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Bird communities show resilience to an extreme drought across a large savanna protected area

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ABSTRACT

Extreme weather events, such as drought, are exacerbated by climate change. Drought impacts vegetation directly, but it also indirectly influences taxa, such as birds, that depend on plants. Although the diversity and abundance of birds and other taxa inform protected area (PA) biodiversity conservation mandates and monitoring programmes, in Africa, for example, there has historically been a general disregard for birdlife when PAs were gazetted. Thus, we aimed to understand how an extreme drought during 2015–2016 in the Kruger National Park, South Africa, impacted bird community composition, diversity and sensitivity to finer-scale pulse disturbances. We used bird species occurrence data and subsequent reporting rates (a proxy of abundance) from one of the world's largest citizen science projects, the Southern African Bird Atlas Project (SABAP). We found that bird diversity significantly increased post-drought, but sensitivities were unaffected, suggesting a resilient bird community occupying this relatively large PA. Our findings show that one of Africa's largest savanna PAs plays a seemingly important role in maintaining regional bird diversity in the face of extreme droughts. We urge PA management to monitor their bird communities and continue to support those who take the initiative to detect losses from severe, multi-season extreme weather events that are expected to become more frequent.

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1. Introduction

Globally, extreme weather events, such as drought, are increasing and have been exacerbated by climate change, posing a major risk to ecosystems (IPCC, 2001; Spinoni et al., 2019). For example, climatological stress related to drought can include reduced surface and subsurface water, which in turn relates to decreased vegetation growth and increased heat waves, ultimately influencing animal population growth and movements. The potential effects of these on semi-arid ecosystems (Zomer et al., 2022) and any protected areas (PAs) therein need to be considered, as such an event may ultimately impact overall ecosystem function and productivity. Events such as El Niño, which often result in unusually high rainfall, may have both positive and negative impacts on animal populations (Grant et al., 2000) and vegetation. However, they may also have negative effects, such as the destruction of habitats and the biota they support. Such extreme weather events inherently necessitate consideration of time (i.e. before, during, and after the event) and are related to much-debated theoretical concepts, such as stability and associated resistance, recovery and ultimately resilience in ecology (Lewontin, 1969; Abbott et al., 2023). Moreover, we can consider drought a press perturbation because its effects span a longer timescale (e.g. across one or multiple seasons) that, in turn, can impact shorter pulse perturbations, such as increased daily or weekly frequencies of temperatures above a certain threshold (Kéfi et al., 2019; Malherbe et al., 2020). For systems and their species to maintain normal functioning, like feeding or breeding under these different perturbations, they must 1) exhibit resistance during drought (e.g. limited loss of diversity and function or have specialised survival strategies), and 2) exhibit recovery after drought (e.g. breeding success or fecundity increases). If, in combination, resistance and recovery are high over time (as before, during and after an event), it suggests a resilient individual, species, community or ecosystem (Hodgson et al., 2015; Wilcox et al., 2020).

The response of birds to drought can be marked, and globally, such extreme events have a negative impact on bird demography, especially in more arid parts of the world, given birds' strong dependence on plants for nesting habitats and food provisioning (Fernández-Tizón et al., 2020; Zhang et al., 2024). Specifically, actively growing vegetation provides food for arthropods, which are important food sources for many bird species. Invertebrates have been shown to suffer from the indirect effects of drought because of changes in vegetation (Croy et al., 2021). In systems such as semi-arid savannas and other systems, drought negatively affects precipitation and subsequent net primary productivity as well as the normalised difference vegetation index (NDVI) of the herbaceous layer (Wessels et al., 2006). Areas with high vegetation productivity tend to have bird communities that are more resilient to severe droughts than arid areas with lower vegetation productivity, compared with more mesic areas (Selwood et al., 2018). Globally, bird responses to drought will depend on their interactions with, for example, vegetation. Thus, project and data collection designs, together with robust statistical approaches, will be able to leverage functional traits, such as those related to breeding and feeding, which may provide important insights into the impacts of drought on biotic communities. For example, at the functional trait-level, populations of short-lived birds with smaller clutch sizes have been found to suffer more because of drought impacts (Zhang et al., 2024) and smaller migrant birds (<50 g body mass) in temperate climes generally prefer areas of high NDVI (Iverson et al., 2023).

