habitat structure and variation in food availability (Morrison, 1986; Nkwabi et al., 2011). These responses can vary from losses or gains of individual species to entire assemblage shifts (Liversidge, 1962; Wiens, 1974; Folse, 1982; Erdelen, 1984; Knopf et al., 1988; Martin and Possingham, 2005).

Table 3
Grassland associated bird species with site-specific distributions illustrating habitat preference. Scientific names are provided in Appendix 1.

Species	Site	Observed indicator value (IV)[a]	IV from randomized groups		p
			Mean	Std. dev.	
Jackal buzzard	NRLu	37.5	21.5	8.4	0.042
Pallid harrier	NRLu	44.4	18.7	8.4	0.017
Red-winged francolin	NRLu	34.8	22.5	6.0	0.039
Sentinel rock-thrush	NRLu	48.4	20.0	7.4	0.005
Familiar chat	NRLu	70.8	21.1	9.5	0.001
African stonechat	NRLu	39.9	20.7	6.1	0.005
Cloud cisticola	NRLu	35.6	21.2	7.0	0.044
Yellow-breasted pipit	NRLu	36.7	22.4	6.5	0.033
Cape longclaw	NRLu	22.9	17.8	1.9	0.014
Malachite sunbird	NRLu	35.7	19.7	5.5	0.001
Red-collared widowbird	NRLu	51.1	19.9	8.1	0.006
Common quail	NRL	32.4	20.7	4.8	0.015
Ground woodpecker	NRL	40.6	18.7	9.1	0.044
Cinnamon-breasted bunting	NRL	45.0	19.0	9.3	0.038
Gray-winged francolin	NRHu	54.0	23.3	10.2	0.019
Eastern long-billed lark	NRHu	38.9	22.2	4.9	0.000
Mountain wheatear	NRHu	34.8	20.6	5.6	0.018
Cape canary	NRHu	28.4	20.1	2.7	0.006
Banded martin	BFu	30.6	20.1	2.7	0.002
Amur falcon	BF	57.4	29.4	11.7	0.024
Southern bald ibis	AF	51.1	19.0	9.3	0.008
Ant-eating chat	AF	50.0	20.1	8.5	0.010
Bokmakierie	AF	50.0	19.6	9.9	0.023
Black-headed heron	Com	39.5	20.9	8.4	0.036
Blacksmith lapwing	Com	72.3	18.1	11.4	0.006
Cape wagtail	Com	44.3	19.9	9.0	0.020
African pipit	Com	17.6	15.7	1.1	0.040

[a] Indicator values ranging from 0 to 100. A ‘perfect indicator’ scoring 100 is present in all replicates within a site and not present in any replicates in any other sites.

Table 4
Functional guilds (from Hockey et al., 2005) with site-specific distributions illustrating habitat preferences. All the analyzed guilds are represented but only those guilds in bold exhibited significant, habitat-related differences in distribution.

Guild	Site	Observed indicator value (IV)	IV from randomized groups		p
			Mean	S.D.	
Water-associated species	NRLu	29.7	19.2	2.8	0.001
Rocky outcrop insectivores	NRLu	32.0	21.6	3.6	0.010
Insectivores	NRLu	19.7	15.4	1.0	0.000
Nectarivores	NRLu	35.4	18.1	5.6	0.010
Grazers	Com	57.1	16.0	7.9	0.002
Terrestrial insectivores	Com	37.9	20.5	3.7	0.000
Generalists	NRLu	19.4	18.9	2.6	0.405
Snake predators	NRLu	40.0	13.0	9.1	0.102
Rodent & insect predators	NRLu	26.1	19.9	3.6	0.066
Bird predators	NRLu	25.0	15.7	7.3	0.191
Frugivores	NRLu	20.0	20.0	0.3	1.000
Terrestrial omnivores	NRHu	22.7	20.1	3.5	0.224
Scavengers	NRHu	24.8	17.4	8.1	0.169
Granivores	NRHu	20.6	18.5	2.8	0.160
Aerial insectivores	BFu	19.4	18.0	2.0	0.225

Table 5
Percentage vegetation cover, phytomass (derived from DPM measures) and average horizontal density (out of ten original vegetation structural indices) were extracted by Partial Correlation Analysis as performing best at differentiating between the effects of management types on bird species richness. Overall regression results: $F_{3,144} = 11.159$, $R^2 = 0.189$, $p < 0.001$.

