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White, Joseph; Stevens, Nicola; Fisher, Jolene; Reynolds, Chevonne

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RESEARCH ARTICLE

Woody plant encroachment drives population declines in 20% of common open ecosystem bird species

Joseph D. M. White[1,2] | Nicola Stevens[1,3] | Jolene T. Fisher[1] | Chevonne Reynolds[1,4]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, WITS, Johannesburg, South Africa

[2]Royal Botanic Gardens, Kew, Richmond, UK

[3]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

[4]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

Correspondence
Joseph D. M. White, Royal Botanic Gardens, Kew, Richmond, UK.
Email: j.white2@kew.org

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Abstract

Grassy ecosystems cover more than 40% of the world's terrestrial surface, supporting crucial ecosystem services and unique biodiversity. These ecosystems have experienced major losses from conversion to agriculture with the remaining fragments threatened by global change. Woody plant encroachment, the increase in woody cover threatening grassy ecosystems, is a major global change symptom, shifting the composition, structure, and function of plant communities with concomitant effects on all biodiversity. To identify generalisable impacts of encroachment on biodiversity, we urgently need broad-scale studies on how species respond to woody cover change. Here, we make use of bird atlas, woody cover change data (between 2007 and 2016) and species traits, to assess: (1) population trends and woody cover responses using dynamic occupancy models; (2) how outcomes relate to habitat, diet and nesting traits; and (3) predictions of future occupancy trends, for 191 abundant, southern African bird species. We found that: (1) 63% (121) of species showed a decline in occupancy, with 18% (34) of species' declines correlated with increasing woody cover (i.e. losers). Only 2% (4) of species showed increasing population trends linked with increased woody cover (i.e. winners); (2) Open habitat specialist, invertivorous, ground nesting birds were the most frequent losers, however, we found no definitive evidence that the selected traits could predict outcomes; and (3) We predict open habitat loser species will take on average 52 years to experience 50% population declines with current rates of encroachment. Our results bring attention to concerning region-wide declining bird population trends and highlight woody plant encroachment as an important driver of bird population dynamics. Importantly, these findings should encourage improved management and restoration of our remaining grassy ecosystems. Furthermore, our findings show the importance of lands beyond protected areas for biodiversity, and the urgent need to mitigate the impacts of woody plant encroachment on bird biodiversity.

KEYWORDS
birds, functional traits, grassland, occupancy models, population trends, savanna, woody plant encroachment

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1 | INTRODUCTION

The Anthropocene has transformed the terrestrial biosphere, transitioning it from a predominantly natural state to one primarily influenced by human activities (Ellis, 2011; Ellis et al., 2010; Steffen et al., 2015). This transition has been identified as the most significant driver of biodiversity loss globally (Díaz et al., 2019). Efforts to curb biodiversity loss typically aim to reduce land conversion rates, encourage land restoration efforts, and promote the expansion of protected area networks (Dinerstein et al., 2020). These strategies are premised on the idea that there are important reservoirs of biodiversity remaining in rangelands (used for livestock) or near-natural lands outside of current protected area networks, which are defined as lands with minor levels of transformation, low population densities and limited impacts from livestock or crop-based agriculture (Clements et al., 2024). These rangelands and near-natural landscapes outside of current protected areas will become increasingly important if we are to reduce biodiversity loss and achieve the restoration and conservation targets set out in the Kunming-Montreal Global Biodiversity Framework (CBD, 2022).

Although grassy ecosystems are subject to high rates of land conversion for crop-based agriculture and forestry (Newbold et al., 2016; Potapov et al., 2022), large moderate intensity rangelands and near-natural areas do still remain outside of protected area networks, particularly in Africa (Clements et al., 2024; Stevens et al., 2022). These areas host a rich biodiversity and support an array of valuable ecosystem services (Bardgett et al., 2021; Murphy et al., 2016; Pärtel et al., 2005). However, many of these important areas are experiencing widespread woody plant encroachment (García Criado et al., 2020; Stevens et al., 2017; Venter et al., 2018) as a consequence of interacting global change drivers, from changing disturbance regimes (altered fire and herbivory) to rising atmospheric CO_2 concentrations and climate change (Archer et al., 2017; Osborne et al., 2018; Stevens et al., 2017). As a result, these systems are experiencing a fundamental change in ecosystem structure, function and composition, and will likely have large, regional-scale consequences for the biodiversity dependent on them. Whilst the regional-scale trend of woody plant encroachment is increasingly recognised (García Criado et al., 2020; O'Connor et al., 2014; Stevens et al., 2016), its influence as a driver of population dynamics at this scale is an under-appreciated impact that needs explicit examination.

Woody plant encroachment changes ecosystem structure, with concomitant changes in biodiversity, ecological function, and ecosystem service provision. In grassy ecosystems, the increasing woody cover shades out the grass layer, resulting in both the loss of herbaceous biodiversity (Wieczorkowski & Lehmann, 2022), their associated ecosystem processes (e.g. fire) and ecosystem services (e.g. foraging; Anadón et al., 2014; Charles-Dominique et al., 2018). It can also cause a shift from a heterogeneous system characterised by multi-structured layers of trees, shrubs and grasses to the extreme of a system that is uniformly dominated by a homogenous layer of woody plants (Sirami et al., 2009). This can have pronounced impacts on the plant and animal communities living in these landscapes. Several local-scale studies demonstrate that homogenisation through woody plant encroachment can reduce species richness across a range of communities, from plants and insects to small carnivores and birds (Blaum et al., 2007, 2009; Ratajczak et al., 2012; Sirami & Monadjem, 2012). A global meta-analysis on vertebrates, suggested that mammals and herpetofauna may be most vulnerable, while birds are more resilient to the effects of encroachment, due to their greater flexibility in nesting and foraging strategies (Stanton et al., 2018). The structural and compositional shift in the plant community caused by encroachment can also act as an ecological filter for certain functional groups (Andersen & Steidl, 2023). For example, at a local scale, increased woody cover can cause reorganisation of mammalian herbivore communities, benefitting smaller bodied browsing herbivores over larger bodied grazers (Smit & Prins, 2015). Similarly, reorganisation of bird communities can occur with encroachment, often favouring leaf gleaning, smaller bodied invertivorous passerines over larger bodied, non-passerine ground dwelling birds (Andersen & Steidl, 2019, 2020; Péron & Altwegg, 2015; Sirami & Monadjem, 2012). It is likely that open system specialists will be disproportionately impacted as they are area sensitive and require large open area habitats to reproduce (Andersen & Steidl, 2020; Reino et al., 2009).