Protected areas, such as Kruger National Park and others across Africa, operate in complex socio-ecological environments, and often, there was little to no consideration given to birdlife when these PAs were gazetted, leading to suboptimal placement, e.g. threatened bird species (Beresford et al., 2011). Thus, the protection benefits bird communities receive through PAs do not necessarily come from targeted conservation projects, but rather from maintaining intact habitats aimed at conserving or preserving more charismatic, threatened mammals and plant species (Beale et al., 2013). Historically, Kruger National Park has achieved limited in-house monitoring of its birdlife, and only 3 % of 545 publications stemming from externally driven research in Kruger National Park from 2003 to 2013 focused on birds (Smit et al., 2017). Despite these limitations, this protected area (PA) supports several non-governmental organisations (NGOs) and academics that continue to monitor a subset of threatened birds for which PAs are generally considered refugia from land degradation (Beale et al., 2013; Thiollay, 2006; South African National Parks Annual Report (Annual), 2024).

Kruger National Park supported the “Turning Kruger Green” initiative (2014–2016), a second South African Bird Atlas Project (SABAP2) sub-project, led by citizen scientists to achieve increased coverage of bird distribution and abundance records across the PA. More recently, Kruger National Park has begun monitoring bird communities in selected areas of high disturbance, and the recently launched “Birding for Science” BirdLasser initiative across South African National Parks (SANParks) will contribute to the national SABAP2 database. Moreover, this PA is a stronghold for faunal and floral conservation in semi-arid savannas, harbouring 2800 animal and plant species. It is among the 20 ($n = 3610$) and five ($n = 345$) largest savanna protected areas across Africa and southern African countries, respectively (UN Environment Programme World Conservation Monitoring Centre UNEP-WCMC and IUCN, 2025). The park has a mean annual precipitation of 541 mm, with alternating wet and dry cycles occurring approximately every five years (MacFadyen et al., 2018).

Southern Africa, including Kruger National Park, experienced an extreme weather event (i.e. drought) based on the extreme climate index during 2015–2016 (Malherbe et al., 2020). This drought epoch was identified as one of three events with the largest impacts across the park over the last ~35 years, with such extreme weather events expected to become more frequent in South Africa (Yuan et al., 2018). For example, the number of heat waves as well as the number of heat wave days during the recent drought (2015–2016) were twice as many as compared with the prior three drought periods of the region (i.e. 1982–1983, 1991–1992, 2002–2003; Malherbe et al., 2020). This specific extreme weather event thus provided an important opportunity to investigate the responses of bird communities comprising varying functional traits (such as body mass and diet) over a more extended period by examining prior and post-drought patterns in this locally understudied taxon (Smit et al., 2017). Such results could contribute to the strategic adaptive management approach, which requires scientific findings to enable PA management to develop mitigation strategies for future drought events that may impact lesser-known taxon groups, such as birds (McGeoch et al., 2011; Beale et al., 2013; Smit and Bond, 2020).

We expected the 2015–2016 drought to have negatively impacted the bird community, driving a decline in bird diversity across Kruger National Park, as birds rely on vegetation both directly and indirectly for food, shelter, and breeding. Firstly, we aimed to establish whether there were differences in the park's bird community before, during, and after this extreme weather event. We predicted that species richness, diversity, community composition and functional uniqueness/redundancy would be somewhat resistant to the drought. These would display reductions in abundance (due to, for example, low vegetation productivity and associated reductions in food) during the drought (Albright et al., 2010; Roberts et al., 2019). Following the drought, increases in vegetation productivity may have led to the recovery of bird community abundances, ultimately demonstrating the resilience of the PA's birds to the drought. Secondly, we investigated the degree to which bird functional trait group abundances within Kruger National Park were sensitive to changes in environmental variables (i.e. short-term pulse perturbations) such as maximum ambient temperature, precipitation, and vegetation greenness (a proxy for vegetation productivity). For example, hydrological processes, such as soil moisture resulting from precipitation, which drive habitat attributes, have been shown to relate to key life history traits of small birds (Cady et al., 2019). We predicted that changes in conditions from pre-drought to drought to post-drought would impact bird trait group sensitivities to pulse perturbations. For example, small species with high metabolic rates, such as granivores and insectivores, that rely directly or indirectly on vegetation conditions for food, may be negatively impacted by unusually high and frequent ambient temperatures or low NDVI values. Similarly, we expected these short-lived species with smaller clutch sizes to have lower abundances during or after the drought (lag effects) because of reduced breeding and the influences of the drought.

2. Methods

2.1. Data acquisition

We employed one of the world's largest citizen science databases for bird occurrence data: SABAP2 (Brooks et al., 2022), which has approximately 22.3 M bird distribution records from mid-2007 to the start of 2024. The data collection protocol involves volunteers traversing pentads (5 by 5 min latitude/longitude coordinate grid cells covering ~81 km²) and recording the bird species observed therein. Our study focused on 181 pentads completely contained within the boundaries of Kruger National Park. However, for our first aim (bird community composition and diversity), we only considered pentads with more than 10 checklists submitted during each drought epoch. These epochs were classified as pre-drought (2011–07–2015–06; 48 months), drought (2015–07–2016–06; 12 months) and post-drought (2016–07–2019–06; 36 months; [Supplementary Information Fig. S1](#)).