	Beta	Tolerance	r^2	t (144)	p-Level
% Veg.	0.361	0.475	0.525	3.316	0.020
DPM	0.335	0.635	0.365	3.561	0.001
AvHorDen	−0.652	0.407	0.593	−5.535	0.000

Some studies of bird assemblage responses to habitat disturbance have been carried out in South Africa (Mentis and Little, 1992; Little and Crowe, 1994; Cameron, 1999; Jansen et al., 1999; Ratcliffe and Crowe, 2001; Little et al., 2005; Fox and Hockey, 2007). To date, however, none of these studies has focused on the direct and relative effects of grazing and burning on grassland fauna and flora.

In terms of the arthropod population on which many grassland birds depend, grazing can lead to decreases in some arthropod orders, including spiders, which in turn can lead to concomitant decreases in the species richness and abundance of grassland insectivores (Dennis et al., 2008). Heavy grazing also leads to decreases in forage palatability, suggesting that high stocking density can also reduce the carrying capacity for livestock (Milchunas et al., 2005).

The arthropod biomass of MHGs was dominated by Orthoptera: these accounted for 78% of the total arthropod biomass throughout the study period. All arthropod taxa declined markedly immediately following a burn (Swengel, 2001; Nkwabi et al., 2011). In this study, overall arthropod biomass increased from early spring

