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Dynamic multi-species occupancy models of birds of high-altitude grasslands in eastern South Africa

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Moist, high-altitude grasslands of eastern South African harbour rich avian diversity and endemism. This area is also threatened by increasingly intensive agriculture and land conversion for energy production. This conflict is particularly evident at Ingula, an Important Bird and Biodiversity Area located within the least conserved high-altitude grasslands and which is also the site of a new Pumped Storage Scheme. The new management seeks to maximise biodiversity through manipulation of the key habitat variables: grass height and grass cover through burning and grazing to make habitat suitable for birds. However, different species have individual habitat preferences, which further vary through the season. We used a dynamic multi-species occupancy model to examine the seasonal occupancy dynamics of 12 common grassland bird species and their habitat preferences. We estimated monthly occupancy, colonisation and persistence in relation to grass height and grass cover throughout the summer breeding season of 2011/12. For majority of these species, at the beginning of the season occupancy increased with increasing grass height and decreased with increasing grass cover. Persistence and colonisation decreased with increasing grass height and cover. However, the 12 species varied considerably in their responses to grass height and cover. Our results suggest that management should aim to provide plots which vary in grass height and cover to maximise bird diversity. We also conclude that the decreasing occupancy with increasing grass cover and low colonisation with increasing grass height and cover is a results of little grazing on our study site. We further conclude some of the 12 selected species are good indicators of habitat suitability more generally because they represent a range of habitat needs and are relatively easy to monitor.

1 Dynamic multi-species occupancy models reveal individualistic habitat preferences
2 in a high-altitude grassland bird community.

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13 ABSTRACT

14 Moist, high-altitude grasslands of eastern South African harbour rich avian diversity and
15 endemism. This area is also threatened by increasingly intensive agriculture and land conversion
16 for energy production. This conflict is particularly evident at Ingula, an Important Bird and
17 Biodiversity Area located within the least conserved high-altitude grasslands and which is also
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20 and grazing to make habitat suitable for birds. However, different species have individual habitat
21 preferences, which further vary through the season. We used a dynamic multi-species occupancy
22 model to examine the seasonal occupancy dynamics of 12 common grassland bird species and
23 their habitat preferences. We estimated monthly occupancy, colonisation and persistence in
24 relation to grass height and grass cover throughout two summer breeding seasons. At the
25 beginning of the season, occupancy increased with increasing grass height and decreased with
26 increasing grass cover in most species. On average, persistence and colonisation decreased with
27 increasing grass height and cover. However, the 12 species varied considerably in their responses
28 to grass height and cover. Our results suggest that management should aim to provide plots which
29 vary in grass height and cover to maximise bird diversity. We also conclude that the decreasing
30 occupancy with increasing grass cover and low colonisation with increasing grass height and
31 cover is a result of reduced grazing on our study site. We further conclude that some of the 12
32 selected species are good indicators of habitat suitability more generally because they represent a
33 range of habitat needs and are relatively easy to monitor.

34 *Key-words: hierarchical occupancy models, habitat suitability, Grazing and fire, grass*
35 *height and cover, monitoring.*

36 INTRODUCTION

37 In South Africa the grassland biome and its associated biota are increasingly becoming threatened due
38 to expansion of agricultural activities, human settlements and associated road infrastructure (Allan et
39 al., 1997; Reyers et al., 2001; Egoh et al., 2011). The growth of the human population in southern
40 Africa is accompanied by increasing demands for water and electricity. These threats are likely to

impact on bird species richness in remote eastern, moist, high-altitude grasslands (eg. Maphisa et al., 2016). This area is a centre of endemism for both plants and animals (Zunckel, 2003) and has the highest concentration of Important Bird and Biodiversity Areas (Barnes, 1998; Marnewick et al., 2015b) in southern Africa. These grasslands are currently predominantly used to support livestock farming accompanied by annual burning followed by heavy grazing (Maphisa et al., 2016, 2017). However, at the start of the 21st century, the area is increasingly targeted for development of large water schemes (eg. Davies & Day, 1998), and electricity projects to meet increasing demands for water for human consumption (Maphisa et al., 2016, 2017). These developments result in habitat loss with possible negative impact on biodiversity.

Because of socio-political pressure and despite objections from environmental organisations, development in the area may not be completely prevented (Bennett et al., 2017). As a result of these threats facing mountain grassland habitats, there is now an urgent need for biodiversity information to identify and protect habitat for threatened fauna and flora of the area. Management needs to predict which areas of conservation importance are most vulnerable to transformation in order to put effective conservation measures in place (Reyers, 2001; Neke & Du Plessis, 2004).

Grazing and fire are two key ecological factors maintaining habitat suitability for different bird species within the grassland biome (Griebel, Winter & Steuter, 1998; Maphisa et al., 2016, 2017). In particular, grazing by mixed livestock and fires of different intensities create a habitat mosaic in grass height and cover which benefits a variety of species across the landscape at different times of the year (Hobbs & Huenneke, 1992; Parr & Chown, 2003; Tews et al., 2004; Vandvik et al., 2005; Fuhlendorf et al., 2006; Evans et al., 2006; Fahrig et al., 2011). Understanding how species of management concern respond to these disturbances is essential for sustainable ecological management of the species (Driscoll et al., 2010). In the absence of herds of roaming wild antelopes which are thought to have been responsible for creating a habitat mosaic in pristine times (Hockey et al., 1988), planned man-made fires and grazing by domestic livestock are now important tools that grassland managers can use to manage grasslands for biodiversity.

Dynamic site occupancy models were initially developed as an approach to investigate the dynamics of species occurrence and to understand how factors of interest affect the vital rates that determine occurrence (rates of local persistence and colonization) (Mackenzie et al., 2011). Site occupancy models offer opportunities to frame and solve decision problems for conservation that can be viewed in terms of site occupancy (Royle, Kéry & Ke, 2007; Martin et al., 2009) and are

well suited for addressing management and conservation problems (Martin et al., 2009). Non-detection of a species at a site does not imply that the species is absent unless the detection probability is one (MacKenzie et al., 2003). Occupancy models account for imperfect detection, which is the inability of investigators to detect a species at a site with certainty (Zipkin, DeWan & Royle, 2009). Incorporating detection probabilities into estimates of species richness is important for obtaining unbiased estimates of species numbers, particularly in communities with large numbers of rare or elusive species (Mackenzie et al., 2011; Govindan, Kéry & Swihart, 2012; Oedekoven et al., 2013). Accounting for detectability is particularly important amongst grassland birds because many grassland birds are hard to identify or highly elusive.

Russell et al. (2009) used a Bayesian hierarchical, multi-species occupancy analysis, to identify the effects of prescribed fires on wildlife communities. These same models can be used for other management-induced habitat changes such as effects of grazing intensity or burning on avian occurrence within the moist high-altitude grasslands. Understanding the drivers of occupancy dynamics in grassland bird species is necessary for grassland management to decide on actions that favour certain target species (eg. MacKenzie et al., 2003), and limit undesirable species, depending on the set management objectives.