Specific to the second aim (bird functional trait groups and their sensitivities to environmental perturbations), we considered pentads that had more than four bird checklists submitted each month during the different epochs. According to Underhill and Brooks (2016), four checklists are considered a minimum for analyses, as this equates to at least 8 h spent actively recording bird species within a pentad ([Supplementary Information Figure S1](#)). The bird checklists used conformed to the “full protocol” criteria, which involved spending a minimum of 2 h and a maximum of 120 h (five days) recording bird species within a pentad. Although the selection of pentads based on a minimum of 10 and four checklists, respectively, results in a large time range spent recording bird species in these grids, we assumed this ‘mixed effort’ applied to all three drought epochs. We also demonstrated that varying sample sizes across our study area had negligible effects on the results (Lerm et al., 2023). We included only resident bird species ($n = 334$) considered to be residing in the park year-round and affected by park-wide processes across seasons, and we employed each species' reporting rate as a proxy of abundance ([Supplementary Information Table S1](#)). Using two sources, we also utilised remotely sensed environmental data to support our second aim. Firstly, we obtained maximum monthly ambient temperature and total monthly precipitation data from the WorldClim database (<https://www.worldclim.org/>). Secondly, we obtained vegetation greenness data in the form of the NDVI (a proxy for productivity; MODIS Combined 16-Day dataset) for the same period and on a monthly frequency for the study area.

2.2. Data analyses

We employed non-metric multidimensional scaling (NMDS), which is one of the most robust techniques for uncovering the compositional dimensions of communities associated with environmental gradients (Kruskal, 1964; Minchin, 1987). In our case, it was used to investigate whether the respective drought epoch bird communities were composed differently by visualising pentads (sites) in ordination space based on their bird species composition. Specifically, we selected a dimension (k) that reached a stress value of ~ 0.05 , which can substantially reduce the risk of false inferences (Clarke, 1993), and goodness of fit tests resulted in $p < 0.05$ across pentads. We employed permutational multivariate analysis of variance (PERMANOVA) using distance matrices and 999 permutations to account for multivariate normality and variance homogeneity (McArdle and Anderson, 2001), testing whether the observed differences in bird species composition across the epochs were significantly different. We employed a beta diversity measure based on the distances of each pentad to the relevant epoch centroid (Anderson et al., 2006) to detect how each epoch's pentads were dispersed (variances) based on their species composition (because sample sizes were unbalanced). A permutation test was then performed to detect the homogeneity of multivariate dispersions (i.e. whether the distances from the overall centroid differed significantly). The vegan package (Oksanen et al., 2022) was employed to perform the above analyses in R (R Core Team, 2023).

Secondly, we computed three commonly used diversity metrics (i.e. species richness, quadratic diversity/entropy, and Simpson diversity) to detect trends from pre- to post-drought using the qualifying pentads ([Supplementary Information Fig. S1](#)). The fourth metric calculates bird community-level uniqueness or functional redundancy based on the traits of resident bird species, as per Lerm et al. (2023), and also allowed us to compare its values across the drought epochs to detect the influence of drought. Moreover, we

employed this framework of four metrics to summarise the different facets of bird community composition before, during, and after the drought, using well-known, traditional metrics as well as more recent developments, such as the aforementioned uniqueness framework. Specifically, species richness refers to the simple total count of species. Simpson's diversity is a well-known taxonomic diversity metric that incorporates species richness and evenness, but not dissimilarity (Simpson, 1949). Rao's quadratic diversity, on the other hand, includes a dissimilarity matrix (Rao, 1982). These metrics are independent of species richness except for small values of uniqueness, which was not the case in our data configuration (Ricotta et al., 2016). A characteristic of this uniqueness (functional redundancy) proposal is that a direct relationship emerges between functional diversity and vulnerability. This means that if a community is highly diverse, it is also highly vulnerable (Ricotta et al., 2016). The computation of all four indices followed the *uniqueness* function produced by Ricotta et al. (2016) in conjunction with the *ade4* R package (Dray and Dufour, 2007). The bird functional traits used for uniqueness/redundancy computation were obtained from Lerm et al. (2023), who derived the traits from those described by Hockey et al. (2005). Specifically, they included the mean body mass, primary diet, nest shape, and primary nesting location for each resident species. We performed a Kruskal–Wallis rank sum test with a Bonferroni-corrected post-hoc Dunn's test to detect differences between epoch pairs that existed and among the epoch diversity metrics (Kruskal and Wallis, 1952; Dunn, 1964; Hochberg, 1988).

