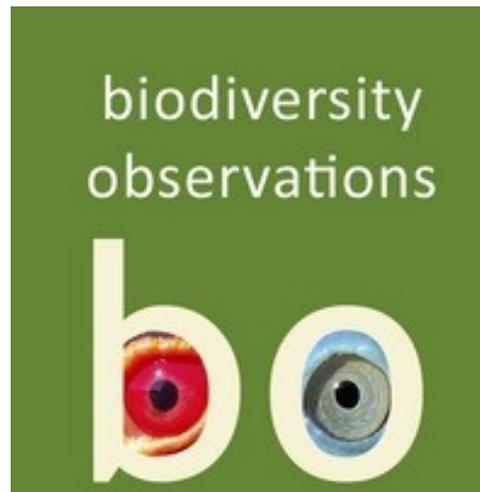


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Ornithology

Birds as indicators for the environmental impact of anthropogenic activities on Onguma, Namibia

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Abstract

Protected areas must be managed to maintain biodiversity. Management strategies can be optimized by assessing the impact of implemented management tools and land uses.

This study assesses the environmental impact of the major anthropogenic forms of disturbance that occur or have occurred on Onguma Nature Reserve, including the presence or absence of game, cattle farming, manual plant removal, chemical plant control, and veld fires. Birds were employed as indicator taxon for the state of the environment. Using generalized linear models, bird species richness, diversity, and abundance were predicted by the variables of interest as well

as soil and vegetation gradients to account for the underlying environmental variability. Additionally, the species composition of the different sub-communities was examined with a NMDS ordination.

Manual plant removal increases, chemical plant removal decreases bird species richness and diversity. Veld fires act diversifying on the avifauna. Removing game significantly lowers the species richness and diversity of birds, indicating that the overall game numbers on Onguma are healthy. The species composition differs among land uses, with grassland specialists less present where cattle farming occurred, suggesting that habitat-selective degradation has taken place.

These results must be contextualized to the study site because the environmental effect of a land use depends on the intensity at which it is implemented, and the consequences of a management tool depend on the need and method of the intervention. Furthermore, the environment dictates the choice of treatment and reacts to the latter, ultimately impacting the bird fauna. Thus, the state of the underlying environment mediates the effect of the treatment on the indicator taxon.

Introduction

Adaptive management: An approach to maintain biodiversity in protected areas

Managing protected areas is necessary to maintain biodiversity (Worboys and Trzyna, 2015). Management plans must be adjusted regularly to meet this goal, by evaluating the impact of present and past management actions through monitoring the environment (Nie and Schulz, 2012). The findings obtained from this process can feed back into new management plans. This process is called adaptive management (Primack, 2014).

Birds as indicators for biodiversity

Birds are widely regarded as a general biodiversity proxy (Gregory et al., 2003). They can be a useful indicator taxon for environmental

health as well as short-term sentinels for changes in the ecosystem such as important modifications in the habitat or the contamination with chemicals or disease. While most birds are either primary or secondary consumers, they will display the effects of environmental stressors sooner and in more isolated ways than organisms higher up in the trophic chain, which are more likely to be affected by a more complex array of drivers (Smits and Fernie, 2013). However, the reaction may not always be intuitive. For instance, global climate change, usually regarded as detrimental to the environment, may have different effects on birds in different climatic contexts, which includes to cause an increase of bird abundance (Augustynczyk et al., 2019).

The general mobility of birds is a limitation and an opportunity that one needs to consider when treating birds as indicator taxon. Small passerines are rarely static and may frequent a whole array of different micro-habitats. Although this behavioral constraint may cause the contrasts between treatments to become blurry, it is important to note that on temporal scales of higher resolutions following a specific treatment, birds may be more accurate indicators than other taxa such as plants, as they can choose their habitat on a more day-to-day basis. Of course, the habitat choice will not be uncoupled from the vegetative recolonization process, depending on the nature of the treatment. Several studies have concluded that the response of birds to different drivers are guild- and niche-specific (Basile et al., 2019; Bled et al., 2019). There is, however, a consensus that specialized species are more vulnerable to change (Hansbauer et al., 2008; Mohd-Taib et al., 2020), while generalists can benefit from different forms of anthropogenic influence and are more likely to be predisposed to become synanthropic in the context of anthropogenic change (Johnston, 2001).

