The loss of vegetation cover has distinct but short-term impact on multiple vertebrate taxa in a grassland ecosystem

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A B S T R A C T

Vegetation cover in grasslands typically fluctuates over time, for example, declining with grazing and disappearing entirely with burning. This temporal change in vegetation cover may impact the composition of vertebrate communities by altering habitats or perceived predation pressure. We manipulated vegetation cover in a high-elevation (ca. 1240–1500 m above sea level) grassland ecosystem and measured its effect on the community structure of birds and small mammals using a Before-After-Control-Impact study design. We established 12 plots (each plot 100 × 100 m) at Telperion Nature Reserve, Mpumalanga, South Africa, which were assigned to three treatments: mowed with cut grass left in situ (mowed-litter), mowed with cut grass cleared (mowed-cleared), and non-mowed (control). We sampled birds and small mammals over three sampling periods: before the treatment (August 2019), immediately after the treatment (October 2019), and three months after treatment (January 2020). We used point counts and Sherman live traps to surveys birds and small mammals, respectively. We observed a total of 2801 individuals of 38 species of birds and 98 individuals of eight species of small mammals. Species richness and diversity of small mammals and birds was significantly higher in the non-mowed plots compared with the mowed plots. Birds also showed differences in community composition in mowed and non-mowed treatments immediately after mowing but these differences disappeared three months after mowing, whereas small mammal composition did not differ before and after mowing. The best performing generalized additive model showed that vegetation biomass had a significant positive influence on bird species richness but not rodents. On the other hand, diversity of both taxa was significantly influenced by grass biomass. Our study suggests that loss of vegetation cover in grasslands has significant short-term effects on birds and small mammals, but that these faunal communities rapidly return to pre-loss conditions within a few months. Hence controlled vegetation removal (e.g. mowing) could be considered an appropriate tool for managing these high-elevation grasslands.

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1. Introduction

Grasslands cover approximately 40.5% of the planet's total land area and offer ecological, environmental, and economic functions (Gibson, 2009; Suttie et al., 2005; White et al., 2000). Grasslands are known for their high level of biodiversity and endemism while playing crucial roles in carbon sequestration and storage, water purification, erosion control, and acting as a food source for over a billion people through agriculture and livestock production (Naidoo et al., 2013; Reyers et al., 2005; Skowno et al., 2019). Despite these benefits, grasslands continue to be destroyed globally, mainly due to habitat transformation, which itself is one of the leading drivers of biodiversity loss (Ries et al., 2004). Such transformations in grasslands are largely attributed to anthropogenic activities which include agriculture, urbanization and mining and are also attributed to climate change (Gang et al., 2014).

The grassland biome in southern Africa occurs within South Africa, Lesotho and Eswatini comprising 28% of the land surface (Brown and Bezuidenhout, 2020). It is estimated that between 60% and 80% of this biome has been irreversibly transformed by anthropogenic activities such as urbanization, rural settlements, agriculture, mining, and forestry (Carbutt et al., 2011; Coetzee, 2012; Neke and Du Plessis, 2004). These activities result in the total destruction of the natural grassland vegetation, alter the soil profile and nutrient content causing habitat and natural resource pathway loss (Brown and Bezuidenhout, 2020). With just 2.3% of the grassland biome formally protected in South Africa, it is in need of conservation attention (Coetzee, 2012), and has been listed as a critically endangered ecosystem (Neke and Du Plessis, 2004; Olson and Dinerstein, 1998; Reyers et al., 2001).

Fire is a natural ecological factor in grasslands and is vital for the maintenance of grassland vegetation in terms of structure and species composition (Brown and Bezuidenhout, 2020). However, incorrect burning strategies and overgrazing of grasslands bring about changes in vegetation structure and species composition, negatively affecting the biodiversity occurring in those habitats (Davidson et al., 2010; Gumbi et al., 2018; Hobbs and Huenneke, 1992; Napoletano et al., 2017). Previous studies have demonstrated negative impacts on biodiversity through removal of vegetation biomass leading to the loss of species and altered community composition, and resulting in the dominance of fire tolerant and grazing tolerant species (Bond et al., 2005; Bond and Keeley, 2005; Sternberg et al., 2000). These two management practices may also lead to the homogenization of habitats, resulting in a loss of biodiversity and ecosystem functioning (Fuhlendorf et al., 2006; McCleery et al., 2018). The changes in habitat structure and reduced biodiversity resulting from the removal of vegetation can be accompanied by loss of food sources and roost sites for some species of fauna together with increases in soil temperature and water loss. Such change in habitat structure may alter the distribution and abundance of animals, affecting community structure at different spatial scales (Davidson et al., 2010; Hobbs and Huenneke, 1992; Mohammadi, 2010; Monadjem, 2005).

Birds and small mammals are widespread and easily quantified components of grasslands, making them suitable model groups for
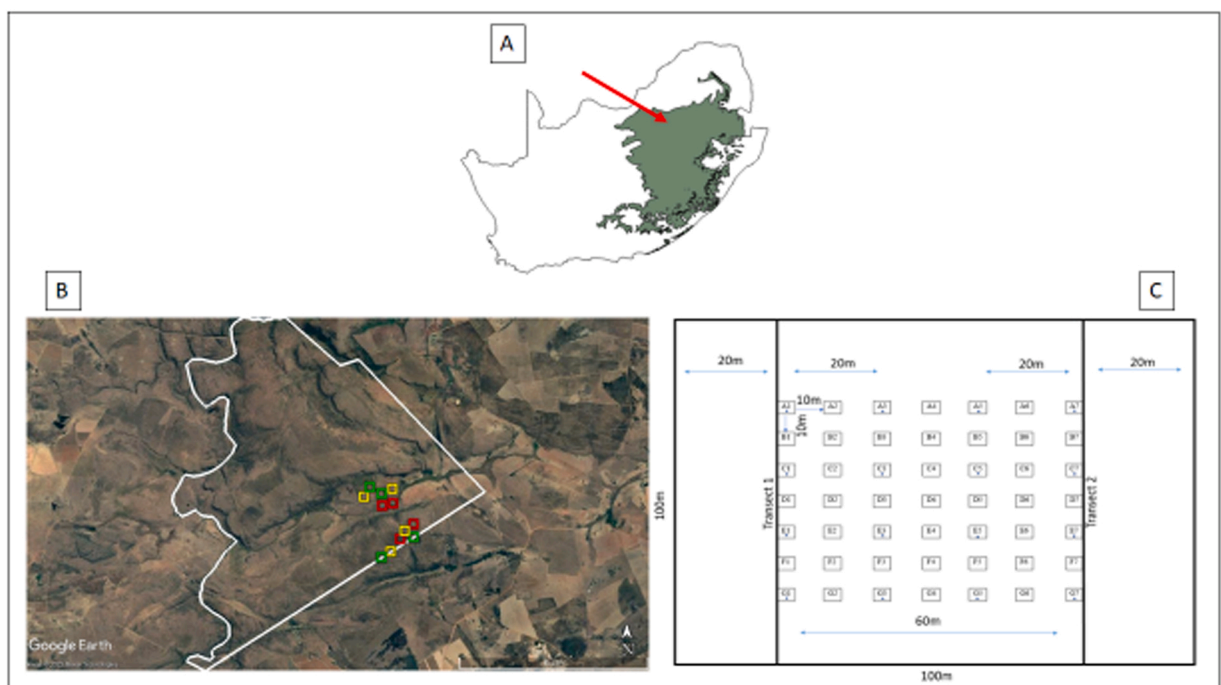
Fig. 1. Presentation of study area showing: (A) the distribution of the grassland biome in South Africa (green shading) with a red arrow pointing at the location of Telperion Nature Reserve; (B) the boundary of Telperion Nature Reserve marked in white with sampling plots shown as squares: non-mowed (red), mowed-litter (yellow), and mowed-cleared (green); and (C) the layout of the transects and Sherman traps in each plot, with the marked squares representing small mammal trapping stations and the squares with stars inside representing trapping stations where vegetation sampling was done.