In this study, we use repeated detection-non-detection data and state-space dynamic occupancy models, to evaluate how grass height and cover influence habitat use by 12 common bird species in high-altitude grassland in eastern South Africa. Grass height and cover are frequently cited as the most important factors influencing habitat selection and nest survival amongst grassland birds (Devereux et al., 2008; Whittingham & Devereux, 2008; Cao et al., 2009; Donald et al., 2010; Fisher & Davis, 2010; Klug, Jackrel & With, 2010). Several species of conservation concern occur with conflicting habitat requirements in the region (Maphisa et al., 2009, 2016). In the case where habitat is managed to maximize biodiversity, management actions that enhance habitat for some species may limit habitat for other species.

Through use of dynamic, multi-species occupancy models (Concepción et al., 2012), management will be able to evaluate and guide conservation decisions needed to maintain avian diversity in the long-term. As an effort to correct past deleterious grassland management (Maphisa et al., 2016) our study area has recently undergone a change from heavy grazing to light grazing while annual burning still persist as before. The land on neighbouring farms is still heavily grazed and annually burned. The response of bird communities to fire is well studied (Driscoll et al., 2010; Watson et al., 2012; Lindenmayer et al., 2016). Individual bird species

differ in their responses. Within habitats that are managed with fire and grazing, the two factors are complementary to create suitable habitat for birds (Fuhlendorf et al., 2006, 2009).

The goal of this study was to examine the response of 12 common grassland bird species to grass height and cover in summer which coincides with high avian species richness and the time when most birds are breeding (Maphisa et al., 2016). The application of fire and grazing was variable in our study area and therefore we indirectly relate bird occupancy to grass height and cover over time. We further incorporate prevailing weather conditions because weather can have effect on birds' detectability during survey (Zuckerberg et al., 2011; Hovick, Elmore & Fuhlendorf, 2014).

MATERIALS AND METHODS

Background

Dynamic, multi-species occupancy models estimate species-specific occupancy, colonisation and extinction probabilities in relation to grass height and cover as the main habitat structuring factors (e.g. Dorazio & Royle 2005; Dorazio et al. 2006; Altwegg, Wheeler & Erni 2008). Using this approach, we examined changes in occupancy from one month to the next over the course of a breeding season while accounting for imperfect detection. We used a dynamic model that estimated for colonisation and persistence from one month to the next month. The basic idea is that (1) non-detection can be distinguished from absence through repeated sampling and (2) species-specific estimates of occurrence can be improved using collective data on all species observed during sampling (Zipkin et al., 2010). The dynamic model describes occupancy as a state process based on: (1) persistence: the probability of an occupied site continuing to be occupied from one month to the next, and (2) colonisation: the probability of an unoccupied site becoming colonised (Popescu et al., 2012).

Study area

This study was conducted at Eskom Ingula Pumped Scheme (Ingula) with few plots randomly selected from the neighbouring privately owned farms (Fig.1). Ingula is located c. 23km north-east (28°14' S, 29°35' E) of the village of Van Reenen at altitudes of 1200 to 1700m asl and covers c. 8 000 ha (Maphisa et al., 2016, 2017). It straddles the escarpment and two provinces: KwaZulu-Natal and Free State (FS). The average altitude below the escarpment is 1200m asl and 1700m asl above the escarpment. The FS side is dominated by sweet and sour grassland vegetation type (Mucina & Rutherford, 2006), characterised by the grass *Themeda triandra*. This area was previously used to support commercial livestock in summer falls partly within an

Important Bird and Conservation Area (Marnewick et al., 2015b). The area below the escarpment is dominated by *Hyparrhenia-Cymbopogon* grasses and has been modified into fields and alien plantations and therefore is considered of less conservation priority compared to the upper site (Maphisa et al., 2016).

The Ingula property and surrounding privately owned farms are designated an Important Bird and Biodiversity Area (Marnewick et al., 2015). Current Ingula management seeks scientific advice on how to manage this area to optimize biodiversity conservation. The surrounding farms are still heavily grazed and annually burned with negative impact on habitats and species. This study was approved by the Ingula Partnership while DHM was an employee of Birdlife South Africa. The Ingula Partnership is made up of Birdlife South Africa Middelpunt Wetland Trust and Eskom. DHM got further verbal permission from the neighboring farm owners to enter their properties and record birds and vegetation for the duration of this study. Commercial farmers' cattle were moved out of Ingula since summer of 2005 so that the area could recover from past heavy livestock grazing and annual burning. However, relatively small herds of livestock belonging to the former land owners' tenants still remain on site with plans to relocate them (Maphisa et al., 2016).

The weather at Ingula is characterised by cold winters with occasional snow and strong directional winds and wet summers dominated by morning mist. Most of the rainfall occurs during the southern hemisphere summer (October to February), sometimes with marked rainfall differences between the upper and the lower parts of the study area. At Ingula, this sharp seasonal contrast in temperatures also affects bird species richness with highest species richness occurring in summer while the winters and spring recorded the lowest species richness (Maphisa et al., 2016). Therefore this study uses summer data for birds and vegetation when species richness is highest.

Vegetation and bird surveys

We laid a grid of 500 × 500 m on 1:50 000 topographic maps of the study area and extended the grid into neighbouring privately owned farms. Then we numbered the plots that were mostly grassland avoiding plots that were too steep, rocky or lie adjacent to the wetlands. We selected 19 plots to be most suitable to survey because they were most accessible from the nearby vehicle

track. Twelve plots were located within the Ingula property itself and seven plots on neighbouring farms (Fig 1; plots P03A, P10, P50, P54, P57, P63, P64 were on private land).

On these plots we surveyed birds and vegetation during austral summer (November to February 2010/11) and summer 2011/12, spanning the entire breeding season (e.g. Maphisa, 2004) (Maphisa et al., 2016, 2017). (eg. Maphisa, 2004)

We walked parallel transect inside each plot 150 m from the edge and recorded birds walking in and walking out of each plot. We assumed that walking rather than point counts would maximize detection of threatened (Taylor, Peacock & Wanless, 2015) and secretive grassland birds such as Yellow-breasted Pipit (*Anthus Chloris*). Each birds was recorded once at the first sighting or when first heard (Dias, Bastazini & Gianuca, 2014) and were assumed to be inside the plots limits. The sighting and recording of birds was done by one person with good experience of habitats of birds of this region. We subsequently recorded vegetation at regular intervals (100 m) along the same route where we recorded birds earlier (eg. Maphisa et al., 2017). Each plot was visited three times each month (November to February) for the duration of this study. Out of the three visits, two were primarily spent recording birds only and lasted up to 30 minutes. We recorded vegetation during the third survey but we also made a list all birds seen and mostly took a little longer than 30 minutes. Bird surveys were undertaken mostly in the mornings, from 07h00–11h00, and sometimes in the afternoons from 15h00–16h00 when weather prevented completion surveys during the morning (eg. Maphisa et al., 2016). Weather permitting, we ensured that the repeat surveys were very close to the first survey.

