

The effects of shrub encroachment on bird occupancy vary with land use in an African savanna

R. A. Stanton¹ , R. J. Fletcher Jr.², M. Sibiyi³, A. Monadjem⁴ & R. A. McCleery²

¹ School of Natural Resources and the Environment, University of Florida, Gainesville, FL, USA

² Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

³ Biological Sciences, University of Eswatini, Kwaluseni, Swaziland

⁴ University of Eswatini, Kwaluseni, Swaziland

Keywords

global change synergies; land-use change; occupancy models; savannas; shrub encroachment; trait-based ecology.

Correspondence

Richard A. Stanton, School of Natural Resources and the Environment, University of Florida, 100 Black Hall, Gainesville, FL 32611, USA. Tel: +1 (352) 846-0632; Fax: +1 (352) 392-6984
Email: richardastanton@ufl.edu

Editor: Res Altwegg

Associate Editor: Viviana Ruiz-Gutierrez

Received 23 January 2019; accepted 28 May 2020

doi:10.1111/acv.12620

Abstract

Land-cover and land-use change are major drivers of global biodiversity loss. Savannas are experiencing shrub encroachment and land-use changes that affect animal communities, yet how the effects of shrub encroachment vary with land use remains unclear. We also need to determine which species traits explain the effects of shrub encroachment and land-use changes to identify potential drivers of community change and predict species' responses to conservation efforts. We sampled birds across gradients of shrub encroachment and land use (protected savanna, pastures, homestead lands, and sugarcane) in the lowveld savanna of Eswatini to: (1) test for the effects of shrub encroachment, land-use change, and their potential synergies on the occurrence of 48 species of birds; and (2) determine which species traits (those associated with nesting, foraging, or vulnerability to predation) explained species' associations with shrub encroachment and land-use change. We used Bayesian multispecies occupancy models to account for imperfect detection, interpret species responses, and understand the effects of species traits. We found evidence for community-wide synergies between shrub encroachment and land-use effects on birds that varied with species' diets. Agricultural intensification had negative effects on the occurrence of most species examined, while shrub cover typically had positive effects which were stronger in pastures and homestead lands than in protected areas. The negative effects of land-use change were greatest for insectivores and cavity nesters, whereas insectivore occurrence increased with shrub cover, collectively indicating that nesting and foraging traits best explained species responses to land-use and land-cover change in the region. Our results suggest that shrub cover management for bird conservation should vary with land use: shrubs could be thinned in protected areas without reducing bird occupancy but shrubs in homesteads should be retained.

Introduction

Humans are changing the world at an unprecedented pace, leading to rapid loss of biodiversity (e.g., Mooney *et al.*, 2009). Land-use and land-cover change are two of the world's most widespread and important drivers of biodiversity loss (Sala *et al.*, 2000; Lambin, Geist, & Lepers, 2003). Land-use change is often associated with increased material inputs or labor applied to landscapes, such as when rain-fed subsistence agriculture is converted to plantation monoculture (Ellis & Ramankutty, 2008). Land-cover change, on the other hand, occurs when the prevailing vegetation structure in a landscape shifts to a different state, irrespective of land use (Turner, Lambin, & Reenberg, 2007). Common examples of land-cover change include the conversion of forest land

cover to non-forest (e.g., grassland) and the drainage of wetlands (Lambin *et al.*, 2003). However, vegetation cover can also change within a land-cover type, such as shrub encroachment occurring in savannas worldwide (Lambin *et al.*, 2003; Eldridge *et al.*, 2011; Stanton *et al.*, 2018).

Savannas cover 20% of the Earth's terrestrial land mass, provide livelihoods for >1 billion people, and include multiple biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Lehman & Parr, 2016). However, savanna biodiversity appears to be under threat from widespread and simultaneous land-use and land-cover changes. Land-use change in savannas is characterized by a combination of: (1) conversion of native vegetation to pasture and subsistence agriculture to directly support human populations; and (2) conversion of native vegetation, pastures, and

subsistence agriculture to plantation monocultures to support economic development (Holden & Otsuka, 2014). Land-cover change in savannas is largely characterized by shrub encroachment, an increase in woody cover beyond that expected under historical variation which is occurring across multiple land uses as a result of atmospheric CO₂ enrichment, overgrazing by livestock, loss of browsing by wild megaherbivores, and fire suppression (Roques, O'Connor & Watkinson, 2001; Stevens, Erasmus, Archibald, & Bond, 2016).

Changing land use and land cover in savannas may have serious consequences for native animals. Land-use change can affect animals by altering food resources and adding anthropogenic stressors such as pesticides, poaching, and noise pollution (Foley *et al.*, 2005). Shrub encroachment also alters animal occurrence, reducing some species and promoting others, perhaps by changing available nest substrates, altering food resources and foraging niche space, or providing cover that affects species' vulnerabilities to predation or desiccation (Seymour & Dean, 2010; Sirami & Monadjem, 2012; Dorado-Rodriguez *et al.*, 2015; Soto-Shoender *et al.*, 2018; Stanton *et al.*, 2018; Hering *et al.*, 2019). Shrubs provide stable cover and food resources that may mitigate the effects of predators, human disturbance, and capture of primary production for human use in intensive land uses for many species (Hinsley & Bellamy, 2000; Frid & Dill, 2002). Yet, whether the effects of shrub encroachment on animal occurrence vary among land uses is currently unknown.

Animal traits provide a potentially generalizable and predictive basis for understanding variation in responses of vertebrates to shrub encroachment and land-use intensification. Species traits also suggest possible mechanisms for responses to environmental changes and several traits have been associated with extirpations and extinctions (McGill, Ehnquist, Weiher, & Westoby, 2006; Brook, Sodhi, & Bradshaw, 2008). Furthermore, knowing which species traits are associated with changes in occurrence can inform conservation practice. For example, changes in trophic relations among animals can stymie restoration efforts focused on vegetation management (Suding *et al.*, 2004; e.g., Jeppesen *et al.*, 2007), so whether predatory species respond consistently to shrub encroachment matters for predicting if shrub thinning can restore species characteristic of open savanna. Likewise, whether species' occurrences are better explained by diet or nest substrate can indicate whether restoration efforts should be tailored to providing specific food items or creating suitable nesting structure (Rotenberry, 1985). Despite the potential scientific and conservation utility of species' traits, community composition in response to shrub encroachment has seldom been evaluated in terms of animal traits across land-use gradients (Kutt & Martin, 2010; Seymour & Dean, 2010).

To understand the influence of land-use change and shrub encroachment on animals with different traits, we surveyed birds in a savanna landscape across gradients of land use (agricultural production gradients ranging from protected areas to monoculture sugarcane plantations) and land cover

(shrubs encroachment) in southern Africa. Our objectives were to: (1) determine the additive and interactive effects of shrub encroachment and land use on the occurrence of common bird species and; (2) determine if species traits (nesting substrate, diet, and mass) explained heterogeneity in effects among species. Relative to other vertebrate taxa, birds are widespread, with traits that vary considerably and have been well described, making them an ideal model to investigate how land-use change and shrub encroachment affect animals with different traits (Newbold *et al.*, 2013). We predicted that the community-level effects of agricultural land use (pasture, homestead lands, and sugarcane) would be negative compared to protected savannas and that the community-level effect of shrub encroachment would be positive, as found in a recent meta-analysis (Stanton *et al.*, 2018). Furthermore, we expected that most species would exhibit land use by shrub encroachment interactions, specifically that species' positive responses to shrub cover would be weakest in protected savanna and strongest in subsistence agriculture because shrub encroachment may provide predator refugia and additional resources in otherwise homogeneous agricultural areas. We also predicted that species responses to land use and shrub encroachment would be explained by species traits (Owens & Bennett, 2000; Hockey, Dean, & Ryan, 2005; Kutt & Martin, 2010; Sirami & Monadjem, 2012). For example, we predicted that shrub encroachment effects on bird occupancy would be negative among species with poor maneuverability and positive among insectivores. Specifically, we treated the relative effects of nesting, foraging, and vulnerability-associated traits as (1) indicators of which stressors are driving common species' responses to land-use change and shrub encroachment, and (2) predictors of common species responses to shrub cover management that could generalize to other species and locations.