Although local-scale studies clearly demonstrate that woody plant encroachment impacts population dynamics and can restructure communities, comparative studies at broad scales are rare (although see Péron & Altwegg, 2015 for a relevant example). Current broad-scale studies do the important task of examining the impacts of climate change or land use on communities such as birds (Coetzee et al., 2009; Hockey et al., 2011), but they fail to address how one of the most significant symptoms of global change in grassy ecosystems (i.e. woody plant encroachment) impacts species' populations. This insight is urgently needed as high rates of encroachment are occurring in these systems and are projected to continue (Kumar et al., 2021; Pfeiffer et al., 2020). Additionally, many open grassy ecosystems are mistakenly targeted for afforestation and tree 'restoration' suggesting that these ecosystems have the potential to become significantly woodier at large extents (Bond et al., 2019). Though encroachment and afforestation are driven by different processes, these disruptions to grassy ecosystems have the potential to drastically impact faunal communities, due to changes in habitat composition and structure (Allan et al., 1997; Castaño-Villa et al., 2019; Stanton et al., 2018). We therefore need to understand the broad-scale impact of significantly woodier grasslands and savannas on population dynamics, which may act as an early warning system for biodiversity loss in these systems. Birds represent a key taxon to investigate the impact of woody plant encroachment on biodiversity because they are well surveyed (Brooks et al., 2022), they are sensitive to changes in vegetation cover and structure (Tews et al., 2004)

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and may act as biodiversity indicators for other taxa (Gregory et al., 2003). Therefore, declines in population trends for open ecosystem birds may act as a good proxy of broader biodiversity loss in the face of large-scale land cover changes due to woody plant encroachment.

The grassy ecosystems of southern Africa are an important focal region when it comes to woody plant encroachment, as they have experienced a strong increase in woody cover (up to 1%/year in some regions; Stevens et al., 2017), have high faunal biodiversity, are under conserved (Skowno et al., 2019) and provide valuable ecosystem services (White et al., 2022). Better computational capacity, increased access to remotely sensed data and wide-scale citizen science sampling efforts have improved our ability to look for generalisable changes in biodiversity due to extensive woody plant encroachment beyond the site or habitat scale. Here, we draw on the rich resource of the Southern African Bird Atlas Project 2 (Brooks et al., 2022), a citizen science project that maps bird species occurrence across South Africa, Lesotho and eSwatini (from 2007 to present), to examine how trends in bird species occupancy in grassy ecosystems are influenced by woody plant encroachment. Additionally, we examine if different functional groups, focusing on nesting sites, diets and habitat specialisation, are disproportionately impacted. We hypothesised that ground nesting, non-invertivorous, open ecosystem specialists would show the greatest occupancy declines. Lastly, we project future occupancy change for vulnerable species based on current woody cover occupancy and responses under a scenario of continued encroachment. Our spatio-temporal analysis allows us to inform efforts to mitigate the impacts of woody plant encroachment on biodiversity and promote land management strategies that support the sustainable conservation of open ecosystem biodiversity.

2 | MATERIALS AND METHODS

We used dynamic occupancy models (Bled et al., 2013; MacKenzie et al., 2017; Royle et al., 2005) to analyse changes in bird species occupancy in response to woody plant encroachment over a 10-year period (2007–2016). We chose this period as it best overlapped with the start of the second Southern African Bird Atlas Project (SABAP2) in 2007 and the end of the available woody cover product from Venter et al. (2018) in 2016. We used the citizen science bird observation data (SABAP2) to fit models for species occurring in South Africa, Lesotho and eSwatini's open, grassy ecosystems, with woody cover and the rates of woody cover change as our primary covariates of interest. After data and model vetting, we present the analysis for 191 commonly occurring open ecosystem bird species. This led us to identify species that were either winners, losers or indifferent in their occupancy response to increased woody cover (Table 1), explore how different functional groups may be impacted, and project future impacts for vulnerable species under a business-as-usual scenario.

TABLE 1 Lookup table for categorising population trends and woody cover responses.

Population trend	Woody cover response	Outcome
Increasing	Positive	Winners
Decreasing	Negative	Losers
Stable	Positive/negative/neutral	Indifferent
Increasing/decreasing/stable	Neutral	Indifferent
Increasing	Negative	Indifferent
Decreasing	Positive	Indifferent

2.1 | Data

2.1.1 | Bird atlas

Bird occurrence at the species level was estimated using data from SABAP2 (sabap2.birdmap.africa). SABAP2 is large-scale citizen science programme, which began in 2007 and is ongoing, and has been extensively used to investigate bird distributions and responses to environmental drivers (Altwegg & Nichols, 2019; Bled et al., 2013; Broms et al., 2016; Chamberlain et al., 2019; Péron & Altwegg, 2015). The programme is open to volunteer observers who submit species lists (hereafter atlas cards) with recorded presences of all birds detected during timed visits to predefined grid cells, which in effect means absences are recorded. Each cell, called a pentad, is 5 min by 5 min in area (ca. 9 km north–south and 7 km east–west in southern Africa). The SABAP2 protocol requests that observers visit all habitats within a pentad. It further requires that pentads need to be visited for at least 2 h and can only be visited once every 5 days by the same observer. Additionally, SABAP2 has a rigorous data vetting procedure to filter out errors in atlas cards before they are added to the database (Brooks et al., 2022). We downloaded full protocol card data with null counts (all cards where the species were both present and absent) for all South African, Lesotho and eSwatini species in the database, totalling 843 species.

2.1.2 | Woody plant encroachment

Woody cover data were obtained from Venter et al. (2018) and processed using Google Earth Engine (Gorelick et al., 2017). Venter et al. (2018) predicted fractional woody cover across sub-Saharan Africa using all Landsat surface reflectance data between 1986 and 2016. Random forest regression models were trained on 6 five-year epochs and included spectral bands and derived vegetation indices and were tested on internal and independent data, showing good overall accuracies (adjusted $R^2 > 0.9$; Venter et al., 2018). The dataset includes a woody cover layer for the year 2016 and a woody cover linear trend layer for a 30-year period (1986–2016) at 30 m resolution across sub-Saharan Africa. We

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aggregated this to a pentad level metric by calculating the mean woody cover for 2016 and 30-year trend layer for near-natural, non-masked pixels in each pentad. We used the existing masking layer from the Venter et al. (2018) woody cover data to exclude pixels classified as forests (natural or plantation), urban surfaces, wetland, cropland, and natural-cropland mosaics. To identify pentads with largely rangeland or near-natural landscapes, we calculated the percentage of masked pixels per pentad. Pentads with >75% masked pixels ($n = 553$) were removed, which excluded pentads with limited near-natural land cover, leaving a total of 10,861 pentads in the study area (Figure S1a). To calculate woody cover data for each pentad, for each year, we hindcast the pentad-based woody cover change trend. We cumulatively subtracted the linear trend for each pentad, starting from the 2016 woody cover value and moving backwards in time to hindcast values iteratively from 2015 to 2007 for each pentad (see White et al., 2022 for a full description of the hindcasting approach).