Thirdly, we employed several analytical procedures in a stepwise manner to detect whether the abundances of different bird functional trait groups were influenced by pulse perturbations, such as ambient temperature, precipitation, and NDVI, from pre- to post-drought. Firstly, bird species reporting rates (%) were averaged across pentads and months and used as a proxy for their abundance in Kruger National Park (Lee and Hammer, 2022; Lee et al., 2022; Supplementary Information Fig. S2). Then, we performed hierarchical clustering to group bird species into functional trait categories/groups based on all the resident species reported in the PA that had functional traits classified according to Lerm et al. (2023), which were derived from natural history information for southern African bird species (Hockey et al., 2005). Specifically, the traits we employed included body mass, primary diet, primary nest shape and primary nest location. This diversity of traits may be influenced by various environmental factors. For example, small-bodied species react differently to larger birds in terms of heat tolerance (Gerson et al., 2019), and ball-shaped nests are more prevalent in hot environments (Englert Duursma et al., 2018); a scenario simulated by the 2015–2016 drought that may have caused shifts in species distributions. Furthermore, we categorised the bird species body size values into three classes: small (1–100 g), medium (101–1000 g) and large (>1000 g). We employed the *vegan* package to perform the clustering (Oksanen et al., 2022).

We employed different empirical dynamic modelling (EDM) techniques to measure the sensitivity of each bird functional trait group to external perturbations. Briefly, EDM encompasses a suite of nonlinear time series tools for analysing and forecasting population dynamics from time series data (Munch et al., 2023). We first used convergent cross mapping (CCM) to detect causal links between bird groups (i.e. interactions such as predator-prey or competition), and between bird functional trait groups and environmental variables. This mapping method tests for causation by measuring the extent to which the historical record of Y-values (environmental variables in our case) can reliably estimate the state of X (bird abundance in our case; Sugihara et al., 2012). These statistical procedures address the ubiquitous, nonlinear relationships that may exist over time among variables. We performed CCM separately for each pair of bird-environmental variables using monthly time series (the length referred to as library size) for each variable pair (functional trait groups as identified by hierarchical clustering and the three environmental variables) from July 2011 to June 2019 ($n = 96$ months and a prediction-time interval of $T_p = 1$ with a final library size of 100). Optimal embedding dimensions (E) were chosen for each variable pair by plotting a range of embedding dimensions as a function of the forecast accuracy and selecting the largest value of E (i.e. where the forecast accuracy peaks along the range of E -values; Sugihara and May, 1990).

We were specifically interested in identifying significant causal links where the three environmental variables drove functional group abundances (i.e. environment-species interactions, rather than illogical species-environment interactions). We followed recent protocols (Ushio et al., 2018; Liu and Gaines, 2022) and considered a causal link to be significant if (1) the cross-prediction accuracy (ρ) was higher than the correlation coefficient between the time series pair and (2) the cross-prediction accuracy for the observed data was higher than 95 % of the cross-prediction accuracy values for surrogate time series data generated from a seasonal null model based on 12 months, 1000 surrogates and an alpha value of three. We then used the set of bird functional trait groups and environmental variables that were significantly causally coupled to each other to estimate the sensitivity of each bird group to perturbations. To achieve this, we employed a locally weighted linear regression method, known as the S-map (Deyle et al., 2016), to reconstruct a time-varying Jacobian matrix. From this matrix, we computed the sensitivity of each bird functional trait group to pulse perturbations in each month (Medeiros et al., 2023). We performed the S-map using only the bird groups and environmental variables causally coupled to each other, and used the exponential regression weight (θ) that maximised leave-one-out prediction accuracy (i.e. θ at maximum mean R^2). All time series data were standardised to a zero mean and unit standard deviation before the CCM and S-map analyses. We performed these analyses using the *rEDM* package (Park et al., 2023). All pairwise post-hoc test results display Bonferroni-adjusted significance values.

3. Results

The species composition of the bird communities differed significantly between the drought epochs based on the bird species recorded during each epoch, albeit inconspicuous across ordination space ($F = 3.158$, $Df = 2$, $p < 0.01$). However, because our sample sizes (the number of pentads included) across the epochs were unbalanced (Supplementary Information Fig. S1) the mean dispersion distance (variance) to the centroid of all pentad communities based on the bird species composition in each epoch had to be determined. We found that these dispersion distances did not differ significantly and that each epoch's communities were homogenous ($F =$