Methods

Study area

We sampled birds across gradients of shrub encroachment and land use throughout lowveld savanna in the Kingdom of Eswatini (formerly known as Swaziland; study area extent: ~6900 km²; Fig. 1). Lowveld savanna is characterized by a grass layer interspersed with woody plants (Mucina, Rutherford, & Powrie, 2005). Several native woody plants have been increasing and contributing to shrub encroachment (e.g., sicklebush, *Dichrostachys cinerea*, buffalo thorn, *Ziziphus mucronata*, and prickly acacia, *Vachellia nilotica*; Monadjem, 2000; Loffler & Loffler, 2005). The lowveld of Eswatini experiences a mean monthly temperature of 26°C in January when most bird species are breeding and typically receives 550–725 mm of rain annually (Goudie & Price Williams, 1983; Sirami & Monadjem, 2012). The land-use mosaic in the lowveld was mainly comprised of four common land uses: protected areas, community pastures, homestead lands, and sugarcane plantations. Protected areas in the Swazi lowveld were primarily comprised of native vegetation (Hurst *et al.*, 2014). Community pastures were degraded

savannas where people reared livestock. Homestead lands occurred where people kept their homes, practiced subsistence agriculture, and retained varying amounts of savanna vegetation. Sugarcane plantations were intensive monocultures; plantations have been present since the 1950s and have increased in extent (Bailey, McCleery, Binford, & Zweig, 2016).

These land uses represent a qualitative gradient of land-use intensity. At the low end of this intensity gradient are savannas in protected areas. Pastures have moderate land-use intensity mainly from cattle grazing. Homestead lands have the highest human density but inputs of water and chemicals for agriculture are limited. Sugarcane plantations have the largest irrigation and chemical inputs of any land use and form monocultures but have lower human densities than homestead lands (Ellis & Ramankutty, 2008; Gaugris & Van Rooyen, 2010). Land uses in savannas also differ in their susceptibility to shrub encroachment (Twine & Holdo, 2016). Where substantial land-use change has occurred, such as savanna conversion to plantation monoculture, shrub encroachment is unlikely to occur. Yet where less-intensive changes have occurred, such as initiation of cattle grazing or planting of subsistence crops in protected savannas, shrub encroachment can be common (Bailey *et al.*, 2016; Fig. 1).

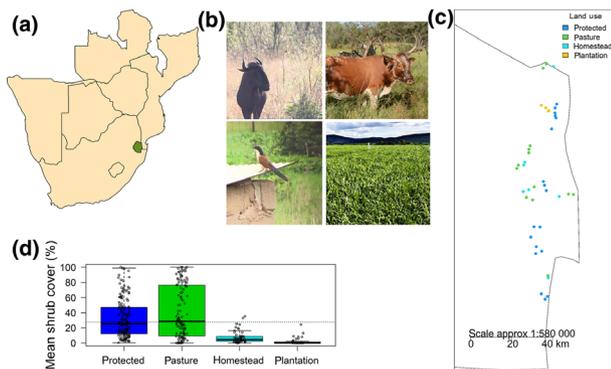


Figure 1 (a) Eswatini (dark polygon), in southern Africa includes a land use mosaic of (b) protected areas, community pastures, homestead lands, and sugarcane plantations (shown from top left to bottom right). We sampled birds in lowveld savanna across (c) 42 grids (colored circles indicate different land uses) comprised of 5–10 sampling points (mean: 8.83) from December 2014 to March 2015. The left margin indicates the approximate western limit of lowveld savanna in Eswatini while the irregular line near the center marks the border between Eswatini and Mozambique. (d) Shrub cover was highest and most variable in protected areas and pastures, but was lower in homestead lands and nearly absent from sugarcane plantation. The dotted horizontal line represents study-wide mean per cent shrub cover while the solid horizontal lines indicate group-level medians, and boxes group-level inter-quartile ranges (25th and 75th). Bubbles represent individual values at each of the 371 points where we measured shrub cover and recorded bird occurrence.

Sampling design

Stratification by land use and shrub encroachment

We sampled across the four predominant land uses—protected area savannas, community pastures, homestead lands, and sugarcane—and the full range of shrub cover present within each land-use type by employing a stratified sampling design. We visited six protected areas (range: 700–16,000 ha; United Nations Development Programme Global Environment Facility, 2013, <https://www.thegef.org/project/strengthening-national-protected-areas-system-swaziland>), seven community pastures, seven adjoining homestead lands, and a large sugarcane plantation (3,800 ha; <http://www.hulets.co.za/ops/swaziland.asp>). We sampled protected areas and the sugarcane plantation in the Swazi Lowveld with permission from the appropriate authorities and in neighboring villages with permission from local chiefs. We attempted to gain access to four sugarcane plantations, but only one allowed access for surveys. We distinguished community pastures from homestead lands and associated farm fields in each village by consulting with local chiefs and their designees, treating pastures and homestead lands separately because of differences in human and livestock activity as well as vegetation structure. All research followed an animal care and use protocol approved by the University of Florida (protocol #: 201509045).

We sampled diurnal bird communities in protected areas, pastures, homestead lands, and a sugarcane plantation, and across a gradient of shrub encroachment where present (protected areas, pastures, and homestead lands) by selecting patches of low, medium, or high shrub cover. We defined low, medium, and high shrub cover as $< \sim 20\%$, $\sim 20\text{--}60\%$, and $> \sim 60\%$ mean cover as determined by visual estimation of two perpendicular ~ 1 km transects within a given protected area or community. We then established at least one grid, ideally comprised of nine points/grid, arranged in a 3×3 square design with all points ≥ 250 m apart (range: 5–10, mean: 8.83 because the vagaries of sampling on the ground required minor modifications of our protocol; Table S1.1). Homestead land grids followed footpaths or roads because each homestead was fenced, but we attempted to replicate a square shape whenever possible. Points within a grid were placed an average of 2.3 km from the nearest neighboring grid to maximize independence among grids (range: 0.85–5.3 km). We created more than one grid within a shrub cover category on the same property when we could not establish grids in each shrub cover category on the same property to secure additional samples (Table S1.2). Samples with similar shrub cover were therefore nearer to one another on average than may have been the case otherwise.

Bird surveys

We conducted repeated 10-minute point counts at each point, counting all birds detected within 50 m. We recorded the

observer, date, time, and wind speed on a Beaufort scale, twice each morning. We visited each point three to four times (mean: 3.97) during the breeding season, 11 December 2014–15 March 2015. We rotated two observers (RAS and MDS) among grids and surveyed between 30 mins before sunrise and 5 hrs after, or within 3 hrs of sunset. We did not survey when it was raining or wind speeds were >20 km/hr. We ran grids in a different sequence each visit so points within a grid were visited at different times of day and so early and late sampling dates were not concentrated in a particular part of the study area.