2.1.3 | Study area

We confined our study area to South Africa, Lesotho, and eSwatini's open, grassy ecosystems (Grassland and Savanna biomes), delineated by the 2018 Vegetation Map of South Africa, Lesotho, and Swaziland (South African National Biodiversity Institute, 2018; data available at bgis.sanbi.org). We treated these biomes as a continuum, as they showed comparable woody cover and rates of woody cover change (Figure S2).

2.2 | Modelling

The modelling process had four steps: (1) data screening, (2) occupancy modelling and extraction of focus estimates, (3) analysis of functional groups, and (4) future projections for vulnerable species.

2.2.1 | Data screening

We downloaded all available atlas cards for all species via the SABAP2 data portal (sabap2.birdmap.africa). Atlas cards were filtered to include only those with a survey duration of at least 2 h, the minimum time required for a full protocol submission. For each year between 2007 and 2016, we filtered the pentads to only include summer atlas cards (October–March), allowing for the inclusion of migrants and overlapping with the peak period for surveying in southern Africa's summer rainfall season. The citizen science data from SABAP2 data have a strong spatial bias in card sampling effort closer to urban areas and along major arterial roadways (Hugo & Altwegg, 2017). We therefore further screened each pentad to include a minimum of three atlas cards and a maximum of 40 cards over the full 10-year period, with each pentad limited to having four atlas cards per summer. We chose to use four atlas cards per summer as (1) the median value of atlas cards over the 10-year period was 38 and (2) restricting the analysis to only include the summer season reduces the likelihood of closure violations. To account for different movement behaviours across species, atlas cards were sampled to maximise the time between each card within each respective summer. After this screening, the sampling design included 3199 pentads, with a total of 31,609 sampled atlas cards (Figure S1a). These 3199 pentads showed a 9.02% overlap with the protected areas (i.e. including only formal protected areas and excluding other effective area-based such as biosphere reserves, botanical gardens and World Heritage Site buffer areas) of the region, meaning 91.98% of the pentad area covered was outside of protected areas, in near-natural landscapes (Figure S1b; protected areas downloaded from Department of Forestry, Fisheries, and the Environment (2023) for South Africa and from UNEP-WCMC & IUCN (2023) for Lesotho and eSwatini).

Following the screening process, we calculated the percentage of presence values for each species in the sampled atlas cards. The median presence percentage was 2.69%. All species with no values (i.e., no presences in the spatial-temporally filtered dataset) and less than 2.69% presence were excluded from further analysis due to low presence-absence ratios and the likelihood of non-convergence in the models. Additionally, species that are strongly associated with water bodies, wide-ranging scavengers (e.g. vultures) and exotic species were excluded from the analysis. This left a total of 266 species for occupancy modelling.

2.2.2 | Population trends and response to woody cover

We used dynamic occupancy models to describe population trends in relation to changes in woody cover, while accounting for imperfect detection (Kéry & Schmidt, 2008; MacKenzie et al., 2017). These models allow for the inclusion of several covariates that influence occurrence and detection, including static variables across sites, variables that change annually, and those that influence the likelihood of observing a species. Initial occupancy was modelled as a function of 2007 woody cover and two climatic variables, related to temperature and evapotranspiration. Colonisation and extinction were modelled as functions of woody cover. The detection parameter was modelled as a function of year, woody cover, Julian day, survey duration and road density.

For site-level covariates for initial occupancy, we included the following variables in our analysis: initial woody cover in 2007, minimum temperature of the coldest month and the ratio of precipitation to potential evapotranspiration. Huntley et al. (2006) found that four climatic variables performed consistently well in predicting African bird distributions: minimum temperature of the coldest month, maximum temperature of the warmest month, the ratio of actual to potential evapotranspiration and the ratio of precipitation to potential evapotranspiration. We extracted the temperature variables from the WorldClim dataset (Hijmans

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et al., 2005) and the precipitation-evapotranspiration from the TerraClimate dataset (Abatzoglou et al., 2018) using Google Earth Engine. After performing a Pearson correlation test with a threshold of $r = 0.7$, we only included minimum temperature of the coldest month and the ratio of actual to potential evapotranspiration (R-index) as climatic predictors for initial occupancy. As an additional environmental predictor for site-level covariates, we used initial woody cover in 2007. This sets a baseline for woody cover for each species' model. For colonisation (probability of occupying an empty pentad) and extinction (probability of becoming locally extinct from a pentad) parameters, we included the hindcasted woody cover for each year. Woody cover and climatic covariates were standardised before modelling, by subtracting the mean and dividing by standard deviation.

As citizen science data are prone to imperfect detection, we modelled the observation covariates as a function of four variables: year, Julian day, survey duration, and the road density for each atlas card. Year, Julian day and survey duration were associated with each atlas card, while road density per pentad (km/km^2) was derived in QGIS from Africa Infrastructure Country Diagnostics (World Bank Group, 2009). Julian day was first converted to degrees and then radians to account for its circularity and leap years were accounted for.

Dynamic occupancy models were fit for each species using the *colext* function from the unmarked package (v.1.3.2) in R (Fiske & Chandler, 2011; R Core Team, 2020). We extracted the following coefficients from the occupancy models: (1) woody cover estimates of initial occupancy, (2) predicted population level estimates of annual occupancy to calculate average rate of occupancy change, (3) woody cover estimates of colonisation and extinction. (1) Woody cover coefficients for initial occupancy were classed as either positive, negative or if 90% confidence intervals (CIs) overlapped with zero—neutral. (2) Average rate of occupancy change (λ) was calculated using the predicted annual occupancy probabilities from the below equation:

$$\lambda_t = \frac{\hat{\Psi}_{t+1}}{\hat{\Psi}_t}$$

where λ_t is the change in occupancy at time t, $\hat{\Psi}_t$ is the occupancy estimate at time t, and $\hat{\Psi}_{t+1}$ is the occupancy estimate at time $t+1$ (Hedlin & Franke, 2017; MacKenzie et al., 2003). Mean occupancy trends (λ) with 90% CIs greater than one were classed as increasing, less than one as decreasing and if 90% CIs overlapped with one—stable. From these extracted model coefficients, we categorized birds as either winners, losers or indifferent in response to woody cover using a simple lookup table (Table 1). For indifferent species, we could not draw a correlative link between their population trends and woody cover responses. Occupancy models that did not converge were excluded from further analysis ($n = 2$). (3) We examined the correlations between the woody cover estimates of initial occupancy, colonisation and extinction across species.