studying the response of vertebrates to vegetation change. Many species of rodents utilize grass cover to escape predation (Banasiak and Shrader, 2016; Loggins et al., 2019; LoGiudice and Ostfeld, 2002), while many bird species prefer low grass cover to allow them to improve visibility and avoid predators (Lima, 1990). Hence, birds and rodents may show opposing preferences to vegetation cover, making it important to include both of these groups in studies that manipulate vegetation cover (Lima, 1990; Slade and Crain, 2006).

Grasslands have important uses around the world. For example, grasslands act as an important source of meat and milk (Boval and Dixon, 2012; Egoh et al., 2011). Grazing forms an important part of grasslands with both livestock and wild game being the most common grazers in these biomes (Carlier et al., 2009). Grasslands also act as providers of honey (as bees also occur in these biomes) and are also used for game hunting, and extraction of medicinal plants and fruits. Williams et al. (2000) estimated that 30% of the plants used and sold as traditional medicine grow in grasslands. Grasses in grasslands are also cut and used for thatching, making handcrafts like baskets and mats (Williams et al., 2000). Grasses are also cut and removed through mowing and burning as a grassland maintenance strategy to maintain grasses at low successional stages, to ensure sustenance of patches with high palatable grasses for wild grazers and to reduce woody encroachment by limiting tree recruitment from reaching maturity (Lemen and Clausen, 1984; Norton-Griffiths, 1979; Salvatori et al., 2001). The different land uses such as grazing in this biome tend to impact vegetation parameters such as litter, bare ground, and shrub cover which may have different impacts on grassland species.

We used a BACI (before-after-control-impact) study design (Castro et al., 2021; Gigliotti et al., 2022) to examine the effects of mowing on bird and small mammal communities occurring in a high-elevation grassland ecosystem, used mainly for wildlife grazing, in South Africa. The areas neighboring the study site are used for livestock rearing and crop farming. Our objectives were to: (1) compare species richness and diversity of birds and small mammals occurring in mowed and non-mowed plots, before and after mowing; (2) compare community composition of birds and small mammals in mowed and non-mowed plots, before and after mowing; and (3) identify important vegetation parameters influencing the structure of bird and small mammal communities. We hypothesized that species richness, diversity and composition of both taxa would be higher in non-mowed plots as we assumed that there would be more food resources and a reduced predation risk associated with these areas. We also hypothesized that grass cover would be the most important vegetation parameter influencing the structure of bird and small mammal communities as it might offer shelter from predators for both birds and small mammals.

2. Methods

2.1. Study area

The study was conducted at Telperion Nature Reserve, a privately owned protected area located approximately 24 km north-east of Bronkhorstspruit on the border of Gauteng and Mpumalanga provinces of South Africa (Fig. 1A and B). The reserve is located between latitudes 25.63° S and 25.75° S and longitudes 29.05° E and 28.92° E, and covers an area of approximately 11,000 ha (Gumbi et al., 2018). The reserve is bordered by privately owned cattle ranches to the north and south, and by the Ezemvelo Nature Reserve to the west. Farmlands surrounding the reserve practice mainly cattle production, game ranching and crop agriculture (Chantal Vinisia et al., 2006; Coetzee, 2012). Elevation varies from 1240 m to 1500 m above sea level. January is the warmest month with daily mean temperatures of 26.1 °C in summer whilst July is the coolest month with daily mean temperatures of 14.6 °C, with seasonal frost occurring during winter (Coetzee, 2012). The region has a distinct wet and dry season with most of the annual rainfall (mean 625 mm) falling during the summer (Gumbi et al., 2018). Telperion Nature Reserve falls within the South African grassland biome and its vegetation type is the Rand Highveld Grassland (Mucina et al., 2006), which is typically found between 1500 m and 2100 m above sea level. This region is considered transitional between the grassland and savanna biomes (Mucina and Rutherford, 2006).

2.2. Sampling design

We sampled birds and small mammals in 12 plots to cover the range of heterogeneity of the grasslands present at Telperion. We randomly selected these 12 plots, each measuring 100 × 100 m. Three of the plots had grass cover manipulated by mowing of grass and the litter left in situ (mowed-litter), while another three plots had grass mowed and the litter was cleared from the plots (mowed-cleared), and the other three were control plots whose grass was not manipulated (non-mowed) (Fig. 1B). Each plot was at least 200 m from the closest neighboring plot, to reduce the movement of small mammals and birds between plots (Dunn et al., 2006; Monadjem and Perrin, 2003). We mowed grass in the manipulated plots using a rotary cutter mounted on a tractor and raked plots by hand using normal garden rakes. We surveyed birds and small mammals during three sampling periods, starting with a pre-treatment period (Pre-T) conducted in August and September 2018 prior to any manipulations of the vegetation. The second sampling period, hereafter referred to as the 'immediate post treatment' (IPT) period, was conducted in October and November 2018 immediately after mowing and raking of the treatment plots. The final sampling period, hereafter referred to as the 'late post treatment' (LPT) period, was conducted in January and February 2019 two months after the vegetation manipulations.