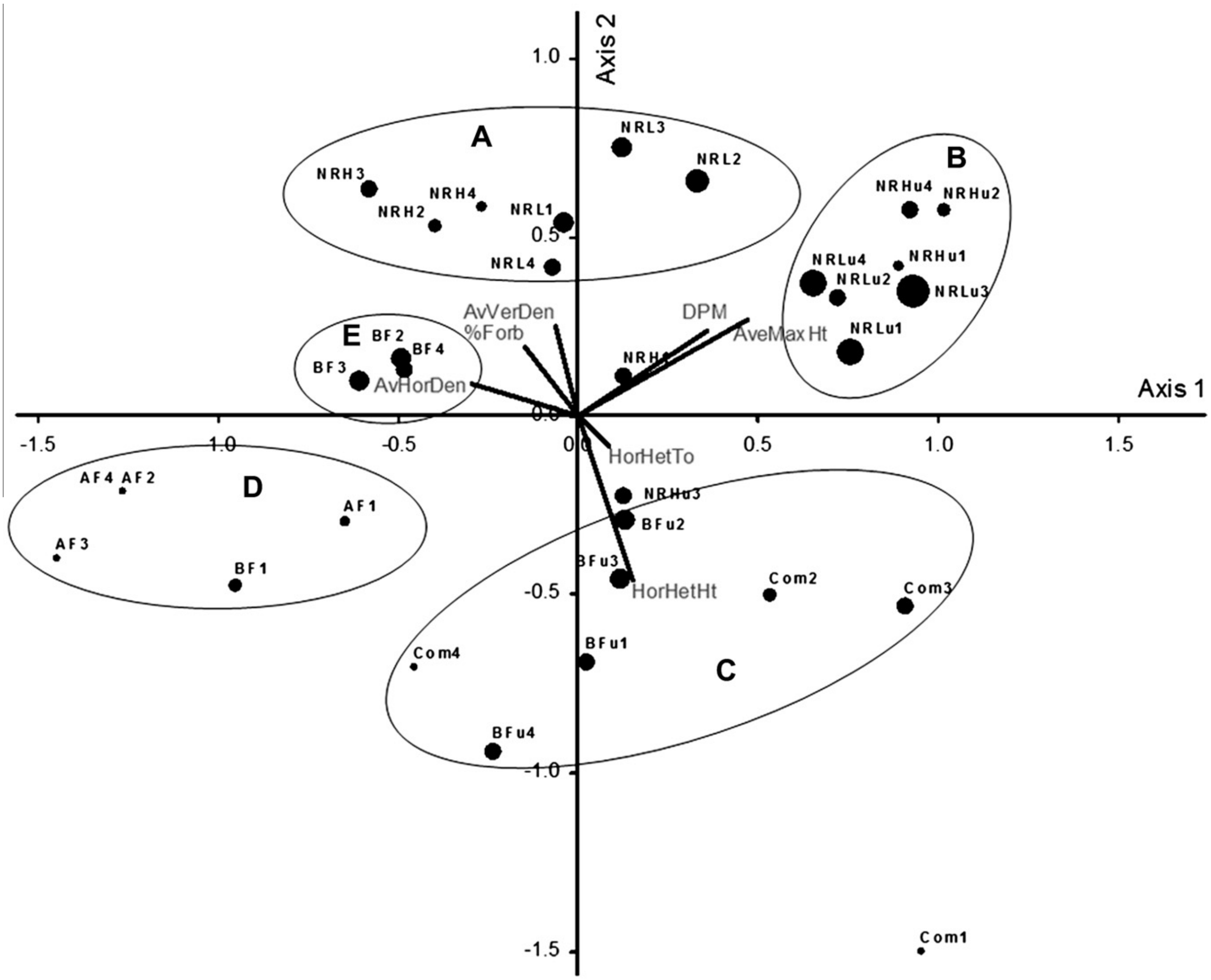

Fig. 5. Non-metric Multi-dimensional Scaling Ordination with ordination space based on bird species counts. Symbol sizes are based on overlaid vegetation biomass values, with larger circles indicating higher vegetation biomass. Axis 1: $p = 0.036$, Axis 2: $p = 0.012$. The influence of vegetation structure on bird assemblage is illustrated as a biplot (lines extending from the center of the graphic), the direction and length of the lines illustrate the strength of the influence of each vegetation structural index on bird assemblages within sites. The groupings A–E were selected subjectively to illustrate the separation of bird assemblages in ordination space.

through to late summer, with the most rapid and substantial increases occurring in sites that were burnt at the start of the current season. This response is a result of grasshopper prevalence in the late summer months in burnt sites, probably explained by their preference for grazing new growth (Swengel, 2001). Livestock stocking density does not appear to have a marked effect on any arthropod order, even though heavy grazing leads to habitat simplification (Swengel, 2001). Vegetation structure, largely controlled by burning, seems to have some effect on arthropod biomass, with vegetation density and arthropod biomass being positively, but weakly, correlated (Table 2). Similarly, forb cover is high soon after burning because large-leaved forbs re-sprout rapidly after fire (Everson et al., 1989). However, as the growing season progresses, grasses become increasingly dominant. The vegetation structural changes referred to here have been written up for publication and are in review (Little et al., in preparation). The non-grasshopper arthropod biomass is dominated by Coleoptera, Hemiptera and Lepidoptera larvae. These groups respond negatively to burning in that season and prefer areas that have remained unburnt for more than a year (Fig. 2).

Bird assemblage structure shifts seasonally. Within sites (regardless of burning or grazing regimes), assemblages at the end of the season differ significantly from those at the start of the season (Fig. 3), but much of this shift may reflect the completion of breeding attempts, with species breeding more successfully becoming increasingly numerically dominant and some species forming flocks. A comparison of time since burning, however, shows very clear differences between sites that were burnt in the current season and those that were not, especially at the start of the breeding season. As the summer season progresses, however, the importance of stocking density increases and, by late summer, grazing has a strong influence on bird assemblage structure (Fig. 3). Derner et al. (2009) suggest that domestic livestock can be manipulated as ecosystem engineers for the benefit of avian communities. However, if grazing and burning are treated as separate extrinsic forces and compared throughout the season, burning frequency overrides stocking density as the main driver of species assemblage structure. Contrary to what was found by Nkwabi et al. (2011) in the Serengeti, both bird abundance and species richness were higher in all unburnt sites relative to sites that had been burnt in that season. A distinct cluster of bird species showed sensitivity to both stocking density and burning frequency (Group A in Fig. 4a and Group B in Fig. 4b). These species have high indicator values (Table 3) specific to the NRLu, suggesting that they are the species most prone to disturbance. Within this assemblage of species, the yellow-breasted pipit (*Anthus chloris*) is regionally and globally *Vulnerable* (Barnes, 2000) and the pallid harrier (*Circus macrourus*) is globally *Near-threatened* (Barnes, 2000).