Interactions between the avifauna and anthropogenic interventions in earlier studies

The presence or absence of domestic or wild herbivores can influence the diversity and abundance of birds. The stocking rate at which herbivores occur seems to be key: It has been suggested that most native herbivores are compatible with a healthy bird fauna, as are do-

mestic animals such as cattle when held at low stocking rates (Ogada et al., 2008). The impact of grazing on birds occurs mostly indirectly through the alteration of the vegetation structure and can become negative when the grazing pressure is too high (Bleho et al., 2014). The exclusion of large herbivores such as the African savanna elephant (*Loxodonta africana*) may increase the diversity and abundance of the avifauna, as the canopy area as well as the biomass of ground-dwelling arthropods do not get reduced (Ogada et al., 2008). In all contexts, some species might benefit from the prevailing conditions and can decrease following the change between land uses (Ludwig et al., 2009).

The effect of removing vegetation on birds appears to be guild-specific (Basile et al., 2019). Furthermore, the reaction can be very different, depending on how the vegetation is removed. A certain homogenization of the bird fauna with an overall decline of species richness all resulting in a domination of common, generalist species can be the consequence of herbicide treatment. On the other hand, manual plant removal may increase the overall species richness and may act to increase the diversity of birds (Easton and Martin, 1998).

Fire is a key disturbance and – at the same time – a management tool in many natural and semi-natural grassy ecosystems in the region. Often suppressed in settled or protected areas while implemented at too extensive levels in others, the frequency, intensity, and season, among other factors, seem to be key for a healthy fire regime (Archibald, 2016). The interplay with herbivores is another important component. Different studies came to different conclusions concerning the effect of fire on the bird fauna. Fire does not necessarily support the predictions from the intermediate-disturbance hypothesis, as in some instances the frequency of fires is directly negatively correlated to bird species richness (Lindenmayer et al., 2008). In other studies, fire did not seem to affect overall species richness and even acted to diversify communities from an ornithological perspective (O'Reilly et al., 2006). Also, the bird fauna appears to recover quicker in structurally more complex vegetation after a fire (Lindenmayer et al., 2008).

The variation of the underlying environment influences the avifauna as well. Vegetation structure is often more important than anthropogenic factors when determining the diversity of the bird fauna (Cherkaoui et al., 2009; Hamza and Hanane, 2021; Lacko et al., 2018). The structurally more complex the vegetation, the higher the diversity of the bird fauna (Tworek, 2007). The exact species composition of the vegetation seems to be of secondary importance (MacArthur, 1964), although tree diversity can stabilize habitat usage over time (May-Uc et al., 2020).

Objectives

This study will attempt to quantify how the management tools and land uses that have been implemented over space and time in the study area affect the avifauna. The ultimate objective is to feed conclusions on the environmental impact of past management strategies and land uses back into management plans that will ensure the protection of the area's biodiversity in the future.

As it is expected that the reaction of the avifauna to various management tools and land uses will be guild-specific, both a general abundance model and an approach that discriminates between species will be included.

The pre-implementation choice as well as the resulting effect of a management tool or land use often depend on and influence the underlying state of the environment. It is thus important to eliminate this bias and to isolate the effect of the factors of interest by including environmental variables in the approach. Vegetation structure can be of considerable importance when trying to determine bird species richness and diversity and may influence the probability of detection when collecting bird data.