2.3. Capture of small mammals

At each plot, we set up 49 trap stations arranged in a 7 × 7 configuration with traps 10 m apart (Fig. 1C). We employed one Sherman live trap (7.6 × 9.5 × 30.5 cm, H.B. Sherman Live Traps. Inc, Tallahassee, Florida) at each station for the capture of small mammals. We carefully placed each trap and covered it with vegetation to protect captured animals from excessive heat. We trapped at each plot for four consecutive nights during each of the three sampling periods.

We used a mixture of oats and peanut butter as bait and checked traps in the early morning commencing at sunrise. We processed captured animals at the station where they were trapped. We identified captured animals using Monadjem et al. (2015) and then marked them using uniquely-numbered ear tags. We weighed the captured animals using a Pesola spring scale and took standard museum measurements including head-body, tail, ear, and hindfoot length using a Vernier caliper. The animal was then released unharmed at the point of capture. The ethics committee for the use of animals from the University of Swaziland approved the protocols used in this study.

2.4. Bird surveys

Birds occurring in very low densities at our study site and the elusive nature of some of the grassland birds, especially during the dry season in the per-treatment sampling period, made them even less detectable. As a result we surveyed birds using the line transect method to cover as much of the plot as possible (Bazzi et al., 2015). At each of the 12 plots, we established two parallel transects that ran from one end of the plot to the opposite end such that each transect was 100 m in length, and each of these transects was placed 20 m away from the other two perpendicular sides of the plots (Fig. 1C). Birds were counted by the same person (Z. D. Bhembe), who spent 5 min walking each 100 m transect and recorded every bird seen or heard within a 20 m distance on either side of the transect. To avoid double counting, we closely observed any flushed birds that were seen leaving the transect to note whether they returned or not. Furthermore, birds that flew into the transect from beyond, and those that flew over the transect, were not recorded. The observer made sure to walk carefully and quietly to avoid flushing birds that were far ahead in the transect. Additionally, by noting the position and movement of birds that were counted in one transect, they could be identified and not recorded in the next transect on the same plot. This was possible because of the low densities of birds in our study area, where we typically only recorded one or two birds per transect.

Bird counts were conducted over a duration of one-month per sampling period, with six plots surveyed per day. Bird and small mammal surveys were running concurrently, so to avoid disturbances between the groups, six consecutive days were spent surveying the same six plots for birds while small mammals were sampled on the remaining six plots. Then after six days the groups would swap plots and the surveys would go on for another 6 days. This process was repeated twice such that we surveyed each plot for birds twelve times in total per period. Since six plots were surveyed per day, then a cycle of six days was followed where the plot that was surveyed first (at sunrise) was subsequently surveyed last (around mid-morning) the next morning, and the plot that was surveyed second the previous morning was surveyed first the next morning. The cycle was repeated so that all plots were surveyed twice per phase of the morning per sampling period.

2.5. Vegetation sampling

At each plot, we selected 16 small mammal trapping stations (four stations in four rows) for vegetation sampling, which were the first, third, fifth, and seventh stations in which rodents were trapped (Fig. 1C). At each of these stations, a 1 m × 1 m quadrat was randomly placed, and the following habitat variables were estimated as the proportion of the quadrat that each variable covered, which was recorded as a percentage: grass cover (grasses covering the ground), forb cover (non woody herbaceous plants which are not grasses), shrub cover (small woody plants which are not trees), bare ground (patches of the ground without any vegetation), litter cover (decaying leaves and grasses on the ground) and rock cover (patches of the ground covered by rocks). In addition, grass biomass was measured using a disk-pasture meter (Bransby and Tainton, 1977; Trollope and Potgieter, 1986).

2.6. Data analysis

We presented a visual representation of species richness and diversity recorded across the study from the three treatments. We then compared species richness and diversity between treatments in the different sampling periods and confirmed the habitat variables that significantly influenced animal communities occurring in the different plots. In order to visually present the summary of the accumulation of species richness and diversity recorded across the study, we used rarefaction and extrapolation curves for Hill numbers in the iNEXT package (Hsieh et al., 2016b). Hill numbers are mathematically unified group of diversity indices which only differ among themselves only by an exponent q and they incorporate relative abundance and species richness (Chao et al., 2014). We used rarefaction and extrapolation of Hill numbers because it accounts for differences in sample size when comparing species diversity across multiple assemblages (Chao et al., 2014). Species richness, Shannon diversity, and Simpson diversity are represented by $q = 0$, $q = 1$, $q = 2$, respectively, where q is a parameter which determines the measures' sensitivity to species relative abundances or frequencies (Chao et al., 2014; Hsieh et al., 2016a).

We performed a two-way analysis of variance (2-way ANOVA), to test for significant differences in habitat variables in the treatments between the three samplings periods and presented the p-values. We calculated species richness as the total number of species recorded in each plot and species diversity was calculated using Shannon-Wiener diversity index in the R package Vegan (Oksanen et al., 2019). Generalized Additive Models (GAM), that do not assume any specific form of relationship between response and explanatory variables (Zuur et al., 2009), were then run to compare species richness and diversity between treatments in the different sampling periods and confirm the habitat variables that significantly influence animal communities occurring in the different plots, using the package "gam", models with the highest R^2 were selected as the best performing models (Hastie, 2020). We then plotted significant habitat variables in a linear model to visualize their influence bird and small mammal communities.

We also tested whether community structure of either birds or small mammals were significantly associated with vegetation

parameters. For a visual representation of community structure of birds and small mammals, we employed non-metric multidimensional scaling (NMDS) by calculating Bray Curtis similarities using the function 'metaMDS' in the 'vegan' package (Oksanen et al., 2020). The stress value of the ordination was used to determine the reliability of the NMDS; a stress value of less than 0.2 shows good conformity in the data (Clarke, 1993). Ellipses were calculated with function "VeganCovEllipse" which was calculated using Vegan package in R, ellipses indicated 95% confidence intervals fitted into spatial ordination. An analysis of similarities (ANOSIM) was used to determine whether there were significant differences in community structure of birds and small mammals with regards to the vegetation. We ran all statistical analyses in version 4.0.4 (2021/02/15) of the program R (R. D. C. T., 2018).