We recorded grass height and cover using similar method as that of (Maphisa et al., 2009, 2017). This consisted of throwing a 30 cm × 30 cm quadrat (divided into nine equal squares) twice at random every 100 m along the transect line (Maphisa et al., 2017). We recorded grass cover as the squares with grass out of nine. Each square that was at least 75% grass was considered grass. We recorded grass height at four corners of the grid which was averaged in our analysis. This field protocol enabled the two variables to be measured over a relatively large area (Fig. 1). Recording only these two variables also allowed us to cover a relatively large area with variable grazing and burning within a short space of time.

Weather conditions affect detectability of birds (Zuckerberg et al., 2011; Hovick, Elmore & Fuhlendorf, 2014; Sliwinski et al., 2016). During each survey, we recorded cloud cover (clear,

partly cloudy or cloudy) and temperature (cold, cool, warm or hot), together with wind conditions (calm, moderate or strong) (Harms et al., 2017). Because of our small data set, we reduced these weather covariates into a single variable representing observability by subjectively scoring their effects based on our ability to detect birds (Appendix S1). The purpose of the observability covariate was simply to capture some of the variability in the detection probabilities (Royle, 2006). No survey was carried out when poor visibility would impact the identification of birds. Other plot attributes that were recorded during the vegetation survey were grazing and burning. However, because management did not have full control over these two factors (Maphisa et al., 2016, 2017), grazing and burning happened in a haphazard way and therefore we decided not to include this information in the model but rather focus on grass height and cover as more proximate habitat variables influencing species habitat selection.

We used multi-species dynamic occupancy models using the 12 bird species that we found to be the commonest during the survey. These birds could serve as indicator species to evaluate future management decisions through adaptive monitoring. The justification for choosing these species is that they are all typical grassland species with a diversity of habitat requirements that should also support rarer grassland species (Maphisa et al., 2017). Our second justification is that because these birds are widespread and relatively common, they should be relatively easy to monitor during future routine surveys. With a view to the monitoring of bird diversity in the future, all these species breed in the region in summer (Maphisa et al., 2016), when they can be detected fairly easily. This in turn could provide more precise occupancy estimates (Ruiz-Gutiérrez, Zipkin & Dhondt, 2010). We assumed that low plot occupancy, persistence or colonisation would therefore mean that plots are not suitable for breeding (eg. Nocera, Forbes & Milton, 2007).

The species were, from the most common to the least common (based on preliminary data analysis): African Pipit *Anthus cinnamomeus*, Cape Longclaw *Macronyx capensis*, Wing-snapping Cisticola *Cisticola ayresii*, Red-capped Lark *Calandrella cinerea*, Zitting Cisticola *Cisticola juncidis*, Yellow-breasted Pipit *Hemimacronyx chloris*, Common Quail *Coturnix coturnix*, Long-tailed Widowbird *Euplectes progne*, African Quailfinch *Ortygospiza atricollis*, Banded Martin *Riparia cincta*, Ant-eating Chat *Myrmecocichla formicivora* and Eastern Long-billed Lark *Certhilauda semitorquata*. Of these species, the Yellow-breasted-Pipit is considered nationally threatened (Barnes, 2000; Taylor, Peacock & Wanless, 2015).

Model description

We developed a multi-species hierarchical model (Appendix S2) using a state-space formulation. The true site-specific occupancy state for species $j = 1, 2, \dots, N$ at site $i = 1, 2, \dots, J$, is denoted $z_{i,j}$, where $z_{i,j} = 1$ if species j occurs at site i and otherwise $z_{i,j} = 0$. The occupancy state $z_{i,j}$, is assumed to be constant across the three surveys within each month. It is the stochastic binary outcome governed by the occupancy probability (Ψ) of species j at site i assumed to be the outcome of Bernoulli random variables :

$$z_{i,j} \sim \text{Bern}(\Psi_{i,j})$$

We assumed that a species can only be detected at a site if it actually occurs there, i.e. there are no false positives (eg. Dorazio & Royle, 2005; Dorazio et al., 2006). A detection of species j at site i on visit k depends on the detection probability $\theta_{i,j,k}$ and the occupancy state:

$$x_{i,j,k} \sim \text{Bern}(\theta_{i,j,k} \times z_{i,j}).$$

(Dorazio et al., 2006; Russell et al., 2009; Zipkin, DeWan & Royle, 2009; Ruiz-Gutiérrez, Zipkin & Dhondt, 2010; Sauer et al., 2013).

We were interested in the seasonal changes in the bird communities and therefore we used a dynamic extension of the model above, allowing the occupancy status to change from one month to the next (eg. Iknayan et al., 2014). We modelled occupancy during the first month (November, $t=1$) as above,

$$z_{i,j,t} \sim \text{Bern}(\Psi_{i,j}), \text{ for } t=1.$$

Occupancy during the subsequent months depended on occupancy during the preceding month:

$$z_{i,j,t} | z_{i,j,t-1}, \phi_{i,j,t}, \gamma_{i,j,t} \sim \text{Bernoulli}(\phi_{i,j,t} \times z_{i,j,t-1} + \gamma_{i,j,t} \times (1 - z_{i,j,t-1})), \text{ for } t > 1,$$

where the colonisation probability (γ) is the probability of an unoccupied site to become occupied and the persistence probability (ϕ) is the probability of an occupied site to remain occupied. The occupancy probabilities during December, January and February ($t=2, 3$, and 4) were calculated as derived parameters.

Initial occupancy, colonisation and persistence were constrained to be linear functions of the covariates grass height (avh) and grass cover (cover) on the logit scale:

$$\text{Logit}(\Psi_{i,j}) = \beta_0 + \beta_1 \times \text{avh}_{i,j,t} + \beta_2 \times \text{cover}_{i,j,t} \quad \text{for } t=1$$

$$\text{Logit}(\gamma_{i,j,t}) = \nu_0 + \nu_1 \times \text{avh}_{i,j,t} + \nu_2 \times \text{cover}_{i,j,t} \quad \text{for } t>1$$

$$\text{Logit}(\phi_{i,j,t}) = \mu_0 + \mu_1 \times \text{avh}_{i,j,t} + \mu_2 \times \text{cover}_{i,j,t} \quad \text{for } t>1,$$

where the β , ν and μ are species-specific coefficients. Each of these nine coefficients was modelled as a random effect, i.e. $\eta_j \sim N(\eta_{\text{bar}}, \sigma\eta)$ where η_{bar} is the mean and $\sigma\eta$ the standard deviation of the species-specific coefficients and $\eta = \{ \beta, \nu, \mu \}$.