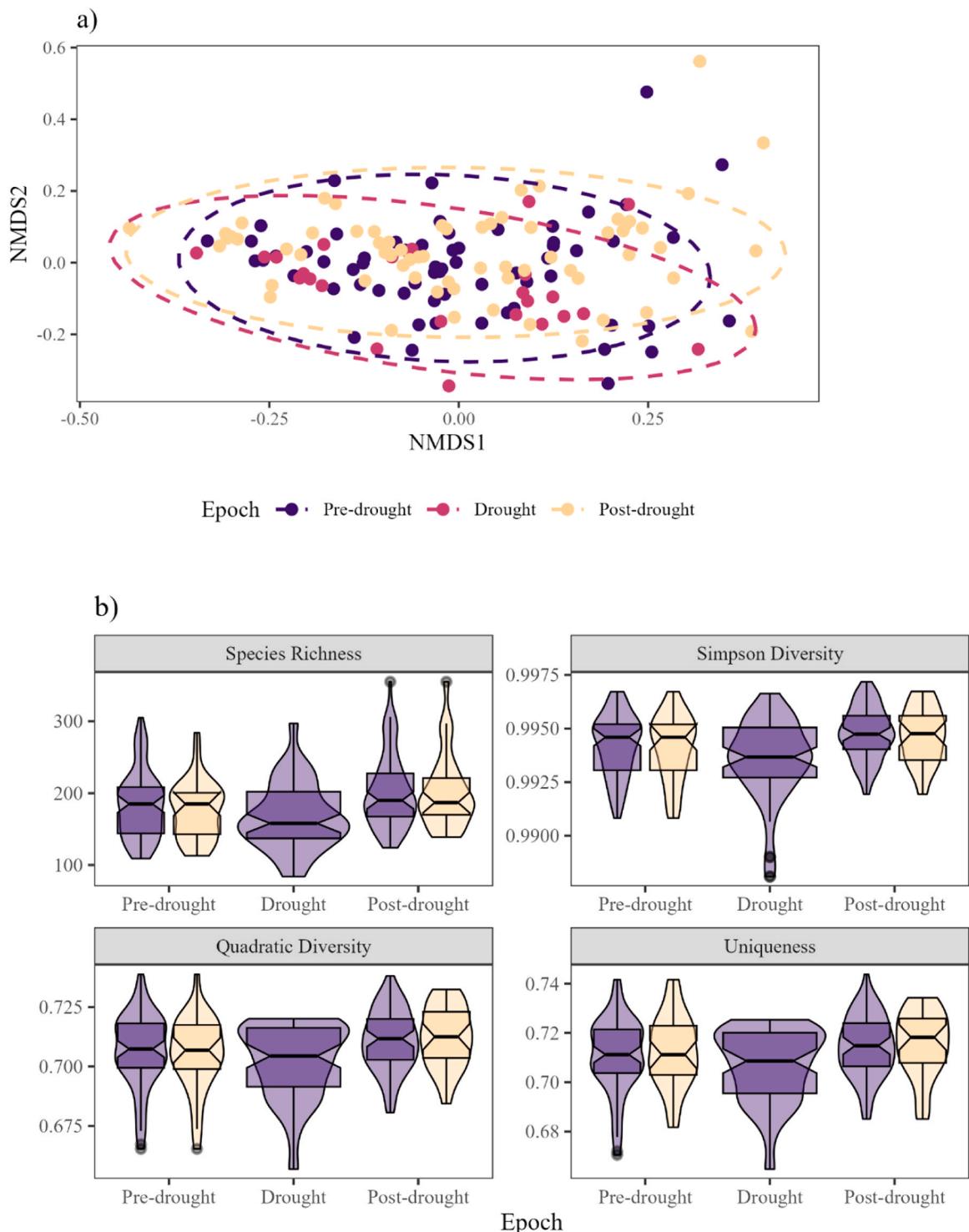


Fig. 1. Outputs of a) nonmetric multidimensional scaling ordination space displays the arrangement of bird communities based on species composition across the three drought epochs (where $k = 12$; ellipses present the 95 % confidence level; final stress value of 0.051), and b) violin- and boxplots display differences in bird diversity patterns across the three drought epochs for the full dataset (dark colours) and the randomly subsampled data (light colours; $n = 12$) from pre-drought and post-drought to match the sample size of the drought epoch. Note for the latter, boxes and whiskers display the interquartile ranges and maximum values, respectively. Dots are outlier pentads, and horizontal lines are the median values. Violin widths display frequency distributions, and the notches on the boxplots display lower (5 %) and upper (95 %) confidence intervals.