3. Results

We recorded a total of 2801 individuals of 38 species belonging to 18 families of birds and a total of 98 individuals of small mammals belonging to two families of the order Rodentia and one family of the order Macroscelidea. For both birds and small mammals, we recorded the highest number of species in the non-mowed plots with 34 and 7 species recorded, respectively (Table 1). *Gerbilliscus leucogaster* was the most abundant small mammal species followed by *Dendromus melanotis* (Table 1). With the exception of

Table 1
The number of bird and small mammal species and individuals recorded in non-mowed, mowed-litter, and mowed-cleared treatments combined across all three periods. The species are shown in descending order of total abundance.

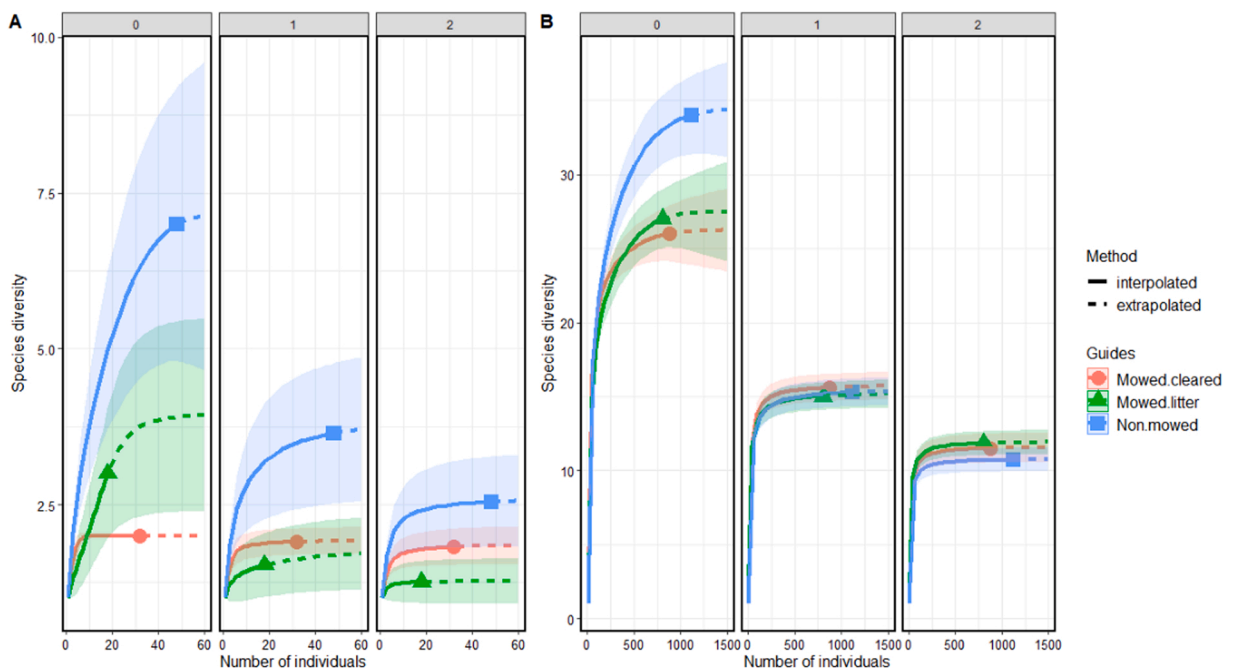| Species	Non-mowed	Mowed-litter	Mowed- cleared	Total
Birds				
Cisticola textrix	192	104	111	*407*
Anthus cinnamomeus	103	111	144	*358*
Cisticola aridulus	190	72	40	*302*
Riparia cincta	80	105	114	*299*
Ortygospiza atricollis	44	68	98	*210*
Cisticola juncidis	103	53	28	*184*
Mirafra fasciolata	62	40	40	*142*
Anthus similis	32	42	37	*111*
Mirafra africana	52	26	31	*109*
Euplectes orix	46	33	22	*101*
Macronyx capensis	45	21	19	*85*
Anthus vaalensis	21	17	34	*72*
Delichon urbicum	22	19	25	*66*
Myrmecocichla aethiops	6	35	20	*61*
Saxicola torquatus	17	9	27	*53*
Euplectes progne	20	6	12	*38*
Anthus eucophrys	3	15	17	*35*
Motacilla capensis	12	5	15	*32*
Coturnix coturnix	19	2	3	*24*
Estrilda astrild	7	3	10	*20*
Vanellus coronatus	2	0	14	*16*
Hirundo rustica	1	8	7	*16*
Cisticola ayresii	2	2	4	*8*
Hirundo albigularis	6	1	0	*7*
Bostrychia hagedash	6	0	0	*6*
Peliperdix coqui	4	2	0	*6*
Scleroptila levaillantii	5	1	0	*6*
Numida meleagris	3	0	2	*5*
Cisticola tinniens	3	0	0	*3*
Pternistis natalensis	3	0	0	*3*
Pternistis swainsonii	3	0	0	*3*
Vidua macroura	1	0	2	*3*
Guttera pucherani	0	3	0	*3*
Bubulcus ibis	2	0	0	*2*
Burhinus vermiculatus	0	2	0	*2*
Eupodotis afraoides	2	0	0	*2*
Circaetus pectoralis	0	0	1	*1*
Total	*1119*	*805*	*877*	*2801*
Small mammals				
Gerbilliscus leucogaster	28	16	21	*65*
Dendromus melanotis	10	1	11	*22*
Mus minutoides	3	0	0	*3*
Mastomys natalensis	2	0	0	*2*
Steatomys pratensis	2	0	0	*2*
Elephantulus myurus	2	0	0	*2*
Gerbilliscus brantsii	1	0	0	*1*
Otomys auratus	0	1	0	*1*
Total	*48*	*18*	*32*	*98*

a single capture of *Otomys auratus* in a mowed-litter plot, the remaining small mammal species were recorded only in non-mowed plots, and their numeric contribution towards total rodent numbers was low (Table 1). Similarly, in birds, with the exception of one species, *Circaetus pectoralis*, all bird species recorded in the IPT period were recorded at least once in non-mowed plots. However, the total number of individuals of each bird species recorded differed significantly between treatments.

Rarefaction curves of treatment study plots generally reached an asymptote, indicating that estimates of species richness and diversity of both taxa were more or less complete, and communities were well sampled (Fig. 2 A and B). There was also considerable variation in the Hill numbers of rodents, where visibly higher species numbers were recorded in the non-mowed plots than the mowed plots, while birds showed relatively similar effective species numbers in species richness and diversity.