As a precautionary, additional assessment of population trends, we used an equality of two proportions test to calculate Z-scores (Underhill & Bradfield, 1996) and measure the confidence of relative reporting rate change over time versus occupancy trends. This statistic relies on the proportion of checklists where a species was reported as present in each pentad and compares two distinct time periods and is commonly used in SABAP2 studies (Hofmeyr et al., 2014; Underhill & Brooks, 2014). It's expressed as:

$$Z = \frac{P_2 - P_1}{\sqrt{P(1-P)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

with P_1 and P_2 representing the reporting rates for each period; n_1 and n_2 representing the total number of cards in each period and P being the pooled reporting rate across periods:

$$P = \frac{n_1 P_1 + n_2 P_2}{n_1 + n_2}$$

we extracted reporting rates from the first 3 years (2007–2009) and last 3 years (2014–2016) to compare trends between the beginning and end of the study period. We used Z-score thresholds of $Z < -1.65$ or $Z > 1.64$ (90% CIs) to filter out species with strongly conflicting trend directions to occupancy trends (e.g. $\lambda > 1$ and $Z < -1.65$, or $\lambda < 1$ and $Z > 1.65$). We filtered out 75 species and results are shown only for the remaining 191 species (72% of 266 species).

2.3 | Functional groups

To identify potential links between functional groups and modelling outcomes, we extracted trait data on (a) habitat specialisation, (b) primary diet and (c) primary nesting sites. All data were extracted from Roberts Birds of Southern Africa 7th Edition (Hockey, 2005). For (a) habitat specialisation we classified species into four classes of habitat specialisation according to Péron and Altwegg (2015). Roberts provides an index of habitat use from 0 to 3, with 0 representing no use, 1 occasional use, 2 secondary habitat and 3 primary habitats. Using this information, we classified birds into either open, intermediate-open, intermediate-closed, or closed habitat specialists based on a lookup table (Table S1). Species with no scores available for any habitat use index were manually classified using information from Birdlife Data Zone (http://www.birdlife.org/datazone/species). For (b) primary diet we classified species into the diet classes carnivore, frugivore, generalist, granivore, herbivore, invertivore, granivore/invertivore and nectarivore based on an index of diet contribution from 0 to 10. This was based on our own diet lookup table (Table S2). For (c) we used primary nesting sites as described in Roberts (Hockey, 2005). Brood parasites were assigned nesting sites based on their major hosts as found in Roberts' species descriptions.

To determine whether loser species were disproportionately represented by different traits we used chi-squared tests. Tests were run on overall contingency tables using all responses and all categories for each trait and then comparing losers and specific traits

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associated with open ecosystem birds (open or intermediate-open habitat specialists; granivores or invertivores; ground or grass nesting sites) with the sum of counts for all other categories. Only 182 species were analysed in the overall test of nesting site behaviour as nine species did not regularly breed in the region.

2.4 | Loser occupancy projections

To test the potential future impacts of woody plant encroachment on population trends if there were to be unmitigated increases in woody cover, we predicted the number of years before a species' occupancy will drop by 50% of its 2016 occupancy across its predicted range. We first predicted species' ranges using the occupancy model beta coefficients, including the slope, initial woody cover, minimum temperature and the ratio of actual to potential evapotranspiration to create probability maps. We generated binary maps using three different species-specific thresholding rules: 10th, 20th and 50th percentile presence threshold (PPT). Under each thresholding rule, pentads with values equal to or above the respective percentile are considered presences, while those below as absences (Radosavljevic & Anderson, 2014). These different thresholds represent progressively more restrictive binary outputs and can be interpreted as broad (10 PPT) to core (50 PPT) ranges of each species. Median woody cover was calculated across the predicted range for 2016 across all presence pentads. Using the median woody cover value, we then found the intersecting occupancy value. This provided the occupancy and median woody cover values for 2016 for each species.

To calculate the number of years until a species would reach 50% of its 2016 occupancy, we first needed to forecast woody cover. To predict future woody cover values, assuming rates of change will be constant at different woody cover values across the time period, we used a general additive model (GAM) of woody cover change versus woody cover for the year 2016 (Figure S2). The GAM model accounts for the bell-shaped distribution of woody cover change across different values of woody cover, with a peak at 47% woody cover. Over short time periods, there is little difference in using GAM predictions rather than linear predictions. But over several decades, values may become distorted with linear models as they would not slow down at greater woody cover. We forecasted the woody cover values iteratively for consecutive years until the median values intersected with the 50% occupancy values for 2016 and calculated the number of years to reach this value. We applied this approach to species that were identified as losers and open or intermediate-open habitat specialists (Figure 4).

3 | RESULTS

3.1 | Changes in woody cover over sampled pentads

Woody plant encroachment was ubiquitous across the study region, with 80% of the pentads showing an increasing trend of at least 0.25%/year. The median value for woody cover was 38.62% across the sampled pentads (Figure 1a). This was representative of the values across the full range of pentads within the study region (Welch's *t*-test; df = 4959.4, $p < .01$; Figure 1b,c). The median value for woody cover change was 0.48%/year (Figure 1d). Similarly, the woody cover change values of the sampled pentads were representative of the full range of pentads (Welch's *t*-test; df = 4959.4, $p < .01$; Figure 1e,f).

3.2 | Winners vs. losers

Focusing only on occupancy trends, 121 species (63% of 191) showed decreasing population trends, with many stable ($n = 61$, 32%) and few increasing ($n = 9$, 5%; Figure 2). For woody cover responses, 74 species (39%) showed positive woody cover coefficients (i.e. greater occupancy probability at higher woody cover), 65 (34%) with negative coefficients and 52 (27%) were neutral due to non-significant coefficients. When combining occupancy trends together with the woody cover responses, 34 (18%) species were losers, where they have both a decreasing occupancy trend and a negative response to increasing woody cover (Figure 2, Figure S3a,b). Only 4 species (2%) were winners (Figure 2, Figure S3c,d). These species have both an increasing occupancy trend and a positive response to increasing woody cover (Figure S3c,d). The remaining 153 species (80%) were indifferent, where their occupancy responses (both increasing and decreasing) appear decoupled from woody cover dynamics. Initial occupancy and extinction estimates for woody cover showed a moderate positive correlation (est. = 0.502, $R^2 = .34$, $p < .001$; Figure S4a), while initial occupancy and colonisation showed a weak positive correlation (est. = 0.271, $R^2 = .05$, $p < .005$; Figure S4b). This suggests that when species have a greater predicted occupancy at greater woody cover (e.g. Figure S3d), they simultaneously experience greater extinction probability with moderate colonisation. Though extinction and colonisation processes were uncorrelated when comparing across species (Figure S4c).

3.3 | Functional groups

Chi-squared tests on contingency tables showed no overall difference between winners and losers for habitat specialisation or nesting sites, and a small difference in diet, driven by nectarivores in winners (Table S3a). Losers had greater counts of open habitat specialisation than other categories (Figure 3; Table S3b) and were found across all classes of habitat specialisations, diets, and nesting sites (Figure 3; Figures S5 and S6), with the most common combination of traits being open habitat, invertivore, ground nesting birds ($n = 4$; Figure S5). However, there were several notable inclusions and exceptions for both winners and losers. No winner species were open habitat specialists. Losers were primarily invertivores, though this was reflective of the broader trends when including indifferent species (Table S3; Figure S5). No winners were granivores. Losers were found across all nesting sites, while no winners were ground, grass or reed nesters.