0.356, $p = 0.705$; Fig. 1a), suggesting that differing sample sizes did not affect the ordination output. The stress value produced for the NMDS analysis was 0.051, which is considered appropriate for making inferences about the differences or similarities in the composition of the different communities (Clarke, 1993). A lack of significant differences between the diversity metrics of the pre-drought and drought epochs suggests that the system was resistant to the extreme weather event. However, species richness, Simpson diversity and quadratic diversity were significantly larger post-drought compared with the drought epoch itself (with Bonferroni p-value adjustments), indicating mostly community recovery. Uniqueness (functional redundancy) was not significantly different between the drought and post-drought epochs. Although none of the diversity metrics differed significantly between the pre-drought and post-drought periods, regardless of whether sample sizes were balanced or not, the NMDS ordination produced results indicating differing species compositions, likely because of species turnover (Fig. 1a, b; Table 1).

Our first step to determine direct environmental impacts (i.e. those of maximum ambient temperature, rainfall and NDVI) on broad bird groups was to classify the PA's species into functional trait groups based on Lerm et al. (2023). Hierarchical clustering identified six such groups: 1) large carnivorous platform nesters, 2) medium to large ground nesters, 3) medium platform nesters, 4) small ball nesters, 5) small cup nesters and 6) small to medium cavity nesters. Small cup-nesting birds [91 species (e.g. the swallow family Hirundinidae)] comprising various feeding traits were the most diverse group in Kruger National Park. Small ball nesters comprised 75 species from the family Estrildidae (e.g. waxbills). Small to medium cavity nesters comprised 35 species, typically African barbets from the family Lybiidae, and hornbills from the family Bucerotidae. Medium platform nesters comprised 31 species, like herons and egrets from the family Ardeidae. Large carnivorous platform nesters comprised 28 species including various endangered vultures and eagles (family Accipitridae). Lastly, the least diverse group of birds was identified via clustering as medium to large ground nesters and included 15 species (e.g. the pheasant family Phasianidae and the Common Ostrich *Struthio camelus*; Supplementary Information Table S1).

Our detection of pairwise causal links via CCM identified two environmental variables (NDVI and maximum ambient temperature) as drivers of three bird functional trait groups, where the prediction accuracies (ρ) were larger than correlation coefficients: small cup-nesting birds (scn), small to medium cavity nesters (smcn), and small ball nesters (sbm). Vegetation greenness (NDVI) was a significant driver of small cup-nesting birds ($\rho = 0.483$; surrogate null model test: $p < 0.001$; $E = 9$) and small to medium cavity nesters ($\rho = 0.453$; $p < 0.001$; $E = 5$), whereas maximum ambient temperature drove small ball nesters ($\rho = 0.474$; $p < 0.001$; $E = 8$; Supplementary Information Table S2). Small to medium cavity nesters were near-significantly ($p = 0.053$) driven by maximum ambient temperature as well. The CCM cross-prediction accuracy for all these cases was larger than the correlation between the time series (Supplementary Information Table S1). Although our CCM analyses identified causal links in both directions (i.e. among the three bird groups comprising medium and large species and the three environmental variables), we disregarded such illogical links where the birds drove the environmental variables.

Continuing from CCM, we reconstructed time-varying Jacobian matrices with the S-map using NDVI, temperature, small cup-nesting birds, small to medium cavity nesters and small ball nesters as state variables. We found no significant differences when we compared the monthly sensitivities of each bird functional trait group across the drought epochs. This lack of significant differences suggest these trait groups were resistant to drought despite being influenced by shorter, monthly environmental perturbations as identified by CCM or some other confounding variable like environmental lag effects (sbm: $\chi^2 = 2.643$, $p = 0.27$; scn: $\chi^2 = 0.503$, $p = 0.78$; smcn: $\chi^2 = 2.656$, $p = 0.26$; Fig. 2a, b).

4. Discussion

Our findings on bird community composition, diversity and sensitivity showed that the 2015–2016 drought across one of Africa's largest PAs (the Kruger National Park) had negligible effects on the park's birds. This suggests that this PA is host to an overall resilient bird population because, the communities did not suffer during the drought and showed post-drought increases, typical of grassland and savanna systems to the West of Kruger (George et al., 1992; Herremans, 2004). Increased phylogenetic diversity inside Kruger National Park compared with the outside landscapes, less infrastructure within its boundaries and its large size (~2 M ha with fewer edge effects than smaller PAs) may have likely contributed to the resilient nature of the bird community, although we cannot say for certain that the PA's bird communities are more resilient to drought than the more anthropogenic landscape outside (Newmark, 2008; Lerm et al., 2023). However, we found that most small to medium-sized birds responded to ambient temperature or vegetation greenness. The lack of differences we found in bird responses to season or across epochs is reinforced by others who found that short-term responses to temperature are more important in driving bird distributions. Although life history traits mediate these

Table 1

Dunn's test results (Z) displaying Bonferroni-adjusted differences between the epochs, for each of the bird diversity metrics using the full dataset (i.e. not sub-sampled to match the drought epoch). Ecological capacity is indicated.