Mowing had a significant negative impact on species richness of birds and small mammals. Species richness was similar on all plots before mowing, however, following mowing, it was higher in the non-mowed than the mowed plots. This difference was reduced over time so that by three months post mowing, species richness was again similar across all plots (Fig. 3A and B). For birds, there was a significant interaction between treatment and sampling period, with species richness higher in non-mowed than mowed-cleared plots in the immediate post treatment sampling period (p = 0.000276, Table 2). Small mammals showed a similar response, except that the interaction was significant for both non-mowed compared with mowed-cleared and non-mowed compared with mowed-litter (p = 0.00316 and p = 0.04841, respectively, Table 3). In addition, the interaction between treatment and period for non-mowed and mowed-cleared plots in the period three months after treatment was significant, showing that small mammal species richness was still higher in the non-mowed plots (p = 0.00949) (Table 3).

Using abundance-based rarefaction and extrapolation curves for Hill numbers (i.e., Hill numbers for q = 0, 1, 2), we showed visually higher small mammal and bird diversity in the non-mowed than in the mowed plots (Fig. 2A and B). Using GAMs we found that small mammal and bird species diversity was similar between non-mowed and mowed plots in the pre-treatment's period (Fig. 3C and D). However, there was a significant interaction between treatment and sampling period, with small mammal and bird diversity higher in non-mowed than in mowed-cleared plots in the immediate post treatment sampling period (p = 0.049227 and p = 0.03293, respectively), non-mowed and mowed-litter plots did not show any significant difference in diversity for both taxa (Tables 4 and 5). Similar to species richness, the difference in diversity across all plots was reduced over time so that by three months post mowing, small mammal and bird diversity was again similar across all plots (Fig. 3C and D).

Study plots showed significant differences in vegetation structure between treatments and sampling periods, with all measured vegetation variables showing significant differences between plots and sampling periods. (Table 6). Only grass biomass and forb cover were significantly associated with bird species richness, with a p value of 0.01331 and 0.00728 respectively. None of the other environmental variables were significantly associated with bird species richness. A linear plot of the two variables against species richness showed a positive relationship for grass biomass (Fig. 4A), and a negative one for forb cover (Fig. 4B). With regards to small mammal species richness, based on the best GAM, none of the environmental variables were significantly associated with small mammal species richness and hence a linear plot was not presented. However, it is worth noting that grass biomass and forb cover

Fig. 2. Rarefaction (solid lines) and extrapolation (dashed lines) curves for (A) small mammals and (B) birds based on Hill numbers (q = 0, 1, 2) for non-mowed, mowed-litter and mowed-cleared plots in a grassland ecosystem, where q = 0 refers to species richness, q = 1 to Shannon's diversity, and q = 2 to Simpson's diversity, respectively. The 95% confidence intervals are shown by the gray shading.
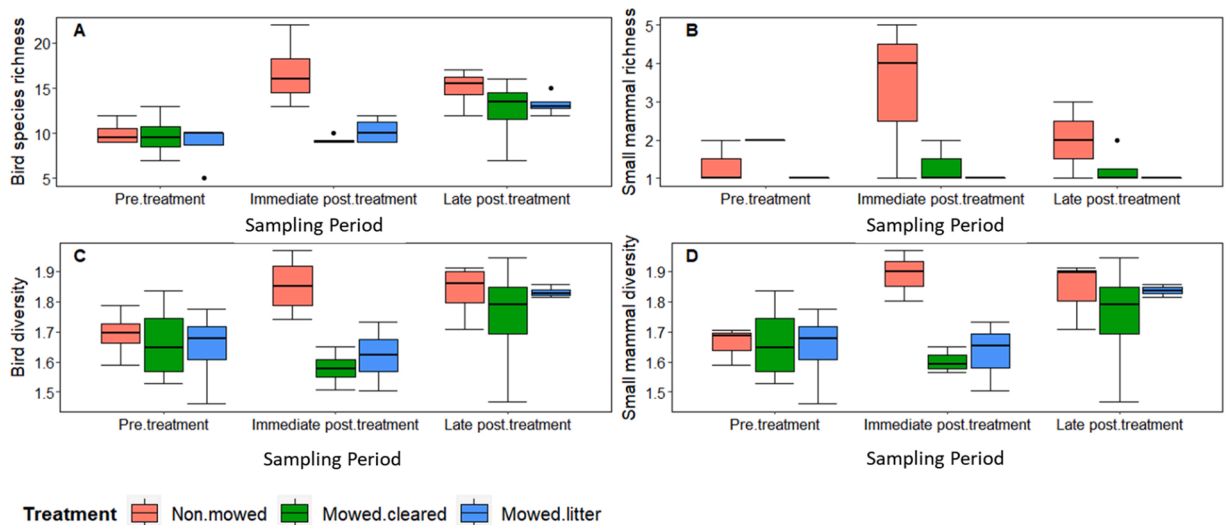
Fig. 3. Boxplots of species richness of (A) birds, and (B) small mammals and diversity of (C) birds, and (D) small mammals in non-mowed, mowed-cleared and mowed-litter plots in the pre-treatment (Pre-T), immediate post treatment (IPT) and late post treatment (LPT) sampling periods.

Table 2
Results of generalized additive models (GAM) comparing bird species richness in non-mowed (baseline), mowed-litter and mowed-cleared plots in the pre-treatment (Pre-T, baseline), immediate post treatment (IPT) and late post treatment (LPT) periods.

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	2.25277	0.07567	29.77	< 2e-16***
TreatmentMowed.cleared	0.05104	0.11535	0.443	0.662123
TreatmentMowed.litter	-0.1866	0.10817	-1.725	0.097509.
PeriodIPT	0.47791	0.10001	4.779	7.48e-05***
PeriodLPT	0.44552	0.10453	4.262	0.004774**
TreatmentMowed.cleared:PeriodIPT	-0.49049	0.115755	-3.113	0.000276***
TreatmentMowed.litter:PeriodIPT	-0.1889	0.14803	-0.276	0.214249
TreatmentMowed.cleared:PeriodLPT	-0.18809	0.01575	-1.194	0.244195
TreatmentMowed.litter:PeriodLPT	0.07598	0.14998	0.507	0.617105

Table 3
Results of generalized additive models (GAM) comparing small mammal species richness in non-mowed (baseline), mowed-litter and mowed-cleared plots in the pre-treatment (Pre-T, baseline), immediate post treatment (IPT) and late post treatment (LPT) periods.