Another distinct bird assemblage exploits disturbed areas. These species appear in group A of Fig. 5b and include species that are characteristic of sites AF and Com (Fig. 5). While the majority of the species that benefit from disturbance are common and widespread, the southern bald ibis (*Geronticus calvus*) (recorded previously as favouring disturbed areas – Jansen et al., 1999) is regionally and globally *Vulnerable* (Barnes, 2000). Overall, however, these farming areas support a lower species richness and abundance of birds than does the conserved area and lack many threatened and specialist species. However, the disproportionate use of farmed areas by even one threatened taxon highlights the need for a large-scale mosaic of habitat management if the focus is to conserve the maximum number of species (Söderström et al., 2001; Fuhlendorf and Engle, 2004; Coppedge et al., 2008). This mosaic can be sustained and supplemented with the use of large fire-breaks as these have been shown to have little impact on the floral component as well as the soil integrity (O'Connor et al., 2004). These fire-breaks act as annually burnt patches and in conjunction with a paddocks of biennially burnt land create the desired mosaic of habitat management.

Even though not all avian functional guilds were significantly influenced by management practices, it is apparent that the majority (71%) of functional groups are concentrated in the reserve sites and, of these, 75% show preference for the conservatively managed (lower stocking density) part of the reserve. In all management types, rocky outcrops provide refuge habitat for a diversity of plants, arthropods and reptiles, because they are a) protected from both fire and grazing (Jansen et al., 1999) and b) provide nesting and feeding habitat for some birds (Milchunas and Noy-Meir, 2004). In the MHGs, nectarivores require intact rocky outcrops for feeding purposes because flowering plants (such as *Leonotis* spp.) are confined to these areas. The grassland specialist red-winged francolin (*Scleroptila levaillantiil)* is also confined to these rocky outcrop habitats because surrounding grazed grasslands are ecologically unavailable due to the short sward height and depletion of food plants. Further work quantifying the effectiveness of these areas as refuges is recommended. Water-associated species are confined to intact wetlands (for which the nature reserve in this study has been recognized as a Ramsar site by the International Convention on Wetlands): these include birds such as flufftails, aquatic cisticolas and warblers. Grassland-nesting insectivorous passerines are sensitive to habitat disturbance resulting in their preference for conserved areas, while terrestrial insectivores (lapwings and thick-knees) and grazers (anatids) prefer open and short-grass areas for foraging, which can lead to disturbed areas being artificially species rich.

Shifts in bird species richness and diversity are driven (at least in part) by vegetation structural change, including phytomass, cover and horizontal density (Erdelen, 1984; Martin and Possingham, 2005; Wiens, 1974; Wiens and Rotenberry, 1981). Phytomass is inversely correlated with stocking density, but this is not the only disturbance effect that drives bird species assemblages. In grasslands, where nesting birds require vegetation cover in which to conceal their nests, phytomass is critical for territory selection and effective reproduction (Batáry et al., 2006). Average horizontal density of vegetation is negatively correlated with bird species richness: this is explained by the structure of growing grasses. In areas that are not heavily grazed, tuft-forming grasses produce a canopy in the later seasonal growth stages. This results in low vegetation density close to the ground (but cover above), providing suitable nesting habitat. Intensive grazing results in a more lawn-like structure with little opportunity for nest concealment.

In conclusion, it is apparent that fire and grazing interplay as factors influencing both bird and arthropod diversity (Fuhlendorf and Engle, 2004; Engle et al., 2008; Fuhlendorf et al., 2008). In moist highland grasslands, however, the influence of fire frequency generally overrides that of stocking density in influencing both arthropod and bird assemblage structures: this is clearly illustrated by the depauperate faunas that characterize annually burnt areas and conversely fire suppression results in moribund grasslands also reducing species diversity (Gregory et al., 2010). Vegetation structural indices are important for predicting both bird and arthropod species richness, as has been shown previously (Wiens, 1974; Wiens and Rotenberry, 1981; Erdelen, 1984; Martin and Possingham, 2005). However, focusing on bird diversity and functional guild richness yields more relevant information to guide conservation action. Thus, from the results of this study, it is recommended that bird counts can (as well as vegetation and arthropod diversity) be used to assess grassland functional integrity. Of the three taxonomic groups, however, birds are the easiest to count and the most responsive to disturbance.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.09.017.

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