	Pre-drought to drought (resistance)	Drought to post-drought (recovery)	Pre-drought to post-drought (resilience)
Species Richness	-1.608	3.058**	1.877
Simpson Diversity	-1.608	3.058**	1.877
Quadratic Diversity	-1.223	2.210*	1.280
Uniqueness	-1.100	2.089	1.280

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

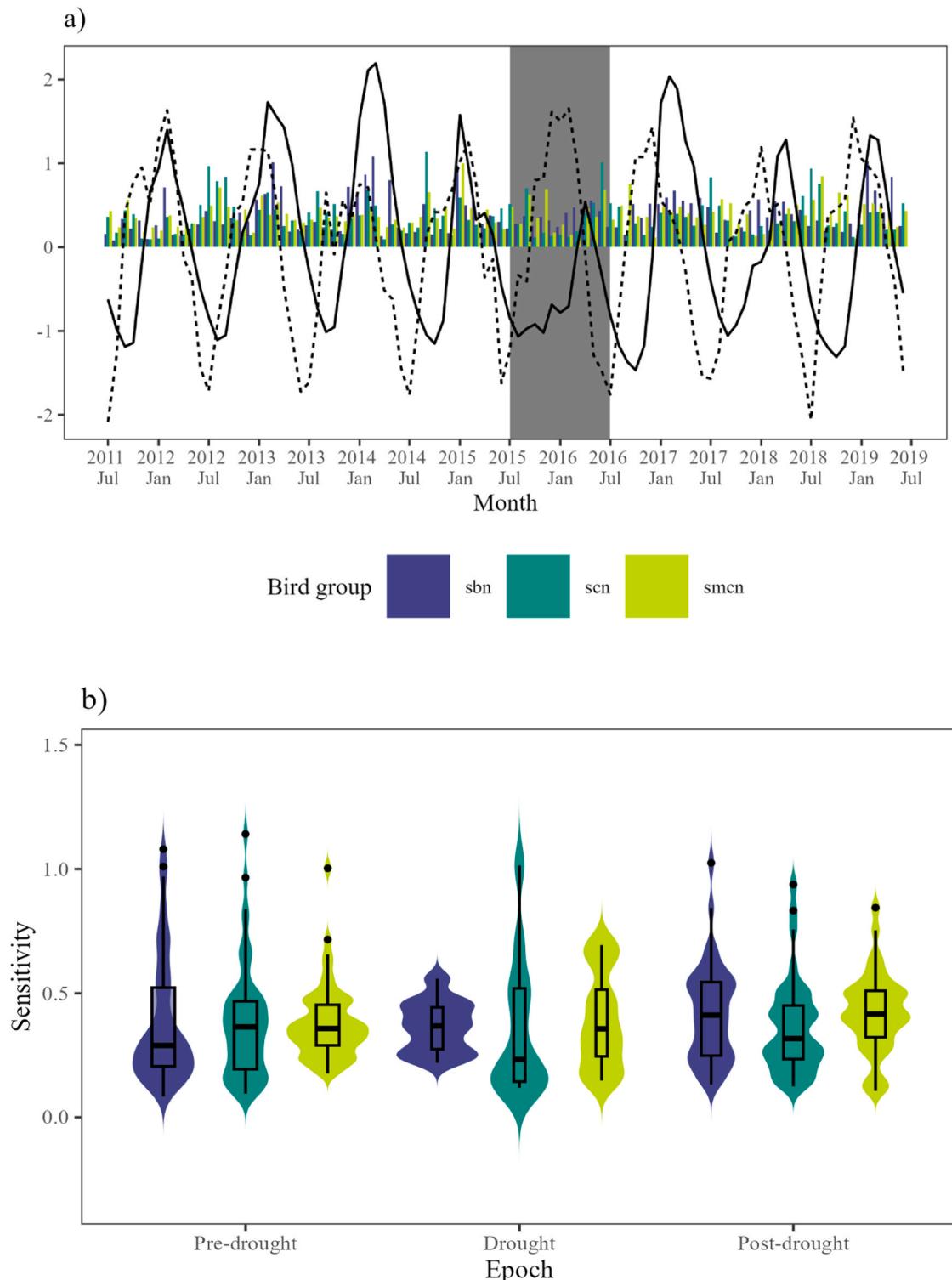


Fig. 2. Outputs showing a) scaled monthly contributions of bird functional trait group sensitivities to observed NDVI (solid line) and maximum ambient temperature (dashed line) where the shaded area indicates the period of extreme drought, as is evident in the environmental trends; b) violin plots (with data distributions in colour) overlaid with box-and-whisker plots (boxes show interquartile ranges around the median and whiskers the maximum values) of scaled sensitivity values across the three drought epochs (colours match trait groups from Fig. 2a). Note: Black dots present outliers. Box plot widths correspond to the sample sizes of each epoch. Bird functional trait group colour and corresponding abbreviations are sbn – small ball nesters; scn – small cup nesters; smcn – small to medium cavity nesters.