Vegetation structure

We sampled vegetation structure surrounding each point by measuring grass, shrub, and tree cover. We defined trees as woody plants >3 m in height and shrubs as woody plants ≤3 m tall after Monadjem (2005) and Sirami & Monadjem (2012). We measured per cent grass, shrub, and tree cover using the line intercept method with three replicates per point and a 50 m tape, recording the amount of each cover type on or above the tape (Tansley & Chip, 1926). We placed the three lines at each point at 0, 120, and 240 degrees orientation. We calculated the mean of the line intercept values recorded at each point for grass, shrubs, and trees and treated them as estimates of per cent cover for each cover type.

Analytical methods

Species traits

We assigned a mass and diet group to each species using Hockey *et al.* (2005; Appendix S1). We binned each species into a diet group based on the most common food type described in Hockey *et al.* (2005). For example, we classified as frugivores any species that ate mainly fruits although most frugivores also consume arthropods. Likewise, 28 species of predatory birds occur in the Swazi Lowveld, including several common non-raptor species amenable to detection on point counts (Hockey *et al.*, 2005). We determined whether each species we detected was a predator of birds and treated predatory status as a trait distinct from diet because predation can have strong effects on community composition (Hairston, Smith, & Slobodkin, 1960; Holt, 1977). We classified trees, shrubs, woody cavities, and grass as nest substrates of interest, coding each species' use of those substrates as 1 if used and 0 if not (Hockey *et al.*, 2005). Some nest and diet traits were represented by many species and others by few species (range: 2–31; Table S1.3). We treated the ratio of each species' mass to wing chord length as a proxy for wing loading, a trait associated with maneuverability (low loading and mass to wing chord ratio) or speed (high loading and mass to wing chord ratio; Norberg, 1990; Hockey *et al.*, 2005). We used mean female masses and wing chord lengths when reported and the mean of mixed or unknown sex samples otherwise (Hockey *et al.*, 2005).

Quantifying occupancy

We estimated occupancy using Bayesian multispecies occupancy models (Dorazio & Royle, 2005; Kéry & Royle, 2015). Occupancy models account for imperfect detection using repeated observations, such as species' detection histories, and can be used to model occupancy as a function of covariates (MacKenzie *et al.*, 2002). Multispecies occupancy models extend single-species models to provide community-level inferences based on model hyperpriors and shrinking species-specific coefficients toward the community-wide mean (Iknayan, Tingley, Furnas, & Beissinger, 2014). Specifically, we fitted a model that used random effects with community-level hyperpriors and hyperparameters defining the distribution of species-level intercepts and covariate effects. Thus, inference regarding community-level effects of shrub encroachment and land-use change can be made directly from the model (Dorazio & Royle, 2005). Occupancy models can be biased for rare species, that is, those detected in fewer than approximately 10% of locations (Royle & Dorazio, 2008), and in multispecies occupancy models patterns for rare species with little occupancy information are largely driven by the community mean because the model parameters undergo shrinkage (also known as 'regularization', Broms, Hooten, & Fitzpatrick, 2016). Furthermore, many bird species are not well suited to point counts because of their behaviors and patterns of space use, and this problem is exacerbated among rare species (Bibby *et al.*, 2000). Given our objective of comparing species and trait-based responses across four land-use types, little to no reliable information would have been gained from detections of rare species so we only modeled species observed at ≥10% of the points we visited (48 species).

We fitted two models to different subsets of our data. First, we fitted a model to all the data and included additive effects of land use and shrub cover plus a random effect of sampling grid on occupancy (to account for spatial dependence within grids) using an 'effects' parameterization with protected areas as the reference land use (Kéry & Royle, 2015). We then tested for shrub cover by land-use interactions by fitting a model with community- and species-level interaction terms to a subset of the data that excluded sugarcane plantation, where significant shrub encroachment did not occur, and checking whether 95% credible intervals for the interaction terms excluded zero.

In both models we defined species occupancy as a binary, partially observed latent variable z_{ik} , modeled as the outcome of a Bernoulli trial with a single parameter (ψ_{ik}), the probability of occurrence, for each species k at location i , and the likelihood of occurrence: $z_{ik} \sim \text{Bernoulli}(\psi_{ik})$. We assumed there were differences in occupancy among species generated by land-use and shrub cover conditions, which we modeled using a logit link function. We accounted for lack of independence among points within each grid, r , by drawing species-level grid effects from a distribution with a shared mean and variance. Similarly, we assumed that species detections (y_{ijk}) followed a Bernoulli distribution with the parameter p_{ijk}

representing the detection probability for species k at location i during sampling period j , which was conditional on the latent occupancy status of the site (z_{ijk}). We used a logit link to model covariate effects of centered and scaled survey date and time with quadratic terms. We modeled covariates on detection as random effects, with species-level estimates drawn from a distribution with a shared mean and variance (i.e., hyperparameters). Consequently, the model statement for the first model was:

$$\begin{aligned}
 y_{ijk} &\sim \text{Bernoulli}(z_{ijk} p_{ijk}) \\
 \text{logit}(p_{ijk}) &= \alpha_k + \alpha 1_k \text{date}_{ij} + \alpha 2_k \text{date}_{ij}^2 \\
 &\quad + \alpha 3_k \text{time}_{ij} + \alpha 4_k \text{time}_{ij}^2 \\
 z_{ijk} &\sim \text{Bernoulli}(\psi_{ik}) \\
 \text{logit}(\psi_{ijk}) &= \beta_k + \beta 1_k \text{pasture}_i + \beta 2_k \text{homestead}_i \\
 &\quad + \beta 3_k \text{plantation}_i + \beta 4_k \text{shrub cover}_i + u_{kr} \\
 \alpha_k &\sim \text{Normal}(\mu_\alpha, \Sigma_\alpha) \\
 \beta_k &\sim \text{Normal}(\mu_\beta, \Sigma_\beta) \\
 u_{kr} &\sim \text{Normal}(\mu_{kr}, \sigma_{kr})
 \end{aligned}$$

The coefficients explaining variation in ψ_{ik} among land uses ($\beta 1_k$, $\beta 2_k$, $\beta 3_k$ and $\beta 4_k$) reflect the difference between occupancy in protected areas (β_k) and each respective land use. Whether the credible interval for an agricultural land-use coefficient excludes zero can therefore be used to infer whether that land use alters occupancy for species k relative to a protected area.