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	0.2617	0.2067	1.266	0.22258
TreatmentMowed.cleared	0.4491	0.2794	1.607	0.12637
TreatmentMowed.litter	-0.3109	0.2882	-1.079	0.29574
PeriodIPT	0.7696	0.2125	3.622	0.00211**
PeriodLPT	0.3567	0.2144	1.664	0.11449
TreatmentMowed.cleared:PeriodIPT	-1.1992	0.3492	-3.434	0.00316**
TreatmentMowed.litter:PeriodIPT	-0.6899	0.3245	-2.928	0.04841*
TreatmentMowed.cleared:PeriodLPT	-0.8277	0.2827	-2.928	0.00940**
TreatmentMowed.litter:PeriodLPT	-0.3237	0.3379	-0.958	0.35144

showed significant differences between the three treatments and also between the three sampling periods.

On the other hand, both bird and small mammal diversity was significantly influenced by biomass ($p = 0.00706$ and $p = 0.03612$, respectively), forb cover ($p < 0.0001$ and $p = 0.000121$, respectively) and litter cover ($p = 0.01880$ and 0.044257, respectively). Linear plots of these variables against diversity showed a positive relationship with biomass and a negative relationship with litter and forb cover (Fig. 5).

A non-metric multi-dimensional scaling (NMDS, stress = 0.17) analysis showed that the composition of bird communities over-lapped extensively between treatments across the three sampling periods (Fig. 6). However, an analysis of similarity (ANOSIM) indicated that treatments differed significantly from each other in species composition ($R = 0.18$, $p = 0.01$) during the immediate post-treatment (IPT) period (Fig. 6B), whereas there were no significant differences in species composition between treatments in the pre-

Table 4
Results of generalized additive models (GAM) comparing bird diversity in non-mowed (baseline), mowed-litter and mowed-cleared plots in the pre-treatment (Pre-T, baseline), immediate post treatment (IPT) and late post treatment (LPT) periods.

|	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	0.590493	0.023505	21.719	< 2e-16***
TreatmentMowed.cleared	0.005278	0.035123	0.150	0.881864
TreatmentMowed.litter	-0.049477	0.033243	-1.497	0.147908
PeriodIPT	0.058864	0.026421	2.228	0.035948*
PeriodLPT	0.097247	0.025292	3.845	0.000826***
TreatmentMowed.cleared:PeriodIPT	-0.092045	0.038935	-2.364	0.026897*
TreatmentMowed.litter:PeriodIPT	-0.030989	0.037330	-0.830	0.414993
TreatmentMowed.cleared:PeriodLPT	-0.045188	0.35872	1.260	0.434486
TreatmentMowed.litter:PeriodLPT	0.07598	0.14998	0.507	0.220415

Table 5
Results of generalized additive models (GAM) comparing small mammal diversity in non-mowed (baseline), mowed-litter and mowed-cleared plots in the pre-treatment (Pre-T, baseline), immediate post treatment (IPT) and late post treatment (LPT) sampling periods.

	Estimate	Std. Error	t value	Pr (>|t|)
(Intercept)	0.550926	0.022819	22.318	< 2e-16***
TreatmentMowed.cleared	0.002834	0.034201	0.083	0.93471
TreatmentMowed.litter	-0.051090	0.032261	-1.584	0.12755
PeriodIPT	0.066713	0.027672	2.411	0.02471*
PeriodLPT	0.103502	0.026430	3.916	0.00074***
TreatmentMowed.cleared:PeriodIPT	-0.089555	0.039343	-2.276	0.03292*
TreatmentMowed.litter:PeriodIPT	-0.043673	0.039585	-1.103	0.28183
TreatmentMowed.cleared:PeriodLPT	-0.029949	0.37879	-0.791	0.43759
TreatmentMowed.litter:PeriodLPT	0.039109	0.36692	1.066	0.29804

Table 6
The p-values from the comparison of the seven environmental variables in the non-mowed, mowed-litter and mowed-cleared treatments and in the pre-treatment, immediate post sampling period and the late post sampling period in 2-way ANOVA.

| Environmental variables	Treatment	Period
Grass biomass	7.42e-11***	2e-16***
Forb cover	0.177	4.91e-8***
Grass cover	0.000724***	0.004213**
Litter cover	2e-16***	2.14e-06***
Shrub cover	5.35e-10***	0.00493**
Grass height	1.25e-08***	0.000282***
Bare cover	5.56e-09***	0.197
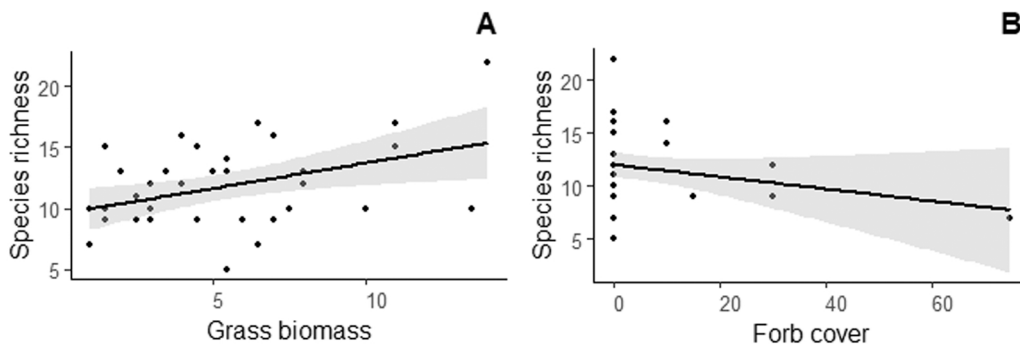
Fig. 4. A linear plot showing the relationship between significant habitat variables (grass biomass and forb cover) and species richness of birds (A, B). The solid line is a line of best fit. The 95% confidence intervals are shown by the gray shading.