responses to extreme weather (Cohen et al., 2020), we found that it was likely traits associated with the larger birds occupying the Kruger National Park which were not affected by heat. Surprisingly, we did not find changes in small bird sensitivities as a result of the heat waves associated with the 2015–2016 drought, because sharp decreases in population growth rates exist among species with smaller thermal ranges (Jiguet et al., 2006). Generally, NDVI has been found to positively and strongly predict bird species richness because of the energy availability in the systems birds occupy (Nieto et al., 2015), more so than, for example, vegetation structure, specifically in predicting drought resistance in birds (Selwood et al., 2018). It is thus surprising that we did not find any significant differences in the bird communities during the drought when NDVI values were unusually low. Likely, confounding factors existed, such as certain functional traits we could not account for, allowing the bird population to resist the drought.

Using citizen science data, such as those derived from SABAP2, requires careful handling, and although we have not explicitly converted reporting rates to abundance, the reporting rate is considered a proxy for abundance. The SABAP's spatial design enabled us to utilise a minimum of eight hours worth of bird record data in each spatial grid (pentad), which are easily traversed and subsequently vetted by expert field ornithologists, providing robust data. This minimum sampling effort is sufficient for obtaining reliable species occurrence data (Underhill, 2016). The drought period, however, was characterised by the uptake of the BirdLasser smartphone app (<https://www.birdlasser.com/>) for submitting SABAP2 records, which resulted in a surge in bird distribution records for Kruger National Park. This increase in card submissions, which peaked in 2017 (the start of the post-drought epoch), then subsided in 2020 to the levels of 2015, likely because of the COVID-19 pandemic. The initial surge likely contributed to increasing the sample size used for the 12-month drought epoch of this study, thereby enhancing confidence in the results presented here (Lerm et al., 2023; Fig. S1; Supplementary Information Fig. S1). Moreover, by using the standard criteria (employing more than four checklists per pentad or eight hours of active bird recording), we showed that not only were ordination variances homogeneous, but also that matching sample sizes of pre- and post-drought epochs to the drought had no difference in effect (Fig. 1a, b). Others have also demonstrated that this reduction or balancing of sample sizes has no effect when applied to this specific dataset across our savanna study area (Lerm et al., 2023).

Finally, regardless of the generally suboptimal placement of PAs, we believe that widespread and abundant species, comprising most of the bird communities we studied, benefit from the Kruger National Park. This PA likely acts as a buffer against climate change and negative land degradation that are typically evident outside PA boundaries. Although in this study we could not show that Kruger's PA fared better than outside when struck by extreme weather events like drought, it has been shown before how this PA contributes to regional bird diversity (Woinarski et al., 2012; Beale et al., 2013; Borges et al., 2019; Ghosh-Harihar et al., 2019; Lerm et al., 2023). It is noteworthy, however, that studies in other parts of the world, such as savanna systems like ours, have shown that bird communities are negatively impacted by prolonged, multi-season droughts (Haslem et al., 2015; Selwood et al., 2018). Well-structured projects, such as the extension of SABAP2 (i.e. the African Bird Atlas Project), however, should be able to identify the impacts of extreme weather events and have already proven useful in other parts of Africa, e.g. by modelling changes over 50 years (Nussbaumer et al., 2025). Thus, despite the bird community resilience we showed to be prevalent across Kruger National Park following a single-season drought and evident across other PA networks, we feel PA management in savanna systems should either develop and implement bird community monitoring programmes in-house or promote and continue to support NGO, academic or citizen science initiatives that are still required in many African countries (Wotton et al., 2020), to detect extreme weather event impacts in PAs.

CRediT authorship contribution statement

Rion Lerm: Conceptualisation, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Investigation, Data Curation, Resources. **Lucas P. Medeiros:** Conceptualisation, Investigation, Formal analysis, Writing - Review & Editing. **Dave I. Thompson:** Conceptualisation, Methodology, Writing - Review & Editing, Supervision. **David A. Ehlers Smith:** Conceptualisation, Methodology, Writing - Review & Editing, Supervision. **Colleen T. Downs:** Conceptualisation, Methodology, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03933.

Data availability

None of the data used in this study were produced by the authors. The sources are cited under "Data acquisition".

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