The analogous model fitted without data collected in the sugarcane plantation was similar but included species-specific shrub cover by land-use interaction terms governed by community-level hyperparameters of primary interest:

$$\begin{aligned}
 \text{logit}(\psi_{ijk}) &= \omega_k + \beta 1_k \text{pasture}_i + \beta 2_k \text{homestead}_i \\
 &\quad + \beta 4_k \text{shrub cover}_i + \beta 5_k \text{pasture}_i \text{shrub cover}_i \\
 &\quad + \beta 6_k \text{homestead}_i \text{shrub cover}_i + \gamma_{kr} \\
 \beta 5_k &\sim \text{Normal}(\mu_{\beta 5}, \sigma_{\beta 5}) \\
 \beta 6_k &\sim \text{Normal}(\mu_{\beta 6}, \sigma_{\beta 6})
 \end{aligned}$$

We used vague priors and hyperpriors for all parameters (e.g., normal with mean = 0 and precision = 0.1 for hyperpriors on the effects of land use, shrub cover, and land use by shrub cover interaction terms). We ran each model with three chains for 60,000 iterations after adaptive and burn-in periods of 5,000 iterations each and thinned each chain by collecting every 20th observation, resulting in 8,250 samples from the posterior distribution for all parameters. We monitored model convergence by examining trace plots and verifying that all Gelman–Rubin r statistics were ≤ 1.1 (Gelman & Rubin, 1992; Gelman & Hill, 2007). We ran all multispecies occupancy models in JAGS called through R version 3.4.4 using the jagsUI package (Plummer, 2003; Kellner, 2016; R Core Team, 2020). There is not a consensus on which model fit diagnostics are best for multispecies occupancy models, but several authors

recommend tailoring model assessment to the inferential goals of each study (Broms *et al.*, 2016; Warton *et al.*, 2017). We therefore investigated whether there was evidence of spatial autocorrelation in the occupancy residuals of our most parameterized model, that is, the model that included shrub cover by land-use interaction terms, despite the fact that we included a random effect of sampling grid in the model (Wright *et al.*, 2019; Appendix S2). Finding no evidence of residual spatial autocorrelation for any species, we were satisfied that the models were appropriate for our data (Appendix S2).

Effects of shrub encroachment, land-use type, and interactions

We calculated categorical trait-based measures (e.g., the average β_{shrub} for cavity-nesting species) as derived parameters. To assess the effects of the continuous traits of mass and maneuverability, we regressed each species effect size of interest (i.e., response to each agricultural land use and to shrub cover compared to a protected area baseline) on each species' trait value for each draw from the posterior distribution, generating a posterior distribution of slope estimates that we used to calculate a credible interval (e.g., Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2009). We log-transformed masses and centered and scaled per cent shrub cover before model fitting. We treated nest substrate, diet, predatory status, maneuverability, or mass as relevant predictors of shrub encroachment effects on bird species occupancy if 95% credible intervals for the appropriate parameters overlapped zero and not important otherwise, although we note where a predictor's 90% credible interval did not overlap zero but the 95% interval did as marginal.

Results

We sampled in 42 grids containing 371 sampling points. Per cent shrub cover differed among land uses, ranging from 0 to 100% in protected areas and community pastures (means $32 \pm 1.3\%$ SE and $41 \pm 1.8\%$ SE respectively), 0–35% in homestead lands, and 0–24% in the sugarcane plantation (means $7 \pm 0.4\%$ SE and $2 \pm 0.3\%$ SE, respectively; Fig. 1; $F_{3, 367} = 38.04$, $P < 0.0001$). We found significant pairwise differences in mean shrub cover between land uses, except between homestead lands and sugar plantation (Tukey's HSD adjusted $P = 0.76$ for homestead lands–sugar plantation versus 0.00–0.03 for all other post-hoc comparisons). We recorded 209 bird species, 48 of which we detected in $\geq 10\%$ (37) of points and analyzed using multispecies occupancy models (Appendix S1). We detected 48, 48, 42, and 34 of the 48 species in protected areas, community pastures, homestead lands, and sugarcane plantation, respectively (mean detected species richness: 18.2 ± 0.32 SE, 17.3 ± 0.26 SE, 14.7 ± 0.26 SE, and 8.2 ± 0.28 SE for protected areas, pastures, homestead lands, and sugarcane plantation, respectively; Appendix S1). Nearly half the species we detected (104 of 209, 49.8%) were recorded on ≤ 10 points, 88 species were detected on ≤ 5 points, and 35 species were detected at a single point; Appendix S1; Figure S1.1).

Contrasting occupancy across shrub cover and all four land uses

From the community model with four land uses and no interaction terms, 19 of 48 species had associations with shrub cover (i.e., the 95% credible interval for β_{shrub} , excluded zero), 14 of which were positive (Fig. 2). In contrast, land-use intensification primarily had negative effects on occupancy. Relative to protected areas, the most frequent negative effects of land use occurred with sugarcane plantation (38 negative, 0 positive), then homestead lands (17 negative, 3 positive), followed by pasture (5 negative, 0 positive; Fig. 2; Table S3.1). We also found marginal occupancy relationships for at least one species with shrub cover and each land use (i.e., the 90% CRIs excluded zero but the 95% CRIs did not; Table S3.2).

We found negative community-wide average effects of non-protected land uses on bird occupancy and marginal positive effects of shrub cover (Fig. 2; Table S3.2). Furthermore, both nest substrate and diet had associations with species responses to shrub cover and land use. Shrubs were positively associated with occupancy among insectivores and species using all nest substrates except cavities (Fig. 3). Community pastures were negatively associated with the occurrence of species using all nest substrates as well as frugivores, insectivores, and seed eaters while homestead lands were negatively associated with the occurrence of tree nesters, shrub nesters, and insectivores (Fig. 3; Table S3.2). Sugarcane plantation had negative effects on the occupancy

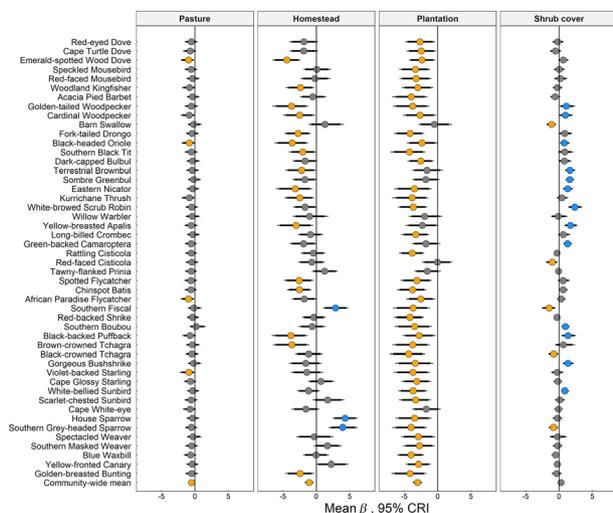


Figure 2 Species occupancy responses (points) of common birds with 90% (thick error bars) and 95% (thin error bars) CRIs to land use and shrub cover relative to protected areas. Species with responses distinguishable from zero are indicated by blue (positive responses) or orange (negative responses) points. Community-wide mean responses are located at the bottom of the plot. Estimates based on a Bayesian multispecies occupancy model fitted to 48 species detected in $\geq 10\%$ of 371 survey stations sampled in low-veld savanna, Eswatini, December 2014–March 2015.

of species using all nesting substrates as well as all diet groups (Fig. 3; Table S3.2). We also found a relationship between response to homestead land use and bird mass that was nearly identical to a marginal relationship between responses to homestead land use and maneuverability because these measures were correlated, but this trait explained no other responses to land use or shrub encroachment (Spearman’s $\rho = 0.95$; Fig. 3; Table S3.3). Predatory species (recorded in [Hockey *et al.*, 2005] as a predator of birds, regardless of primary diet) were less likely to occur in sugarcane than protected areas, but this trait explained no other responses to land use or shrub encroachment (Table S3.1).