We modelled the detection probability (p) as a function of field conditions measured by the continuous covariate obs, and a random effect ε . α_0 and α_1 are coefficients:

$$\text{Logit}(p_{i,k,t}) = \alpha_0 + \alpha_1 \times \text{obs}_{i,k,t} + \varepsilon_{i,k,t}$$

Each covariate was centred and scaled before analysis (Nichols & Boulinier, 1998; van den Berg et al., 2006; Jones et al., 2012; Pollock et al., 2014). We then calculated the number of species, out of the 12, that are present at a site in a given month (local species richness, $r_{i,t} = \sum z_{i,j,t}$) and the number of plots each species occupied in a given month ($o_{j,t} = \sum z_{i,j,t}$) as derived parameters.

Model fitting and analysis

We estimated the parameters using a Bayesian analysis of the model with vague priors (Royle, Kéry & Ke, 2007; Russell et al., 2009; Zipkin, DeWan & Royle, 2009; Banks-Leite et al., 2014) for all parameters. We used a Uniform distribution $U(-10,10)$ for the coefficients and Inverse Gamma (0.01,0.01) for the variances of the random effects. We tested the sensitivity to the choice of priors for the latter by also using $U(0,15)$ as priors for the standard deviations (Zipkin, DeWan & Royle, 2009) (Appendix S2).

We carried out the analysis in JAGS (Plummer, 2003) called via package rjags (Plummer, 2014) from R (R Development Core Team, 2013). The MCMC procedure requires an initial burn-in period for the chains to converge to a stationary process, after which the subsequent estimates can be used to calculate medians and credible intervals associated with the parameters of interest (Sauer et al., 2013). We assessed convergence using the Gelman-Rubin statistic (Gelman & Shirley, 2011) and visual inspection of the chains (Jones et al., 2012). We ran three chains of length 60 000 each; with a burn-in of 30 000 and thinned the remaining results by taking each 20th value from the chains. With these settings, the model converged for all parameters.

RESULTS

Plot occupancy was variable among the 12 species across the four months, with overall high initial occupancy followed by a gradual decline in the number of occupied plots for a majority of the 12 species as the season progressed (Fig. 2). The Wing-snapping Cisticola was recorded in almost every plot throughout the four months and occupancy for this species was estimated to be 1. Four other species, Cape Longclaw, African Pipit, Zitting Cisticola and Banded Martin, exhibited high plot occupancy too throughout the four months. Two other species, Red-capped Lark and Common Quail, were common early during the season but showed a rapid decline to a low number of occupied plots by the fourth month. Long-tailed Widowbird and Eastern Long-billed Lark occupied the fewest number of plots throughout the season, with Eastern Long-billed Lark showing a rapid decline between the third and fourth months (Fig. 2).

Habitat effects on occupancy, persistence and colonisation

Plot occupancy was highest at the start of the season and lowest towards the end of the summer season (Fig. 2). Species varied in their responses to grass height and cover with majority of birds reacting more negatively to increasing grass cover than increase in grass height (Fig. 3). Across the 12 species, persistence and colonisation decreased with increasing grass height and cover suggesting that plots with low, open grass were more likely to be occupied. However, the relationship between the occupancy parameters and habitat variables differed among species, suggesting that the species prefer different levels of grass height and cover (Fig. 3). Overall, colonisation declined with increasing grass height and cover for a majority of the 12 species, with African Quailfinch, Banded Martin and African Pipit being the exceptions because they were little affected by increasing grass cover (Fig. 3).

Four species, Common Quail, Cape Longclaw, Banded Martin and Zitting Cisticola were found on almost all plots and were only marginally affected by increasing grass height and increasing grass cover (Figs 2 & 3), suggesting that variation in grass height and cover affected these four species little. The Common Quail was recorded almost everywhere during the first two months with subsequent decline (Fig. 2). This species was little affected by increasing grass height, but experienced a steep decline with increasing grass cover (Fig. 3). The Yellow-breasted Pipit, the only threatened and endemic species of the 12, was more common at the beginning of the summer but was scarce by the end of the summer (Fig. 2) and its persistence was affected more negatively by increasing grass height than by increasing grass cover, while its plot colonisation was negatively affected by both increase in grass height and increase in grass cover (Fig. 3).

Red-capped Lark was common everywhere during the first month and thereafter showed a rapid decline (Fig. 2), with decline in plot occupancy and persistence with both increasing grass height and cover (Fig. 3). The Long-tailed Widowbird showed an increase in the number of occupied plots over the first two months and then remained steady thereafter (Fig. 2), persisting across increasing grass heights and covers, appearing to be positively impacted by lack of grazing (Fig 3). Of the remaining three species, the African Pipit was found in most plots in all months of the survey (Fig. 2), where its persistence within plots was affected negatively by both increasing grass height and cover. The Ant-eating Chat and Eastern Long-billed Lark occupied small number of plots throughout the summer (Fig. 2). Persistence of Ant-eating Chats was affected more by increasing grass cover than increase in grass height, while persistence of Eastern Long-billed Lark was affected by increase in grass height and cover (Fig. 3).

Species richness: comparing Ingula with neighbouring private farms.

Of the 12 species examined here, eight to 10 were estimated to occur per plot (Fig. 4). Species richness did not vary much over the months and was similar on Eskom's property compared to private farms (Fig. 4).

DISCUSSION

The increasing demand for land for development necessitates more effective management of the remaining ecosystems and biodiversity (Zipkin, DeWan & Royle, 2009; Drum et al., 2015). Detection-nondetection data and multi-species occupancy models (MacKenzie et al., 2003; Popescu et al., 2012) provide a cost effective way of monitoring the response of a collection of species for management of the habitat (Sauer et al., 2013). We examined the response of common grassland species to grass height and cover which has been affected by a recent management change from heavy grazing to little grazing. Habitat structure is a major determinant of how species use a landscape (Nocera, Forbes & Milton, 2007), both in space and time, and affects species diversity (Martin & Possingham, 2005). For grassland ground-nesting bird species that use the grassland for both feeding and breeding, vegetation structure is critical for their use of habitat.

Our study focused on common species because they are easy to monitor and could serve as indicator species to evaluate the effects of management actions (eg. Macleod et al., 2012). Our results suggest that these species varied in their habitat requirements, measured by grass height and cover (Maphisa et al., 2017). We suggest that low colonisation with increasing grass height and cover is a result of little grazing (Fig. 3) since the new Ingula management took over. This is further confirmed by declining occupancy from one month to the next for majority of species.