treatment and late post-treatment sampling periods (Fig. 6A, C) (R = −0.02, p = 0.589, R = 0.067, p = 0.123). In contrast, the composition of small mammal communities was similar between treatments in the pre-treatment period (Fig. 5D), whereas after the vegetation manipulation, there was severe contraction in NMDS space of treatment plots during the immediate post-treatment and late
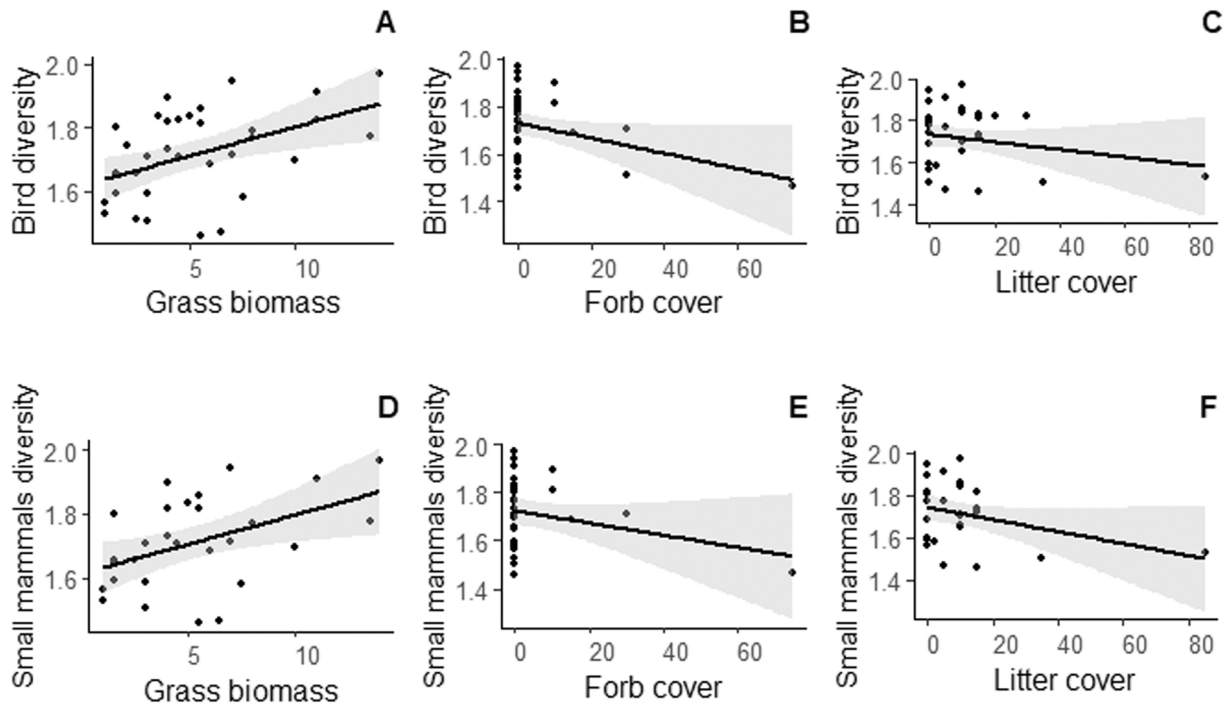
Fig. 5. A linear plot showing the relationship between significant habitat variables (grass biomass, forb cover and litter cover) and bird diversity (A, B, C) and small mammals (D, E, F). The solid line is a line of best fit. The 95% confidence intervals are shown by the gray shading.
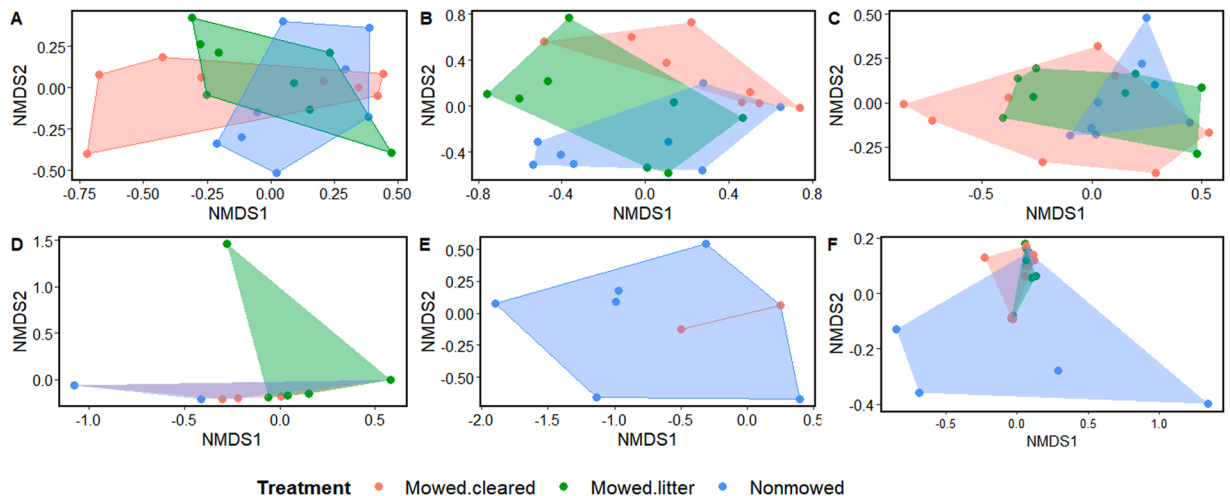
Fig. 6. Non-metric multidimensional scaling (NMDS) of the bird community recorded on non-mowed, mowed-cleared, mowed-litter plot in the pre-treatment period, immediate post-treatment period (IPT) and late post-treatment period (LPT) for: (A) birds in the pre-treatment period; (B) birds in the IPT; (C) birds in the LPT; (D) small mammals in the pre-treatment period; (E) small mammals in the IPT; and (F) small mammals in the LPT. Polygons are convex hulls (see text for further details).

post-treatment periods (Fig. 6E, F), associated with a decline in the number of species remaining in these communities. However, despite this contraction, species composition did not differ significantly between the treatments (ANOSIM: R = 0.05669, p = 0.153, R = 0.033, p = 0.193 and R = 0.010, p = 0.316, respectively). It is clear from the NMDS ordination that species composition of mowed (cleared and litter) plots was a subset of the non-mowed plots (Fig. 6 E, F).

4. Discussion

We found a negative relationship between mowing and species richness in both birds and small mammals, corroborating the

findings of previous studies (Barras et al., 2000; Keesing, 1998; Kotler, 1984; Monadjem, 1997, 1999; Saetnan and Skarpe, 2006). However, we demonstrated that bird species richness was only affected when the cut grass was removed after mowing; mowed plots with litter left in situ did not differ from non-mowed plots. This suggests that despite the grass being mowed, most bird species were still able to utilize mowed areas as long as the cut grass remained in place. This was not the case with small mammals, as their species richness was lower in both mowed treatments compared with non-mowed plots, showing that the presence of cut grass did not improve small mammal species richness. We suggest that the low species richness of birds and small mammals in mowed areas where grass was removed is directly attributable to changes in vegetation structure, more specifically to the reduction in grass biomass. In addition, more seed resources were probably available in non-mowed areas compared to mowed cleared areas, which has been linked to rodent community structure (Taraborelli et al., 2009).