Synergies between shrub encroachment and land use

Because sugarcane plantations had very little shrub cover (2%) and we had no a priori expectation that shrub encroachment was occurring in that land use, we only considered potential interactions between shrub cover and three land uses: protected areas; pastures; and homestead lands. We found evidence for a community-wide shrub cover by land-use interaction, where the effect of shrub cover on occupancy tended to be weaker in protected areas and stronger in homestead lands and pastures (Table S4.1). For most species (26 of 48 species, 54%), mean predicted occupancy had the same trend across all land uses, but the magnitude differed among land uses (Figure S4.1–48). For the remaining 22 species, mean predicted occupancy increased across the range of shrub cover in at least one land use while decreasing in at least one other land use (Figure S4.1–48). The pasture by shrub cover interaction was positive (mean β : 0.52, 95% CRI: 0.12–0.96, Table S4.1), as was the homestead lands by shrub cover interaction (mean β : 1.73, 95% CRI: 0.87–2.64; Fig. 4; Table S4.1). Predicted occupancy across the range of shrub cover within each land use was similar to that obtained in the model without shrub cover by land-use interactions, with the notable exception that shrub cover reduced the occupancy of seed-eating birds in protected areas and pastures but increased it in homestead lands (Figure S4.49).

Discussion

We found that shrub encroachment was associated with increased occurrence for many species and had no significant effect on several others, while land-use intensification was associated with reduced occurrence for nearly all species. However, the effects of shrub encroachment on bird communities were also dependent on land-use context. Studies of shrub encroachment effects on savanna biodiversity seldom span land-use gradients and a recent meta-analysis found no studies that included homestead lands (Stanton *et al.*, 2018). Our results help to fill this gap, providing insight into the effects of shrub encroachment and its relevance for conservation, where shrub encroachment tended to increase

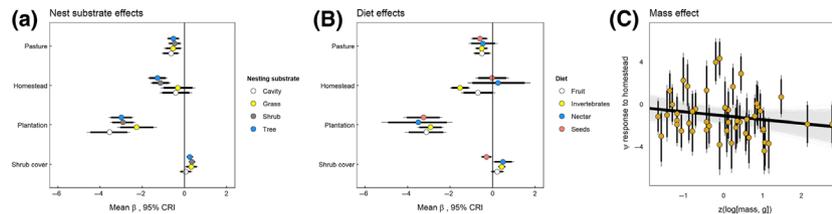


Figure 3 Occupancy responses (points) with 90% (thick error bars) and 95% (thin error bars) CRIs of common bird species to land use and shrub cover relative to protected areas in lowveld savanna, Eswatini, December 2014–March 2015, varied according to (a) nesting substrate and (b) diet. Bird occupancy responses to homestead land use (c) were negatively associated with the scaled and centered log of each species' average mass. Group responses and CRIs for categorical traits were determined by pooling posterior distributions of community occupancy model β s of species sharing each respective trait in common. Response to mass was determined by regressing species' responses to land use and shrub cover on species' average mass for each draw from the posterior distribution. Thin gray lines show the relationship estimated for each regression and the thick black downward sloping line represents the mean result.

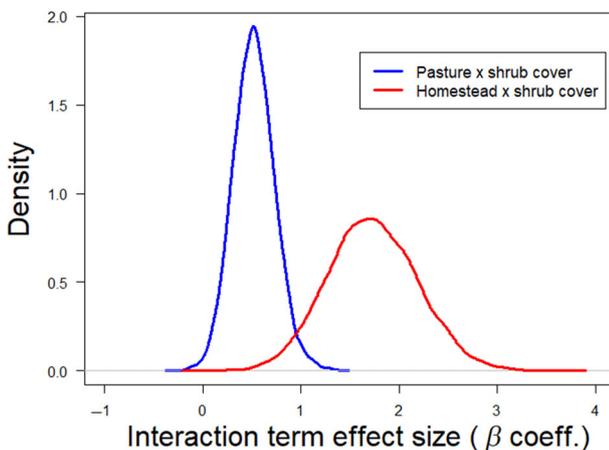


Figure 4 Posterior distributions of community-level shrub cover by land-use interaction terms (hyperparameters) from Bayesian multi-species occupancy models fitted to data from surveys of 48 bird species in three lowveld savanna land uses (protected areas, community pastures, and homestead lands), Eswatini, December 2014–March 2015. The interaction terms had positive effects (increasing predicted occupancy with more intensive land uses) and 95% CRIs excluding zero (Table S4.1).

occurrence of common birds in non-protected land uses. This finding is encouraging, given that relatively little land in sub-Saharan Africa is formally protected (World Database on Protected Areas, <http://www.protectedplanet.net/>). Likewise, our finding that nest substrates and diets explained bird responses to shrub encroachment and land use highlights the value of a trait-based approach for generalizing the effects of land-use and land-cover effects on savanna biodiversity. Our results also have several important conservation implications, which we address below.

Effects of shrub encroachment

We found that the effects of shrub encroachment were generally positive for the 48 species we considered, as expected given bird's ecological traits, and consistent with the weak evidence for positive effects of encroachment on

bird diversity and abundance found in a recent meta-analysis (Stanton *et al.*, 2018). However, it is surprising that shrub encroachment did not reduce the occurrence of grass-nesting species. We speculate that a combination of three non-exclusive factors may explain this result. First, locations with a paucity of shrub cover may also lack grass cover, leaving grass-nesting species with limited suitable nest substrate. Second, it is common for grass-nesting species within savannas to place their nests adjacent to a shrub (e.g., species in the genus *Prinia*; Hockey *et al.*, 2005), which could potentially constrain nest-site selection for one or more species. Finally, shrubs may provide foraging substrate, cover, or perches for grass-nesting species and therefore nest-site selection for some species could be driven by resource complementation (Dunning, Danielson, & Pulliam, 1992).

The effects of shrub encroachment varied among land uses in two ways. In some species, mean predicted occupancy had the same general relationship with shrub cover among land uses but the magnitude of the effect varied. In others, the direction of the mean predicted relationship with shrub cover varied among land uses. We hypothesize that this pattern occurred because the ecological functions of shrubs varied in their relative importance among species and land uses. In some cases, shrubs may have been providing much needed escape cover, food items, or nesting substrates that were lacking in the environment, increasing occupancy in a given land use. In other cases, shrubs may have been replacing grassy herbaceous cover that harbored better quality resources, decreasing occupancy. This suggests that (1) while promoting land-cover heterogeneity within land uses can promote bird diversity, the scale and amount of land-cover heterogeneity to target for conservation remains an open question, and (2) resource complementation may be a common, but understudied, mechanism driving patterns of species occurrence in savannas.

Effects of land use

Sugarcane plantation had markedly negative effects on bird occurrence, which is not surprising given that sugarcane cultivation is an intensive land use that typically leads to

widespread land-cover conversion. Linear features in sugarcane plantations, such as road verges and irrigation channels, provide pockets of floristic heterogeneity that may attract birds, but the value of such features is unclear (Keir, Pearson, & Congdon, 2015). Given the dramatic contrast between sugarcane plantation and all other land-use types, as well as the fact that we found no positive species' associations between sugarcane and occurrence, we suspect that sugarcane is poor habitat for most bird species. It is possible, however, that aerial insectivores benefit from foraging in sugarcane, which is frequently used by some foraging bats (Noer, Dabelsteen, Bohmann, & Monadjem, 2012; Shapiro, Monadjem, Röder, & McCleery, 2020).

Pastures had the full suite of species seen in protected savanna, and only five species were less likely to occur in pastures than in protected savanna. This result suggests that moderate grazing and modest human disturbance is tolerable for many species if vegetative cover resembles that found in protected savanna, consistent with several studies of grazing effects on bird diversity (Martin & McIntyre, 2007; Gregory, Sensenig, & Wilcove, 2010). Homestead lands, however, were distinctly less suitable than protected savanna, likely owing to a combination of human disturbances and removal of native vegetation similar to but less intensive than that found in sugarcane.