With little grazing after early fire season, this results supports our own field expectations regarding the habitat preferences of these birds. Habitat heterogeneity is important for the majority of grassland birds (Reynolds & Symes, 2013). Once settled, navigation of habitat to search for food, nesting and evading predators is critical for ground nesting birds (eg. Devereux et al., 2006, 2008; Whittingham & Devereux, 2008).

Under managed burning and grazing and leaving some areas unburned we would expect more pronounced results indicated by colonization when habitat is suitable and extinction when habitat becomes unsuitable (eg Stefanescu et al., 2014). We suggest that Ingula grasslands and similar habitats in the region be managed with fire and grazing to bring habitat suitability to benefit grassland community in general (Fuhlendorf et al., 2009; Maphisa et al., 2017). Moreover, our results suggest that a suite of common birds can be used as indicators for habitat suitability for other species that are uncommon and yet share habitat with some of these birds. However, a disadvantage of using common species is that they may be less sensitive to changes in habitat (eg. Banks-Leite et al., 2014), especially for those species that occur on all plots. Alternatively, density might be a more sensitive indicator for the effect of habitat change on some species than plot occupancy (Macleod et al., 2012).

The southern African subregion is characterized by seasonal altitudinal migration (Berruti, Harrison & Navarro, 1994) with high-altitude grasslands showing most pronounced fluctuation of species richness between winter and summer (Maphisa et al., 2016). Because of widespread annual burning prior to summer in the region (Maphisa et al., 2016), we expect high occupancy probabilities at the start of the season (Fig. 2). Although our study area was protected and there was little grazing compared to the way this land was used before 2005, arson resulted to burning of almost the entire site year after year. Usually grass is short at beginning of summer and therefore grassland birds should easily be detectable at the beginning of summer but also birds are more vocal when they establish territories (Mattsson & Marshall, 2009). In the case of Ingula as the season progresses and with little grazing we expect low persistence probabilities as the grass grows taller (Fig. 3). The exception would be birds that prefer tall grass and therefore occurred everywhere (eg. Common Quail, Banded Martin and African Pipit). We deliberately included one aerial feeder (Banded Martin), because during fieldwork, we found this bird mostly associated with tall grass where it feeds on flying insects early in the morning. But because, Banded Martin would have likely been recorded in every plot this is one of the few species whose colonization was little affected by increasing grass cover indicating that our model prediction was correct.

Our results are consistent with earlier studies demonstrating an avifaunal shift in response to change in vegetation height (Martin & Possingham, 2005; Tichit et al., 2007; García et al., 2007) as season progresses. When the birds arrive at the beginning of the austral summer season, grass height and cover are important factors that determine whether birds stay to breed or move elsewhere if unsuitable. These two habitat features affect species differently according to their ecological needs and therefore we expected initial occupancy which can be expressed in terms of persistence and colonisation to decline with the months (Fig. 3). Another potential reason describing declining persistence and colonization could be because February marks the end of breeding season when birds move out of the study area. The summer breeding season is short in our study area (Maphisa et al., 2016) compared to similar high-altitude grasslands in Ethiopia (Mamo, Asefa & Mengesha, 2016; Maphisa et al., 2017), which is another relatively well-studied high-altitude grassland area in Africa.

Our previous study spanning three summers (Maphisa et al., 2017) ranks Cape-Longclaw as the commonest species in the area. These contrast with our current study that ranks African Pipit as the first common species followed by Cape Longclaw. This is because neighbouring farms bordering Ingula are still annually burned and heavily grazed and therefore provide habitat typical of African Pipit and Red-capped Lark which prefers short grass. Maphisa et al. (2017) restricted bird surveys to within the Ingula property only. With only half the amount of plots surveyed in neighbouring farms the species richness of the two differently managed areas appears similar (Fig 4). However, we did not study density of the different species here. Density might be more sensitive to habitat differences between Ingula and neighbouring farms (eg. Macleod et al., 2012) . However, since our main objective was to recommend appropriate grassland management and monitoring to current management we feel that our current approach is more appropriate than density or species richness. High species richness might not mean habitat suitability but rather ease of finding food (eg. Devereux et al., 2006).

We modelled occupancy, persistence and colonisation as logit-linear functions of grass height and cover from one month to the next for four months (multi-seasons). This was a simple approach. An alternative approach would have been to consider models with quadratic terms (Zipkin, DeWan & Royle, 2009; Zipkin et al., 2010; Ruiz-Gutiérrez, Zipkin & Dhondt, 2010) to examine species-specific optima in grass height and cover. However, we did not do this due to small sample size (12 plots within Ingula compared to 8 on private land), which was a result of the study site rugged topography and the fact that the survey was undertaken by one person.

MODELLING HABITAT FOR ALL GRASSLAND AVIAN COMMUNITY

Rare species, which are often of conservation priority, are frequently more sensitive to changes in habitat compared to common species (Zipkin et al., 2010). By virtue of being rare, these species are also harder to monitor routinely to inform management (MacKenzie et al., 2005; Zipkin et al., 2010). Our study design and statistical model could be expanded to include rarer species by monitoring more plots with a larger replication of surveys. This would allow estimation of occupancy dynamics for species that are less often encountered. Our study region is a conservation hot spot (eg. Zunckel, 2003) which include species that prefer moderate grazing co-occurring with species that prefer heavy grazing (Maphisa et al., 2016). Both groups include species of management concern requiring habitat heterogeneity.

Often land managers are tasked to make habitats suitable for a variety of species, sometimes with contrasting habitat needs (Sauer et al., 2013). We found that habitat preferences indeed varied among a suite of 12 common species, and changed throughout the season. Managing the habitat for these species thus requires maintaining a mosaic of patches that differ in grass height and cover, which should also benefit other species that are harder to monitor. Fire and grazing is used as management tool in the region on state-owned conservation lands and private reserves (Parr & Chown, 2003). Further work is needed in the region to confirm our current findings under controlled burning and grazing with random replicated plots to capture variability in grazing and burning (Parr & Chown, 2003). But this may not be possible because fire and grazing is applied different by different owners to maximize livestock production and not conservation targets. The recent increase in the number of conservation areas in the region provides further opportunities to study bird's habitat requirements more fully where fire and grazing can be used as management tools to maximize biodiversity targets.

Hierarchical multi-species occupancy models have advantage to other survey methods for monitoring purposed because only detection-nondetection of species is recorded. Repeated surveys provide important information on the observation process. The difficult topography of our study area plus inclement weather makes surveying equal number of plots difficult in some years. Improvements in hierarchical multi-species dynamic occupancy models makes it possible to predict areas that may not be sampled in some years due to logistic factors (Iknayan et al., 2014).