We showed that grass biomass was the most important habitat variable affecting species richness of birds. The only other significant habitat variable was forb cover that was negatively associated with bird and small mammal species richness. Grass biomass is usually associated with increased food resources such as insects and grass seed hence loss of cover may lead to decrease in food availability and quality (Keesing, 1998; Retzer, 2007). We suggest that the low species richness of small mammals in mowed areas is related to cover and the perceived threat of predation for many small mammals in open environments (Loggins et al., 2019), and was in line with our prediction that most small mammals would utilize non-mowed areas. With regards to granivorous birds, finding food may be easier in areas with shorter grasses, which might explain why bird richness did not decline as much as that of small mammals in the mowed areas (Devereux et al., 2004). Furthermore, these birds probably differ in their response to predators by taking flight rather than hiding in the manner of small mammals (Elgar, 1989; Lima and Dill, 1990). Forb cover showed a negative correlation with species richness suggesting that birds and small mammals in grassland habitats distinguish between cover provided by grasses and forbs. Since we found that grass biomass has a strong correlation with species richness for both taxa, our study corroborates the fact that grass cover is a critical feature for most small mammal species occupying grassland habitats (Loggins, Monadjem, et al., 2019; Loggins, Shrader et al., 2019; LoGiudice and Ostfeld, 2002).

The effect of mowing on species richness was evident only for a short period of time. This was observable by the late post-treatment period, which was conducted two months after mowing, when bird species richness was no longer significantly different in non-mowed and mowed plots. The same trend was observed for small mammals, suggesting that by this time grass biomass had recovered sufficiently to recreate suitable conditions for these animals. Hence, our results show that mowing negatively impacts species richness for a short period of time only, measured in weeks or months.

The patterns for species diversity were slightly different from those of species richness; we found lower diversity in mowed-cleared plots for both birds and small mammals immediately after mowing. The diversity for both taxa was however similar in non-mowed and mowed-litter plots. We had expected a higher diversity of both taxa in the non-mowed plots compared to mowed treatments. Thus, our findings suggest that mowing coupled with clearing affected diversity of both taxa whilst mowing alone did not show the same negative impact on diversity. Some studies have shown that grass cover alterations resulting from mowing and grazing can reduce the diversity of insects (Davis et al., 2014; Smith et al., 2015). Hence, the clearing of the mowed plots might have reduced food available for both taxa and consequentially resulted in species being further apart in these plots perhaps due to spreading out more in search of food. The uneven distribution of species for both birds and small mammals is suspected to be the main reason behind the low diversity in the mowed-cleared plots. The higher diversity of both taxa in non-mowed plots was in line with other studies which have reported higher species diversity of birds and small mammals in areas with higher vegetation cover (Fynn et al., 2005). Since sampling occurred immediately after mowing, both taxa might have still foraged in the mowed-litter plots at that point on whatever seeds that were remaining on the cut grasses whilst they abandoned cleared treatments because there was nothing left to forage on after the raking and sweeping of these plots. This might have delayed the reduction in diversity in the mowed-litter plots hence the similarity in species diversity in mowed-litter and non-mowed plots. We were also able to show that grass biomass had a positive association with the diversity of birds and small mammals while forb and litter cover had a negative association with diversity of both taxa. A potential reason for this might be that high forb and litter cover make it difficult for birds to spot prey while at the same time also obstructing the movement of small mammals making navigation difficult. Even though the mowed-litter plots still had high bird and small mammal diversity, the negative association of litter and diversity of both is likely to be a result of diminishing food sources available after mowing as cut grasses were not able to bear seeds.

There was a small, but significant, difference in species composition of birds in non-mowed and mowed areas, suggesting that mowing does not in fact have a big impact on bird community composition at least not at the scale at which we conducted our study. In our study, all the bird species recorded in mowed plots were also recorded in non-mowed plots, however the opposite was not true. For example, we observed some species (such as *Euplectes progne*, *Coturnix coturnix* and *Scleroptila levaillantii*) only in non-mowed plots, showing that the impact of mowing on bird community composition may have been subtle and possibly important. An alternative explanation is that grass biomass (and by association, vegetation cover) is not particularly high in this landscape (classified as medium tall grassland), hence the differences between mowed and non-mowed areas were not important to the bird species typically inhabiting this region. For example, the species *Ortygospiza fuscocrissa* prefers short grasslands (Maphisa et al., 2017), but we recorded it on our non-mowed plots, indicating that even with grass biomass at its fullest, short grassland specialists persist here.

In contrast to birds, small mammals showed a significant difference in community structure in the three treatments, since almost all the species that we recorded were captured in the non-mowed plots, but only two species were recorded in the mowed plots. The numerically dominant species recorded across all the plots, irrespective of treatment, was *Gerbilliscus leucogaster*. This species was able to persist in mowed areas which might have been due to the burrowing behavior of this species (Monadjem et al., 2015) serving as an anti-predation refuge and hence allowing this species to forage in such open environments. *Gerbilliscus* species also have expanded auditory bullae (Monadjem et al., 2015) associated with increased hearing sensitivity of low frequency sounds, which increases their

ability to detect predators (Kotler, 1984; Mason, 2016). The dominance of *G. leucogaster* across our study probably explains the lack of significant differences in the composition of small mammals across our treatments. Since *G. leucogaster* was unaffected by mowing, its numbers did not change radically across mowed and non-mowed plots hence resulting in similar composition of small mammals across treatments. Yet, except for *Dendromus melanotis*, which like *G. leucogaster* utilized mowed and non-mowed areas, the other small mammal species virtually disappeared from the mowed treatments, suggesting that their community structure was indeed affected by vegetation cover.

5. Conclusion

Our study demonstrated that the removal of grass cover by mowing has negative impacts on both bird and small mammal species richness, diversity, and community structure, but that these effects are short-lived. Since grass biomass was an important habitat variable for both these groups, the negative impacts of mowing stem from the removal of cover. However, the impacts of mowing were short-term since the species composition of bird and small mammal communities were once again similar three months after mowing. This suggests that grass mowing can be used as an appropriate management tool in these high-elevation grasslands.

Author contributions

Zamekile D. Bhembe and Monday V. Mdluli contributed equally as first authors of the manuscript and they collected the data. Ara Monadjem designed the study, assisted with data analysis and drafting of the manuscript. All authors provided critical input into various draft versions of the manuscript and approved it for submission.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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