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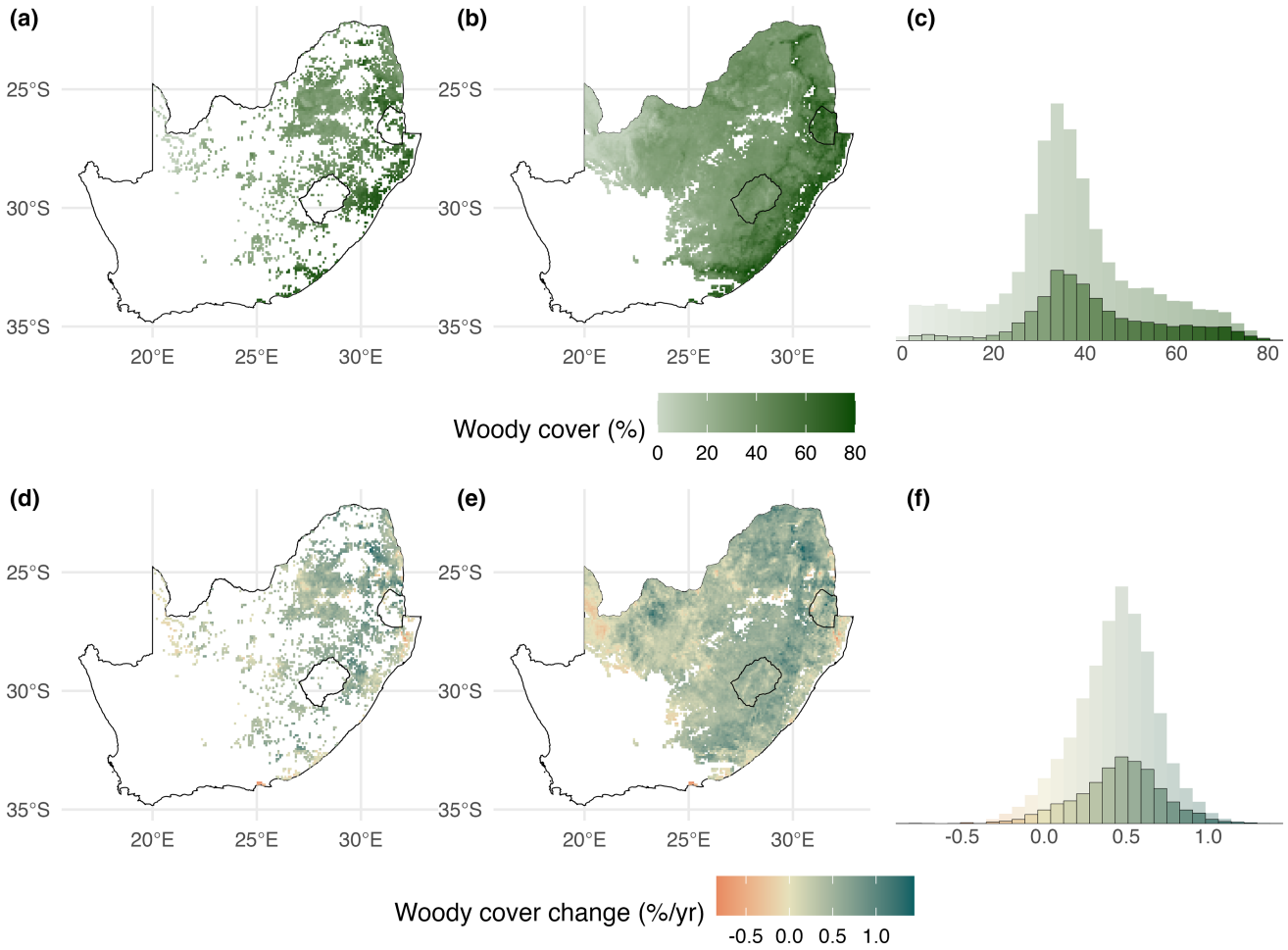

FIGURE 1 Woody cover and the woody cover change across South Africa, Lesotho and eSwatini's grassland and savanna biomes at the pentad scale from Venter et al. (2018). (a, d) show the values across the 3199 sampled pentads used in the occupancy models; (b, e) show the values across all pentads in grasslands and savannas; and (c, f) show the distribution of the values for the sampled (highlighted) and for all (background) pentads. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

3.4 | Loser occupancy predictions

We predicted that species classified as losers and open or intermediate-open specialists will take 52 ± 16 years (median ± SE) to decline in occupancy by 50% from 2016 (Figure 4a) using 20th percentile presence threshold (20 PPT). For example, the Tawny eagle will reach a 50% occupancy decline within 20 years, primarily due to its low occupancy in 2016 (at 20 PPT; Figure 4a). While the Little swift will take more than 250 years to decline to 50% occupancy (across all thresholds), as they started with a greater predicted occupancy in 2016. The number of years to reach 50% of their 2016 occupancy rates relative to woody cover varied across loser species. This is primarily related to their starting occupancy values in 2016 and the shape of the woody cover response curve. For example, despite having similar core spatial distributions and similar starting woody cover values for 2016, the Wing-snapping cisticola (*Cisticola ayresii*; Figure 4bi) had less absolute change in occupancy (0.20 in 2016 to 0.10 in 2049) than the Zitting cisticola (*Cisticola juncidis*; 0.95 in 2016 to 0.47 in 2229). Species with high predicted occupancy at their median woody cover, such the Zitting cisticola (Figure 4bii) and Crowned lapwing (*Vanellus coronatus*; Figure S7) had a much larger absolute decline required to reach 50% of their initial occupancy and therefore may take centuries to decline by 50%.

4 | DISCUSSION

Our study shows that woody plant encroachment is widespread in the open, grassy ecosystems of South Africa, Lesotho and eSwatini, and that this change in vegetation structure is having a concerning negative impact on open ecosystem bird population trends. Over 60% of species in the analysis demonstrated a population decline over the 10-year period, and approximately one fifth of all modelled species were classified as losers and are showing declining population trends in direct response to woody plant encroachment with a concerning ratio of 8:1 losers to winners. These species have higher occupancy in lower woody cover habitat and are losing good quality habitat as encroachment degrades and fragments grasslands and savannas. With most of the region experiencing increases in woody