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SUPPORTING INFORMATION

Appendix S1. Scores allocated to three categories based on personnel field observation, each weighted according to how DHM perceived a variable to influence observability. Conditions were optimal with a clear sky (score 1 = 100), cool temperatures (score 2 = 100) and calm wind conditions (score 3 = 100). For other weather conditions, observability was reduced and we chose the scores according to our subjective judgement of how much it affected our ability to detect birds. For example, observability was similarly reduced in strong winds as in hot weather, etc. We then averaged the three scores to get a single value for observability.

Appendix S2. Multi-Species, dynamic hierarchical model: R and BUGS code used to fit the model. R script with the JAGS model specification for multi-species hierarchical occupancy model with effect of grass height and grass cover on occupancy (Ψ), persistence (ϕ) and colonisation (γ) probabilities with additional effect of environment (cloud cover and wind) on detection probability (p).

Figure 1(on next page)

Map of Ingula study area showing location of our random study plots created with ggplot2

lon and lat on the y and x axis both represents longitude and latitude respectively

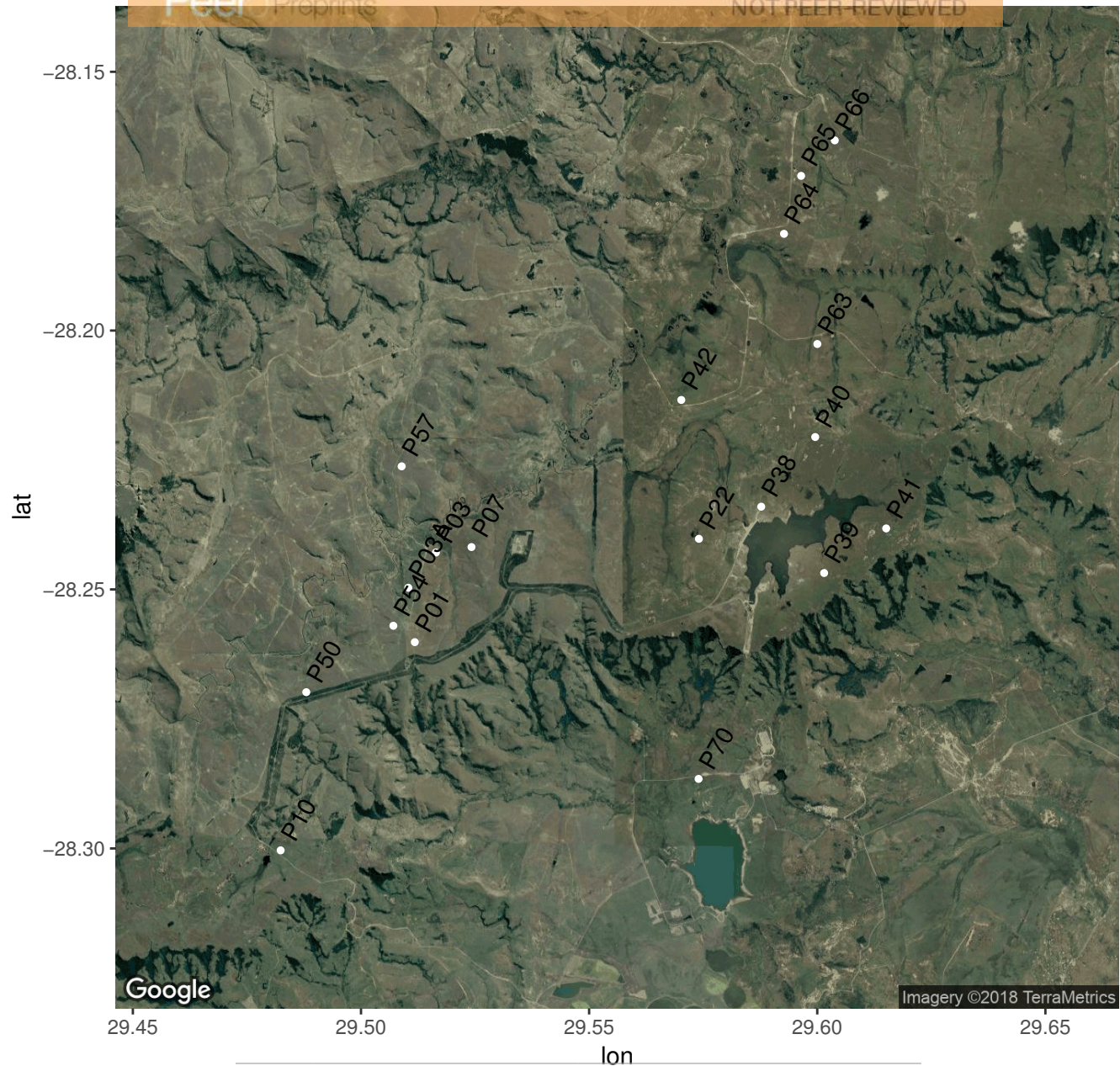


Figure 2(on next page)

Multi-season plot occupancy by month-November to February for the top 12 most common species covering the two austral summers (2010/11-2011/12).