Traits provided more insight about variation in the effects of pasture and homestead land uses: shrub nesters, tree nesters, and insectivores were less likely to occur in homestead lands while users of all nest substrates, as well as fruit, invertebrate, and seed eaters were less likely to occur in pastures. However, it is important to emphasize that the magnitude of the negative effects we observed were considerably greater but more variable in homesteads. We suspect that insectivorous birds were less likely to occupy homestead lands because the quantity and perhaps heterogeneity of vegetative cover was insufficient for many species, although it is also possible prey availability was lower in these areas. One surprising result was that cavity nesters were less likely to occupy pastures but not homestead lands. This pattern may be explained in part by: (1) increased occurrence of cavity-nesting human commensals (House Sparrow, *Passer domesticus*, and Southern Grey-headed Sparrow, *Passer diffusus*) that nest in buildings and other man-made cavities (Hockey *et al.*, 2005); and (2) loss of naturally occurring cavities in pastures caused by widespread collection of wood for fuel and building materials (Twine & Holdo, 2016). Likewise, shrub cover may promote the occurrence of seed-eating birds in homestead lands and discourage seed-eating bird occurrence in other land uses because escape cover is more limiting in intensive land uses, although we cannot say definitively which species will respond in this manner with the data at hand. This is consistent with our finding that bird occurrence in homesteads had a marginal negative association with maneuverability, but since we found nearly the same effect for body mass, we cannot determine whether predator–prey interactions or other indirect factors best explain species' occupancy associations with homesteads.

Caveats and limitations

Prior studies have found bird traits to be a strong and ubiquitous predictor of species responses to land-use change (e.g., Newbold *et al.*, 2013; Burivalova *et al.*, 2015). Methodological differences and historic biodiversity change may have reduced the estimated effects of some of the traits we examined. For example, using full posterior distributions is important for avoiding bias and controlling error rates in models with random effects whereas ignoring posterior distributions can lead to spurious findings (Hadfield *et al.*, 2009). Also, our community sample was restricted to relatively common species amenable to point count surveys, possessing a potentially restricted range of continuous traits which may have reduced magnitude of the mass and maneuverability effects we estimated (Sirami & Monadjem, 2012). Consequently, it is also important to emphasize that our results may not generalize to rare species, and that robust inference regarding the responses of rare species to land-use and land-cover change will often require focused single-species studies because there will be practical limits to what researchers can glean from multispecies modeling. Similarly, it is unfortunate that we were only able to sample a single sugarcane plantation because several plantations denied our requests for access. Nevertheless, we expect that our results would have been similar in other sugarcane plantations, given the monoculture conditions (lack of heterogeneity) and similarity of the plantation we surveyed to other sugarcane plantations in the region (Mulwa, Böhning-Gaese, & Schleunig, 2012; Alexandrino *et al.*, 2019).

Conservation implications

The positive effects of shrub cover were most pronounced in pastures and homestead lands, whereas shrub encroachment had little predicted effect in protected areas, where most species were expected to occur even with little to no shrub cover. This is important for conservation because it suggests that shrub cover can be beneficial to bird communities in agricultural land uses, providing a means for promoting taxonomic diversity in agriculturally dominated landscapes, complementing (1) interspersed land-cover types and (2) heterogeneous canopy cover, both of which have biodiversity benefits (Shaw *et al.*, 2002; Ke *et al.*, 2018; McCleery *et al.*, 2018; Reynolds *et al.*, 2018). Managing shrub cover in protected savanna adjacent to homestead lands and plantations might also increase representation of species in these land uses, as small mammals in Swazi sugarcane plantation differed in their abundance with distance from a protected area with abundant woody cover (Hurst *et al.*, 2014). Similarly, pastures and homestead lands may be providing habitat for species exhibiting negative responses to shrub encroachment, such as Southern Fiscals (*Lanius collaris*) and Barn Swallows, the latter species having experienced population declines in recent decades (Møller & Vansteenwegen, 1997; Peron & Altwegg, 2015).

Collectively, our findings have two major implications for conservation practice. First, shrub cover goals for bird

conservation should vary with land use, honoring the fact that shrub cover is natural in savannas and increases habitat heterogeneity in anthropogenically altered landscapes (Stevens *et al.*, 2016). For example, protected area managers should be able to aggressively thin shrubs to increase the abundance of large-bodied terrestrial mammals without losing bird species (Soto-Shoender *et al.*, 2018), while community leaders on homestead lands (where large-bodied wild mammals rarely occur) may want to encourage people to retain shrubby vegetation, which should attract more birds without displacing the shrub-avoiding species that presently occupy homestead lands. Additional ancillary benefits to retaining shrubs on homestead lands might include: reduction of soil erosion; additional livestock forage; and natural pest control and pollination services provided by birds and beneficial insects that respond positively to shrub cover (Tefera, Dlamini, & Dlamini, 2008; Blaum *et al.*, 2009; Morandin, Long & Kremen, 2016; Xiong, Sun, & Chen, 2018). Second, retaining suitable vegetation structure in community pastures and homestead lands should promote species' occurrence to a similar degree across bird diets, so managers probably do not need to promote specific plant species to see increased bird occurrence. This is consistent with research finding no differences in bird species richness or composition in South African shrublands dominated by *Senegalia mellifera* and *Tarchonanthus camphoratus*, respectively (Sirami *et al.*, 2009). Together, our findings provide actionable information about widespread biodiversity change in savannas and a generalizable foundation for understanding its causes.

Conflict of interest

The authors declare no conflict of interest.

Data Availability Statement

Data and code reported herein are available online as Appendix S1 at: [Data and code will be uploaded to figshare. Please view files provided with the revised manuscript.]

References

- Alexandrino, E.R., Buechley, E.R., Forte, Y.A., Cassiano, C.C., Ferraz, K.M., Ferraz, S.F.B., Couto, H. & Şekerçioğlu, C.H. (2019). Highly disparate bird assemblages in sugarcane and pastures: implications for bird conservation in agricultural landscapes. *Neotrop. Biol. Conserv.* **14**, 169.
- Bailey, K.M., McCleery, R.A., Binford, M.W. & Zweig, C. (2016). Land-cover change within and around protected areas in a biodiversity hotspot. *J. Land Use Sci.* **11**, 154–176. <https://doi.org/10.1080/1747423X.2015.1086905>
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S. (2000). *Bird census techniques*. London: Elsevier.
- Blaum, N., Seymour, C., Rossmanith, E., Schwager, M. & Jeltsch, F. (2009). Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. *Biodivers. Conserv.* **18**(5), 1187–1199.
- Broms, K.M., Hooten, M.B. & Fitzpatrick, R.M. (2016). Model selection and assessment for multi-species occupancy models. *Ecology* **97**, 1759–1770.
- Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460. <https://doi.org/10.1016/j.tree.2008.03.011>
- Burivalova, Z., Lee, T.M., Giam, X., Şekerçioğlu, Ç.H., Wilcove, D.S. & Koh, L.P. (2015). Avian responses to selective logging shaped by species traits and logging practices. *Proc. R. Soc. B Biol. Sci.* **282**(1808), 20150164–<https://doi.org/10.1098/rspb.2015.0164>
- Dorado-Rodrigues, T.F., Layme, V.M.G., Silva, F.H.B., Nunes da Cunha, C. & Strüssmann, C. (2015). Effects of shrub encroachment on the anuran community in periodically flooded grasslands of the largest Neotropical wetland. *Austral Ecol.* **40**(5), 547–557.
- Dorazio, R.M. & Royle, J.A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *J. Am. Stat. Assoc.* **100**, 389–398. <https://doi.org/10.1198/016214505000000015>
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos* **65**, 169–175.
- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F. & Whitford, W.G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* **14**, 709–722. <https://doi.org/10.1111/j.1461-0248.2011.01630.x>
- Ellis, E.C. & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* **6**, 439–447. <https://doi.org/10.1890/070062>
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.K., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science* **309**, 570–574. <https://doi.org/10.1126/science.1111772>
- Frid, A. & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* **6**, 11. <http://www.consecol.org/vol6/iss1/art11/>
- Gaugris, J.Y. & Van Rooyen, M.W. (2010). Woody vegetation structure in conserved versus communal land in a biodiversity hotspot: a case study in Maputaland, South Africa. *S. Afr. J. Bot.* **76**, 289–298. <https://doi.org/10.1016/j.sajb.2009.11.007>
- Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. New York: Cambridge University Press.
- Gelman, A. & Rubin, D.B. (1992). Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–472. <http://www.jstor.org/stable/2246093>