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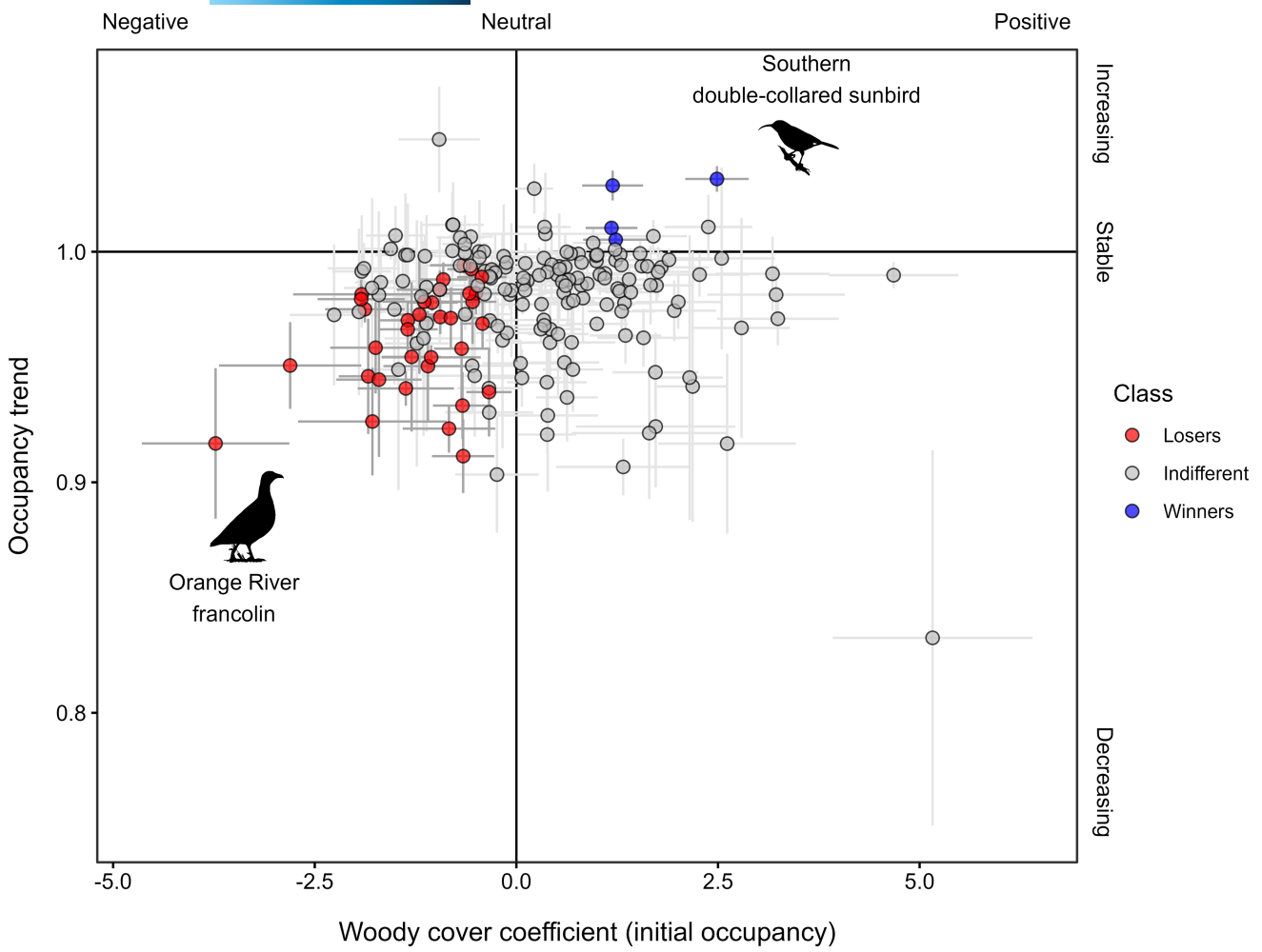

FIGURE 2 The occupancy trend and woody cover coefficients for 191 species. Losers are shown in the bottom left quadrant with a negative woody cover response and declining occupancy trend. Winners are shown in the top right quadrant with a positive woody cover response and increasing occupancy trend. See Figure S3 for examples of occupancy trends and woody cover response curves for the Orange River francolin (*Scleroptila levaillantoides*) and the southern double-collared sunbird (*Cinnyris chalybeus*). Indifferent species were (1) unlikely to have a mechanism linking their occupancy trends to woody cover (top left and bottom right quadrants), (2) showed non-significant responses to woody cover or (3) had 90% confidence intervals overlapping with the stable axes. Bars represent 90% confidence intervals and are shown in darker grey for winners and losers.

cover, we can expect further major declines in some species in as little as 20 years (Figure 4) under a business-as-usual scenario. These findings draw urgent attention to the importance of monitoring the impacts of steady land cover change across the world's grassy ecosystems, in addition to land use or climate change, and designing active restoration initiatives to address the impacts on biodiversity.

4.1 | Winners and losers

Birds are excellent indicators of changes in biodiversity (Gregory et al., 2003), and with their strong response to changes in habitat structure are ideal models for exploring how woody plant encroachment impacts populations (Andersen & Steidl, 2023; Sirami & Monadjem, 2012; Stanton et al., 2018). Responses are expected to impact birds across certain functional groups (open habitat, granivorous, ground nesters) more negatively than others (closed habitat, generalist, tree nesters). Counter to this expectation, we found no distinct trait combinations that linked loser species to grassland-associated life histories (such as open habitat, ground nesting granivores). Birds across all trait combinations were negatively impacted, though there were some important exceptions. Open habitat, ground or grass nesting, invertivores were mostly unique to losers with no winners in this category (Figure S6). We always found open habitat specialists to be losers or indifferent, and never winners, thereby never experiencing any benefit from increased woody plant encroachment, similar to the conclusions of Péron and Altwegg (2015).

In contrast to the study by Péron and Altwegg (2015) we show that woody plant encroachment can elicit strong responses across a variety of bird functional types and is not restricted to open habitat specialists. Similarly, we found most loser species were invertivores

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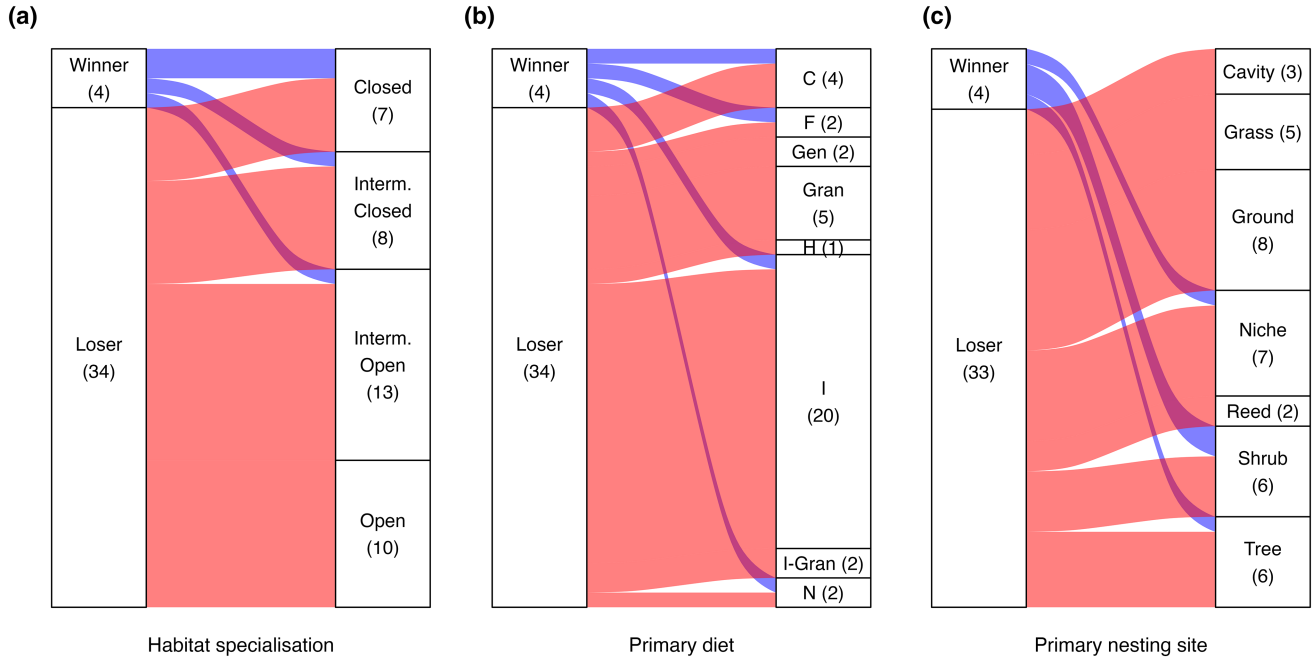