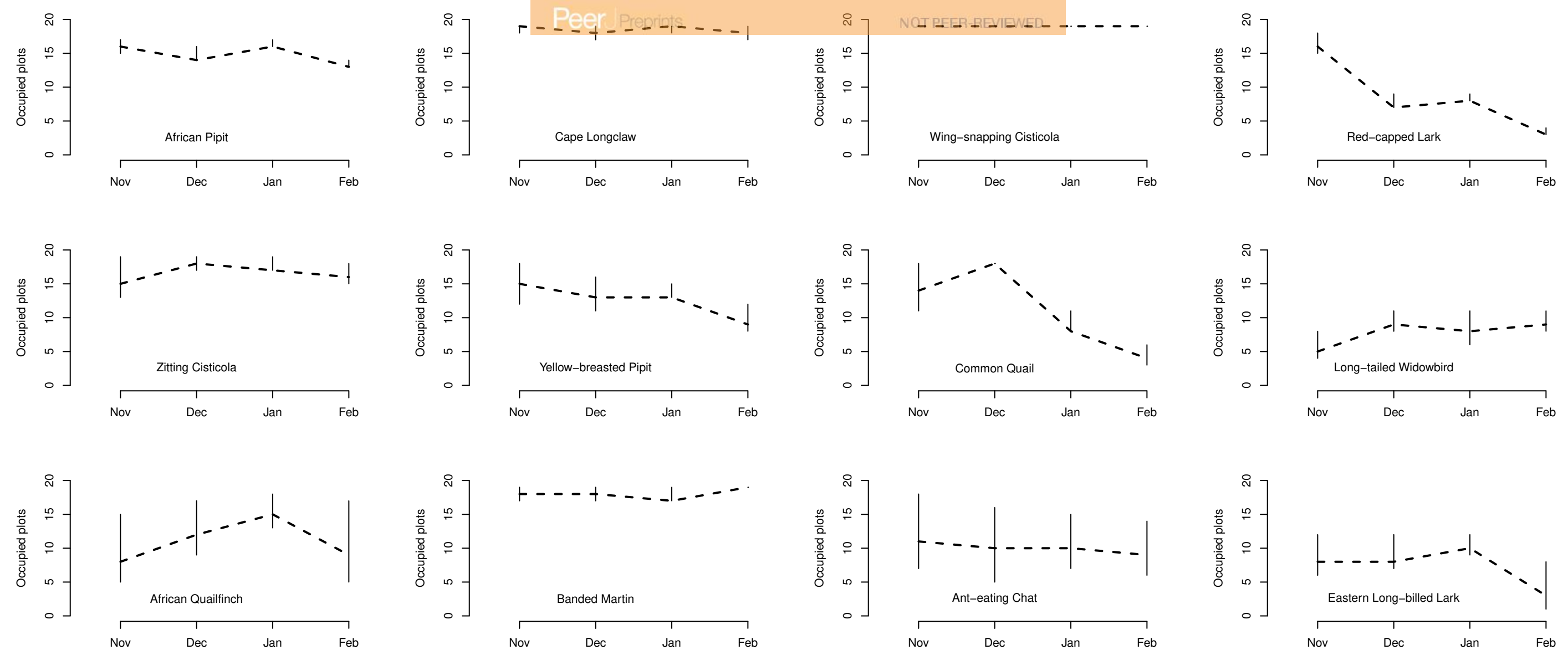


Figure 3(on next page)

Hierarchical plot occupancy of the 12 most common species, showing influence of grass height and cover on persistence and colonization of each species during the austral summer survey for two years 2010/11-2011/12 at Ingula