- Goudie, A.S. & Price Williams, D. (1983). *The Atlas of Swaziland*. Lobamba, Eswatini: Occasional Papers of the Swaziland National Trust Commission.
- Gregory, N.C., Sensenig, R.L. & Wilcove, D.S. (2010). Effects of controlled fire and livestock grazing on bird communities in East African savannas. *Conserv. Biol.* **24**, 1606–1616. <https://doi.org/10.1111/j.1523-1739.2010.01533.x>
- Hadfield, J.D., Wilson, A.J., Garant, D., Sheldon, B.C. & Kruuk, L.E. (2009). The misuse of BLUP in ecology and evolution. *Am. Nat.* **175**, 116–125. <https://doi.org/10.1086/648604>
- Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.* **94**, 421–425. <https://doi.org/10.1086/282146>
- Hering, R., Hauptfleisch, M., Geißler, K., Marquart, A., Schoenen, M. & Blaum, N. (2019). Shrub encroachment is not always land degradation: insights from ground-dwelling beetle species niches along a shrub cover gradient in a semi-arid Namibian savanna. *Land Degrad. Dev.* **30**, 14–24
- Hinsley, S.A. & Bellamy, P.E. (2000). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *J. Environ. Manage.* **60**, 33–49. <https://doi.org/10.1006/jema.2000.0360>
- Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (2005). *Roberts' Birds of Southern Africa*. 7th edn. Cape Town: Trustees of the John Voelcker Bird Book Fund.
- Holden, S.T. & Otsuka, K. (2014). The roles of land tenure reforms and land markets in the context of population growth and land use intensification in Africa. *Food Policy* **48**, 88–97. <https://doi.org/10.1016/j.foodpol.2014.03.005>
- Holt, R.D. (1977). Predation, apparent competition, and structure of prey communities. *Theor. Popul. Biol.* **12**, 197–229. [https://doi.org/10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9)
- Hurst, Z.M., McCleery, R.A., Collier, B.A., Silvy, N.J., Taylor, P.J. & Monadjem, A. (2014). Linking changes in small mammal communities to ecosystem functions in an agricultural landscape. *Mamm. Biol.* **79**, 17–23. <https://doi.org/10.1016/j.mambio.2013.08.008>
- Iknayan, K.J., Tingley, M.W., Furnas, B.J. & Beissinger, S.R. (2014). Detecting diversity: Emerging methods to estimate species diversity. *Trends Ecol. Evol.*, **29**, 97–106.
- Jeppesen, E., Meerhoff, M., Jacobsen, B.A., Hansen, R.S., Søndergaard, M., Jensen, J.P., Lauridsen, L., Mazzeo, N. & Branco, C.W.C. (2007). Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* **581**, 269–285.
- Ke, A., Sibiyi, M.D., Reynolds, C., McCleery, R.A., Monadjem, A. & Fletcher, R.J. (2018). Landscape heterogeneity shapes taxonomic diversity of non-breeding birds across fragmented savanna landscapes. *Biodivers. Conserv.* **27**, 268. <https://doi.org/10.1007/s10531-018-1561-7>
- Keir, A.F., Pearson, R.G. & Congdon, R.A. (2015). Determinants of bird assemblage composition in riparian vegetation on sugarcane farms in the Queensland Wet Tropics. *Pac. Conserv. Biol.* **21**, 60–73. <https://doi.org/10.1017/PC14904>
- Kellner, K. (2016). jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses. R package v. 3.4.3. <https://cran.r-project.org/package=jagsUI>
- Kéry, M. & Royle, J.A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. New York: Academic Press.
- Kutt, A.S. & Martin, T.G. (2010). Bird foraging height predicts bird species response to woody vegetation change. *Biodivers. Conserv.* **19**, 2247–2262. <https://doi.org/10.1007/s10531-010-9840-y>
- Lambin, E.F., Geist, H.J. & Lepers, E. (2003). Dynamics of land-use and land-cover change in tropical regions. *Annu. Rev. Environ. Resour.* **28**, 205–241. <https://doi.org/10.1146/annurev.energy.28.050302.105459>
- Lehman, C.E.R. & Parr, C.L. (2016). Tropical grassy biomes: linking ecology, human use and conservation. *Philos. T. R. Soc. B. Biol. Sci.* **371**, 20160329. <https://doi.org/10.1098/rstb.2016.0329>
- Löffler, L. & Löffler, P. (2005). Swaziland tree atlas; including selected shrubs and climbers, Southern African Botanical Diversity Network Report. <http://www.sanbi.org/sites/default/files/documents/documents/sabonet-report-no-35-swaziland-tree-atlas.pdf>
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255. [https://doi.org/10.1890/00129658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/00129658(2002)083[2248:ESORWD]2.0.CO;2)
- Martin, T.G. & McIntyre, S. (2007). Impacts of livestock grazing and tree clearing on birds of woodland and riparian habitats. *Conserv. Biol.* **21**, 504–514. <https://doi.org/10.1111/j.1523-1739.2006.00624.x>
- McCleery, R., Monadjem, A., Baiser, B., Fletcher, R. Jr, Vickers, K. & Kruger, L. (2018). Animal diversity declines with broad-scale homogenization of canopy cover in African savannas. *Biol. Cons.* **226**, 54–62. <https://doi.org/10.1016/j.biocon.2018.07.020>
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185.
- Møller, A.P. & Vansteenwegen, C. (1997) Barn swallow. In *The EBCC Atlas of European Breeding Birds*: 478–479. Hagemeyer, W.J.M. & Blair, M.J. (Eds). London, UK: T. & A. D. Poyser.
- Monadjem, A. (2000). An avifaunal (Aves) survey of the lower Usuthu River basin, Swaziland. *Durban Museum Novitates* **25**, 25–31. http://hdl.handle.net/10520/AJA0012723X_1790
- Monadjem, A. (2005). Association between avian communities and vegetation structure in a low-lying woodland-savanna ecosystem in Swaziland. *Ostrich* **76**, 45–55. <https://doi.org/10.2989/00306520509485472>

- Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., Mace, G.M., Palmer, M., Scholes, R. & Yahara, T. (2009). Biodiversity, climate change, and ecosystem services. *Curr. Opin. Environ. Sustain.* **1**, 46–54. <https://doi.org/10.1016/j.cosust.2009.07.006>
- Morandin, L.A., Long, R.F. & Kremen, C. (2016). Pest control and pollination cost–benefit analysis of hedgerow restoration in a simplified agricultural landscape. *J. Econ. Entomol.* **109**(3), 1020–1027.
- Mucina, L., Rutherford, M.C. & Powrie, L.W. (eds.). (2005). *Vegetation map of South Africa, Lesotho and Swaziland, 1:1 000 000 scale sheet maps*. Pretoria: South African National Biodiversity Institute.
- Mulwa, R.K., Böhning-Gaese, K. & Schleuning, M. (2012). High bird species diversity in structurally heterogeneous farmland in western Kenya. *Biotropica* **44**, 801–809.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858. <https://doi.org/10.1038/35002501>
- Newbold, T., Scharlemann, J.P., Butchart, S.H., Şekerçioğlu, Ç.H., Alkemade, R., Booth, H. & Purves, D.W. (2013). Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B Biol. Sci.* **280** (1750), 20122131. <https://doi.org/10.1098/rspb.2012.2131>
- Noer, C.L., Dabelsteen, T., Bohmann, K. & Monadjem, A. (2012). Molossid bats in an African agro-ecosystem select sugarcane fields as foraging habitat. *Afr. Zool.* **47**, 1–11. <https://doi.org/10.1080/15627020.2012.11407517>
- Norberg, U.M. (1990). *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. New York: Springer.
- Owens, I.P.F. & Bennett, P.M. (2000). Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl Acad. Sci. U. S. A.* **97**, 12144–12148. <https://doi.org/10.1073/pnas.200223397>
- Péron, G. & Altwegg, R. (2015). Twenty-five years of change in southern African passerine diversity: nonclimatic factors of change. *Glob. Change Biol.* **21**, 3347–3355. <https://doi.org/10.1111/gcb.12909>
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling, Proceedings of the 3rd international workshop on distributed statistical computing. <https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf>
- R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Reynolds, C., Fletcher, R.J., Carneiro, C.M., Jennings, N., Ke, A., LaScaleia, M.C., Lukhele, M.B., Mamba, M., Sibiya, M.D., Austin, J.D., Magagula, C.N., Mahlaba, T., Monadjem, A., Wisely, S.M. & McCleery, R.A. (2018). Inconsistent effects of landscape heterogeneity and land-use on animal diversity in an agricultural mosaic: a multi-scale and multi-taxon investigation. *Landscape Ecol.* **33**, 241. <https://doi.org/10.1007/s10980-017-0595-7>
- Roques, K.G., O'Connor, T.G. & Watkinson, A.R. (2001). Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* **38**, 268–280. <https://doi.org/10.1046/j.1365-2664.2001.00567.x>
- Rotenberry, J.T. (1985). The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* **67**, 213–217. <https://doi.org/10.1007/BF00384286>
- Royle, J.A. & Dorazio, R.M. (2008). *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. London: Academic Press.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Seymour, C.L. & Dean, W.R.J. (2010). The influence of changes in habitat structure on the species composition of bird assemblages in the southern Kalahari. *Austral Ecol.* **35**, 581–592. <https://doi.org/10.1111/j.1442-9993.2009.02069.x>
- Shapiro, J.T., Monadjem, A., Roder, T. & McCleery, R. (2020). Response of bat activity to land-cover and land-use change in savannas is scale-, season-, and guild-specific. *Biol. Cons.* **241**, 108245. <https://doi.org/10.1016/j.biocon.2019.108245>
- Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A. & Field, C.B. (2002). Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* **298**, 1987–1990. <https://doi.org/10.1126/science.1075312>
- Sirami, C. & Monadjem, A. (2012). Changes in bird communities in Swaziland savannas between 1998 and 2008 owing to shrub encroachment. *Divers. Distrib.* **18**, 390–400. <https://doi.org/10.1111/j.1472-4642.2011.00810.x>
- Sirami, C., Seymour, C., Midgley, G. & Barnard, P. (2009). The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Divers. Distrib.* **15**, 948–957. <https://doi.org/10.1111/j.1472-4642.2009.00612.x>
- Soto-Shoender, J.R., McCleery, R.A., Monadjem, A. & Gwinn, D.C. (2018). The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. *Biol. Cons.* **221**, 127–136. <https://doi.org/10.1016/j.biocon.2018.02.028>
- Stanton, R.A., Boone, W.W., Soto-Shoender, J., Fletcher, R.J., Blaum, N. & McCleery, R.A. (2018). Shrub encroachment and vertebrate diversity: a global meta-analysis. *Glob. Ecol. Biogeogr.* **27**, 368–379. <https://doi.org/10.1111/geb.12675>
- Stevens, N., Erasmus, B.F.N., Archibald, S. & Bond, W.J. (2016). Woody encroachment over 70 years in South

- African savannahs: overgrazing, global change or extinction aftershock? *Philos. T. R. Soc. B Biol. Sci.* **371**(1703), 20150437. <https://doi.org/10.1098/rstb.2015.0437>
- Suding, K.N., Gross, K.L. & Houseman, G.R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* **19**, 46–53. <https://doi.org/10.1016/j.tree.2003.10.005>
- Tansley, A.G. & Chip, T.F. (1926). *Aims and methods in the study of vegetation*. London: The British Empire Vegetation Committee and the Crown Agents for the Colonies. <http://krishikosh.egranth.ac.in/bitstream/1/2047455/1/1471.pdf>
- Tefera, S., Dlamini, B.J. & Dlamini, A.M. (2008). Dynamics of savannas in Swaziland: encroachment of woody plants in relation to land use and soil classes and indigenous knowledge on plants utilization. *Res. J. Bot.* **3**(2), 49–64.
- Turner, B.L. II, Lambin, E.F. & Reenberg, A. (2007). The emergence of land change science for global environmental change and sustainability. *Proc. Natl Acad. Sci. U. S. A.* **104**, 20666–20671. <https://doi.org/10.1073/pnas.0704119104>
- Twine, W.C. & Holdo, R.M. (2016). Fuelwood sustainability revisited: integrating size structure and resprouting into a spatially realistic fuelshed model. *J. Appl. Ecol.* **53**, 1766–1776. <https://doi.org/10.1111/1365-2664.12713>
- Warton, D.I., Stoklosa, J., Guillera-Arroita, G., MacKenzie, D.I. & Welsh, A.H. (2017). Graphical diagnostics for occupancy models with imperfect detection. *Methods Ecol. Evol.* **8**, 408–419.
- Wright, W.J., Irvine, K.M. & Higgs, M.D. (2019). Identifying occupancy model inadequacies: can residuals separately assess detection and presence? *Ecology* **100**, e02703.
- Xiong, M., Sun, R. & Chen, L. (2018). Effects of soil conservation techniques on water erosion control: A global analysis. *Sci. Total Environ.* **645**, 753–760.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Data and code.

Appendix S2. Assessment of residual spatial autocorrelation in the model with three land uses and a shrub cover by land use interaction.

Methods S1. Supplementary Methods.

Appendix S3. Tables and figures pertaining to results from the model with four land uses.

Appendix S4. Tables and figures pertaining to results from the model with three land uses and shrub cover by land use interactions.