FIGURE 3 The frequencies of bird species classified as consensus winners and losers across their (a) habitat specialisations, (b) primary diet and (c) primary nesting sites of resident birds ($n = 37$) in response to increased woody cover. Abbreviations in the figures correspond to: Interm. = Intermediate, C = Carnivore, F = Frugivore, Gen = Generalist, Gran = Granivore, H = Herbivore, I = Invertivore, I-Gran = Invertivore-Granivore, N = Nectarivore.

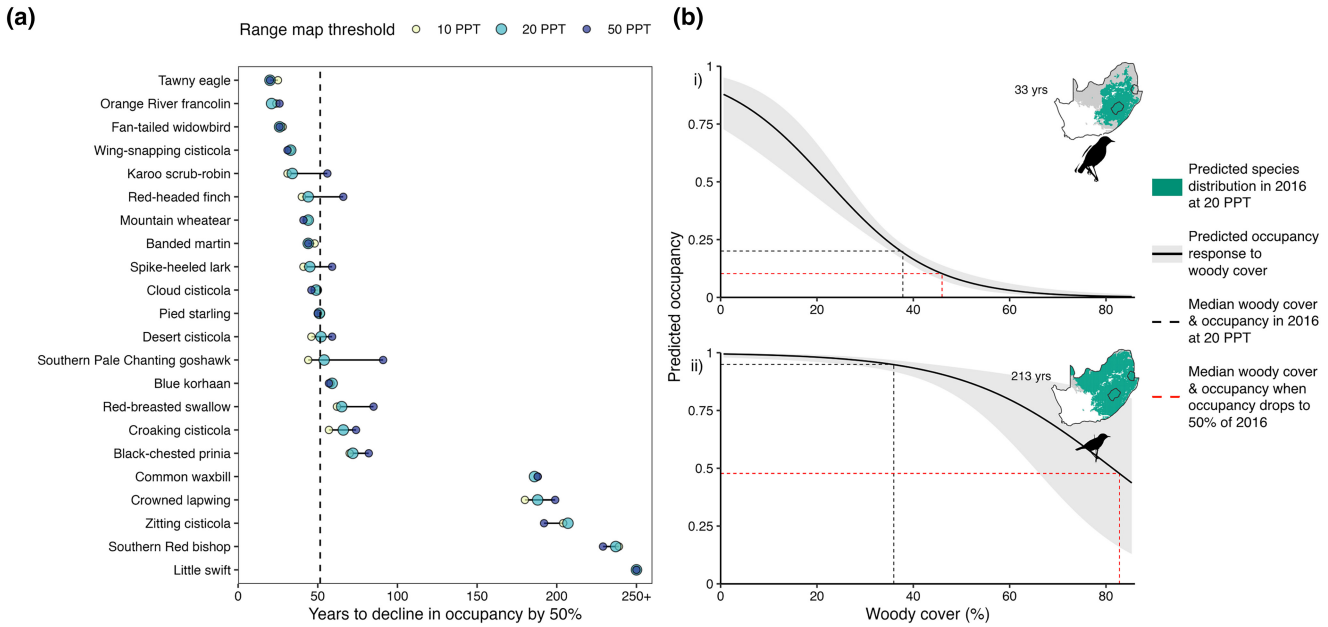

FIGURE 4 (a) The predicted number of years until a species declines in occupancy by 50% from 2016 occupancy levels for open and intermediate-open habitat losers with the dashed line showing the median value. (b) Two cisticola species showing examples of (i) a rapid (Wing-snapping cisticola; *Cisticola ayresii*) and (ii) a delayed (Zitting cisticola; *Cisticola juncidis*) decline. In panel (b) solid curves and grey polygons show their predicted occupancy response to woody cover and 95% confidence interval. Dashed black lines show the median woody cover and their corresponding occupancy values across their range in 2016. Red lines indicate when occupancy reaches 50% of its 2016 level. Maps show species predicted distributions in 2016 at 20th percentile presence threshold (20 PPT).

or granivores, such as the cisticolas. However, the same patterns were found across all species when including all birds in the analysis, suggesting loser species are not functionally distinct from the regional community. The impact of woody plant encroachment likely requires a more detailed understanding of birds' foraging behaviours and prey habitat requirements to untangle the direct mechanisms.

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For example, whether birds glean invertebrates from the woody layer or ground layer versus hawking, and what are the invertebrate host plant requirements (Holland et al., 2006; Kutt & Martin, 2010). Losers also displayed a broad range of nesting behaviours with no clear preference for sites expected to be vulnerable to increased woody cover, such as ground, grass, or reed nesting (Coppedge et al., 2001). Unsurprisingly, winners were not found in these three categories. Habitat specialisation, diet and nesting requirements may well be important functional groupings linking woody plant encroachment to species declines, though we were unable to draw definitive conclusions linking traits to outcomes for winners or losers.

4.2 | Occupancy declines

Concerningly, 121 species showed a decline in occupancy. This mirrors trends found in African savanna raptors, which show severe declines and few gains over the last 20–40 years (Shaw et al., 2024). Shaw et al. (2024) found 37 of 42 raptors declining and these declines were more severe outside of protected areas. Though these trends and those presented in this study were often subtle, it suggests there are several factors influencing bird occupancy in the region beyond only woody plant encroachment (Péron & Altwegg, 2015). While many species were negatively impacted by encroachment, some are declining despite showing greater predicted occupancy under higher woody cover. This finding highlights the difficulty in predicting species response to global change variables and indicates multiple and potentially interacting factors are at play (Stanton et al., 2018, 2021).