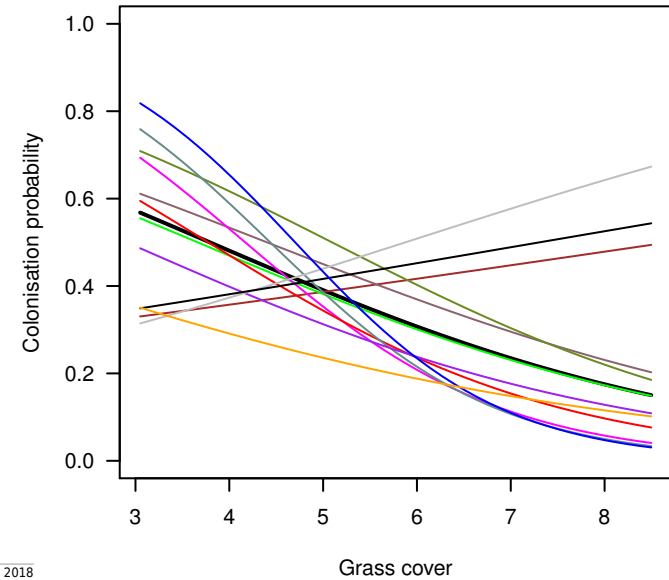
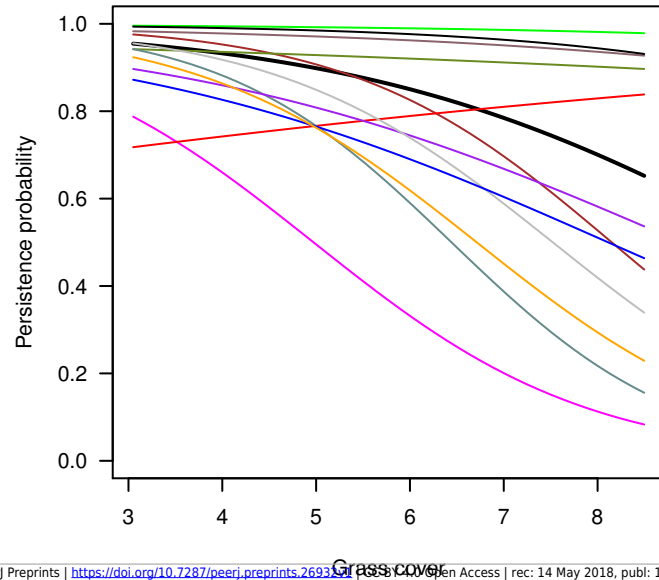
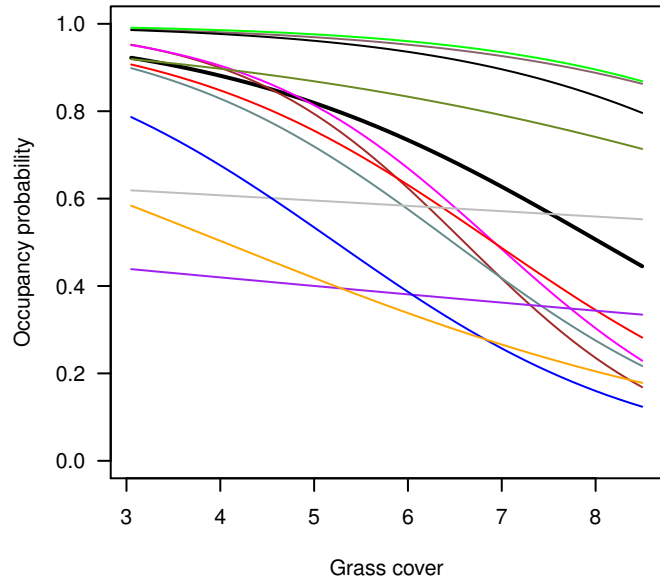
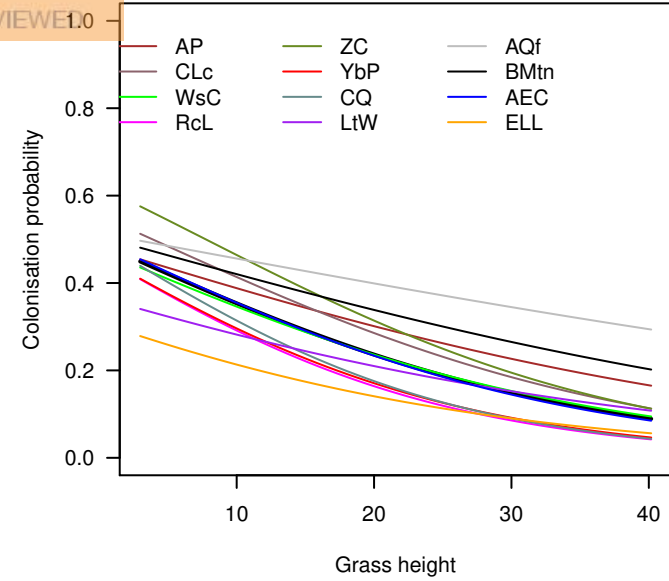
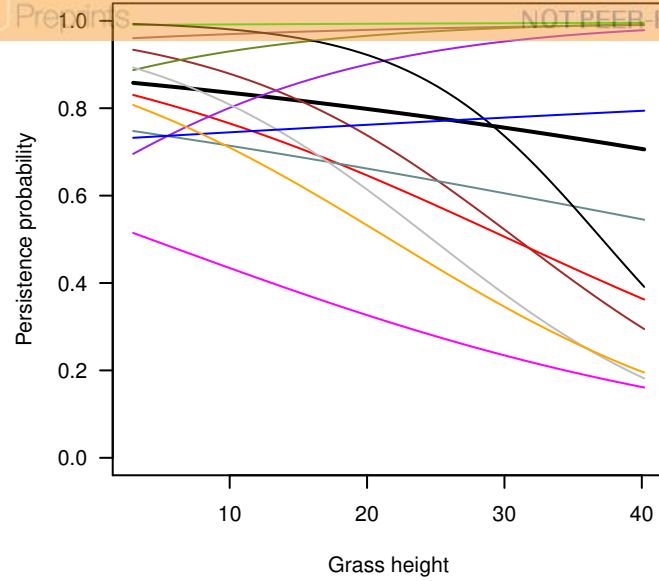
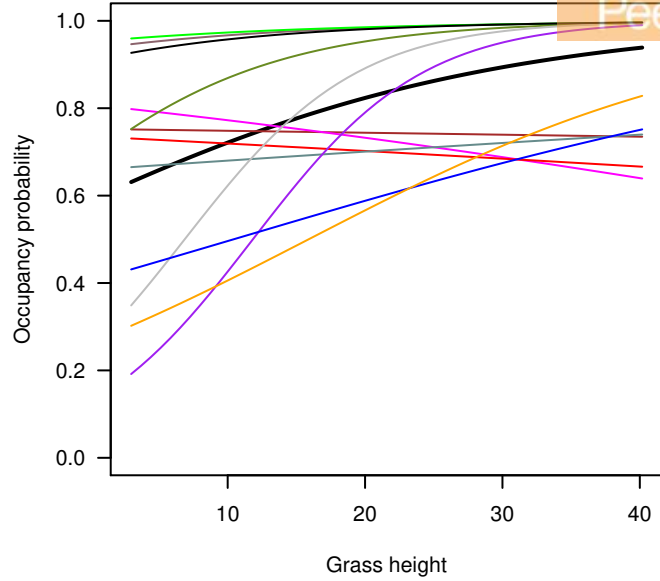
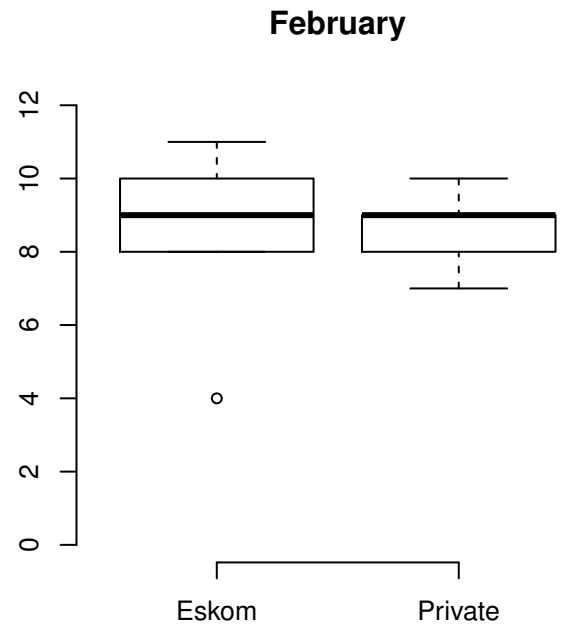
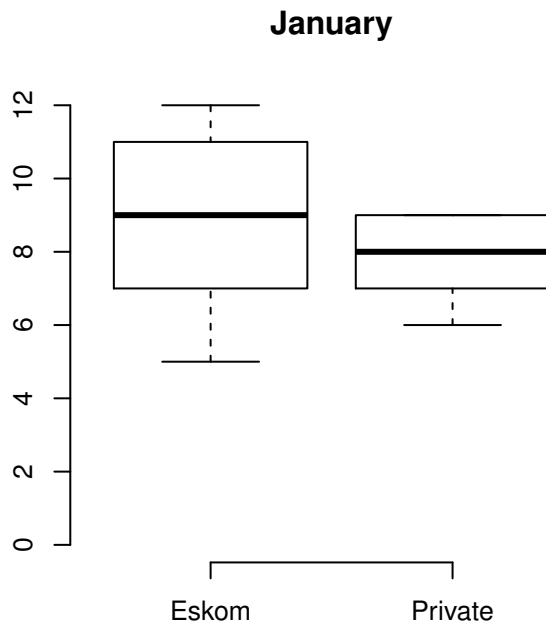
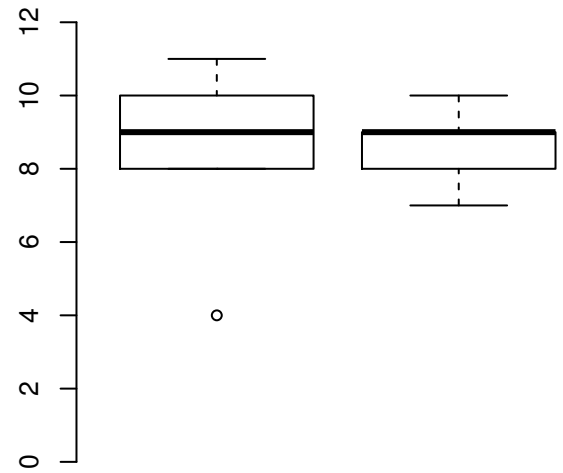
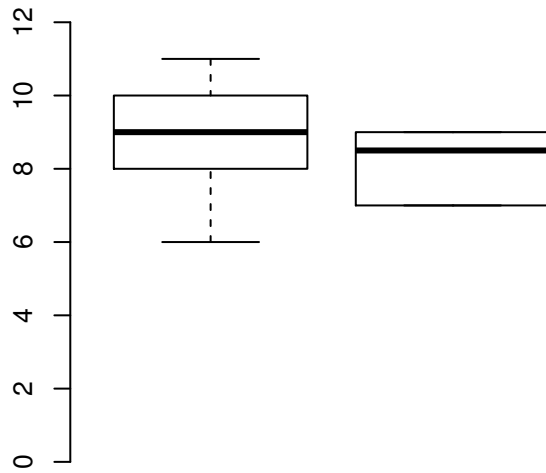


Figure 4(on next page)

Bird species richness comparing Ingula farms that experienced little grazing compared to neighbouring farms which were mostly annually burned and intensively grazed with cattle during two austral summer surveys (2010/11-2011/12). Twelve plots were surveyed



Species richness