For the few species considered indifferent with increasing population trends and a preference for open habitats, encroachment may be a mitigating factor, providing foraging substrate and cover, nesting substrate or perches (Stanton et al., 2021). Additionally, encroachment may interact with increasing temperatures by providing thermal refugia microsites to mitigate heat stress (Carroll et al., 2017; Van de Ven et al., 2019).

However, most indifferent species in our analysis were declining despite showing a greater occupancy at higher woody cover. We speculate that this may be driven by woody plant homogeneity, as encroachment is typically dominated by a single or few woody shrub species (O'Connor et al., 2014; Roques et al., 2001). In these homogenous stands, there is reduced forage variety, forage locations, and potential nesting sites (Coppedge et al., 2001; Kutt & Martin, 2010). This warrants further investigation to identify broad-scale plant community shifts (Raymundo et al., 2023) and bird species-specific mechanisms linked to encroachment beyond just woody cover, particularly for these declining species.

4.3 | Complexity of woody cover responses, occupancy and scale

Our analysis revealed that the impacts of woody plant encroachment on populations are complex, with species impacted at different time scales. Isolating woody cover as a single variable, we predict that the Tawny eagle, already globally listed as vulnerable (Birdlife International, 2021), may lose a further 50% of its regional occupancy within 20 years if woody plant encroachment continues unabated. Many species, such as Wing-snapping cisticola, are already at the extreme end of their tolerance for woody cover and their regional occupancy will continue to be at risk with further encroachment.

The time scales at which species are predicted to decline depends on (1) current woody cover across their range and (2) the shape of their occupancy response curves to woody cover. Concerningly, several species with preferences for more open, grassy habitats show mean woody cover values across their ranges indicative of high woody cover savanna systems (>30% woody cover, Figure S6). Our estimates only used mean woody cover scores across each species' range, which is likely to mask out local occupancy increases, decreases, persistence, extinction, and colonisation across sites (Frey et al., 2016). However, our goal was to explore how species with similar starting woody cover values across their range (such as the two closely related cisticolas) may elicit stark contrasts in their predicted occupancy change to increased encroachment due to their different woody cover occupancy response curves (Figure 4). Zitting cisticolas are predicted to be more tolerant to higher woody cover values, while Wing-snapping cisticolas have a narrower range of suitable habitat. The low relative occupancy values for Wing-snapping cisticolas and similar species make small absolute changes crucial to monitor.

Evaluating population trends at a pentad scale across large regions comes with some limitations. (1) Due to the nature of citizen science data, we cannot be sure that each atlas survey returned the exact same locations within each pentad (Chamberlain et al., 2019). It is therefore important to interpret these results as coarse, region-wide indicators across species and not as localised population dynamics, which may be evaluated far better with targeted, repeated point count studies (e.g. Sirami & Monadjem, 2012). (2) The species filtered out of the analysis due to low presence or non-converging models may have different population trends and are not accounted for here. Additionally, as we did not look at possible mechanisms outside of woody cover, we cannot draw conclusions on the drivers of population change for most species analysed in this study. However, for those species included, we have used both average rate of occupancy and Z-scores to carefully identify the direction and significance of population trends. (3) Woody cover and rates of change were average at the pentad scale, potentially confounding high variance within a pentad. For example, a pentad may be experiencing high increased woody cover while simultaneously being cleared in different sites. However, with over 3000 pentads used in this study, we do not believe this localised variance would greatly affect our outcomes.

4.4 | Implications

We found worrying evidence for population declines in almost 20% of the common southern African birds examined in this

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study and highlighted woody cover as an important driver of this. Our findings draw attention to understanding species-specific responses to biome-level ecological change. In contrast to previous work (Andersen & Steidl, 2019; Péron & Altwegg, 2015; Sirami & Monadjem, 2012) we found no definitive pattern in species traits with birds typically considered savanna- or closed habitat specialists declining along with open habitat specialists. Importantly, in this study we focused on abundant species above a presence threshold to improve modelling reliability. However, there are several hundred rarer species that may be similarly impacted by woody plant encroachment and already be of conservation concern. Changes in occupancy of any of these species has the potential to rearrange community-level interactions (Andersen & Steidl, 2019) and trigger cascading biodiversity changes at higher or lower trophic levels (Bridgeland et al., 2010).

In untransformed systems it is often assumed that biodiversity is going to be most significantly impacted by climate change and land use change. The responses of birds to woody plant encroachment in our study is a strong indicator that drivers beyond climate and land use change can have significant consequences for terrestrial biodiversity. The steady change in vegetation structure seen across continental and biome scales (Skowno et al., 2017; Venter et al., 2018) is a significant driver of biodiversity disruptions and declines. In the rush to respond to climate change and biodiversity loss there is increasing emphasis on tree planting as a mitigation measure, often focused in open grassy ecosystems (Bond et al., 2019; Fagan et al., 2020). Such measures will only intensify the negative responses shown by our study, by further woodifying grass-dominated ecosystems. Our study serves as an important reminder that increasing aboveground woody biomass, through encroachment or afforestation, may lead to trade-offs in biodiversity (Veldman et al., 2015).

Open, grassy ecosystems remain vulnerable to land use and land cover change, with continued degradation and fragmentation across previously untransformed lands (Archer et al., 2017; Skowno et al., 2021). Calls to better manage woody plant encroachment through targeted clearing (Stafford et al., 2017), implementing appropriate fire regimes (Alados et al., 2019) or complementing grazers with browsers in rangelands (Estell et al., 2012) in an integrated land management strategy are crucial for both conserving open ecosystem biodiversity and ecosystem services (White et al., 2022). Additionally, conservation efforts need to manage the complexity of balancing open ecosystems where species may either benefit or lose out due to woody plant encroachment. If the global commitments of halting biodiversity loss, and restoring and conserving up to 30% of terrestrial areas by 2030 are to be realised, significant intervention needs to be directed to the rangelands and near-natural lands outside of protected areas where degradation threatens ecosystems and species.

AUTHOR CONTRIBUTIONS

Joseph D. M. White: Formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Nicola Stevens:** Conceptualization; funding acquisition; methodology; writing – review and editing. **Jolene T. Fisher:** Conceptualization; funding acquisition; methodology; writing – review and editing. **Chevonne Reynolds:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The SABAP2 atlas cards can be downloaded from sabap2.birdmap.africa. The processed outputs that support the findings of this study are available in the supplementary material of this article. The cleaned SABAP2 cards, occupancy models and pentad-level woody cover data are available at https://doi.org/10.6084/m9.figshare.25577460 and the R code to produce these outputs can be found at https://doi.org/10.5281/zenodo.11220477.

ORCID

Joseph D. M. White https://orcid.org/0000-0002-5617-4515
Nicola Stevens https://orcid.org/0000-0002-0693-8409
Jolene T. Fisher https://orcid.org/0000-0002-1626-7610
Chevonne Reynolds https://orcid.org/0000-0002-2345-7017

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