As the effect of a management tool depends on the way and degree of its implementation, this study will seek to quantify the environmental effect of the various anthropogenic factors. But it will also attempt to contextualize each variable by concluding whether the management tools have achieved an environmentally meaningful effect,

whether it was necessary in the first place to implement a certain management tool and whether stocking rates of land uses involving animals have or have had a negative impact on the environment. To spatially sieve out the effect of individual drivers is hypothesized to become the main challenge .

Methods

Study area

The Etosha pan in northern Namibia is an endorheic salt pan spanning almost half a million hectares. This formation tells the story of a mid to late Tertiary lake that dried up about four million years ago (Miller et al., 2010). Among the drainage systems that initially fed into the lake, the Kunene flows today into the Atlantic Ocean and the Okavango drains into a delta in Botswana. Although only flooded seldomly, the pan is listed as wetland of international importance under the Ramsar convention since 1995 (Ramsar Convention, 2021). Annual precipitation only spans from 250 mm in the west to 450 mm in the east (Le Roux et al., 1988). Nevertheless, the area holds a considerable number of natural springs that concentrate mostly on the southern edge of the pan, enabling the presence of large numbers of game. Etosha National Park has been a protected since 1907 and is today a category II protected area or national park according to the standards of the International Union for the Conservation of Nature (IUCN, 2016).

The Omuramba stream that partially fills up the pan once every few years following important rains, enters the park from the east. Where the Omuramba meets Fisher's pan, the easternmost basin of the Etosha pan, lies Onguma Nature Reserve at 18.6-18.8° S and 17.0-17.2° E. Onguma covers 35 970 hectares, borders Etosha to its west and north, Sachsenheim to its east and Mokuti and Mushara to its south. Before being declared a reserve in the early 2000s, Onguma was a cattle farm during most of its written history, which only started well in the 20th century with its first conventional ownership by a German couple called Böhme (Stark, 2021). Today's Onguma is the combination of four merged farms, all of which used to hold cattle along-

side with game, namely Vergenoeg in the south (6 715 hectares), Ruimte in the south-east (6 620 hectares), Operet in the north-east (2 595 hectares) and the original Onguma in the west (20 040 hectares) (Figure 1). Onguma is fenced, with one additional internal fence around Ruimte. This causes Ruimte to be largely game-free. Particularly Onguma's western fence on the border with Etosha is not proof to the movement of game, including megaherbivores such as the African savanna elephant (*Loxodonta Africana*).

This results in a spatial mosaic in which cattle and game are and have been present or absent. Additionally, two forms of plant control have been implemented in selected locations to halt bush encroachment and to open up the landscape, while fires have repeatedly penetrated the reserve over the past years. The environmental value of the location as well as the short anthropogenic history create a good context, in which studying the environmental impact of management strategies and land uses is both important and feasible.

Bird data collection

The bird data were collected between the 5th of August and the 4th of October 2021, thus before the arrival of the summer migrants. The count itself was split into four phases (Figure 2). Phase 1 targeted the atlassing of the roads on Onguma Nature Reserve open for the field guides (1038 datapoints, 133 transect kilometers). Phase 2 covered some of the roads on the reserve of which the use is restricted to the antipoaching unit and the reserve management (743 datapoints, 93 transect kilometers). Phase 3 served to collect a control dataset in Etosha National Park (266 datapoints, 15 transect kilometers). Additionally, in phase four, a total of 9 transect kilometers were walked on the property to calculate a probability of detection by comparing the obtained datapoint densities with vehicle-based atlassing.

The transects were driven at a speed of approximately 20 km/h, with the atlassing times concentrated in early mornings or late afternoons when the birds are at their most active (Silva et al., 2015). In the event of a visual or audible encounter, the vehicle was stopped, and all detectable birds were identified and recorded using the framework

of the citizen science project SABAP2 (Southern African Bird Atlassing Project 2). The app Birdlasser is the principle mobile data gathering tool of SABAP2 and facilitates the collection of the species, the number of individuals encountered, as well as temporal and spatial coordinates.

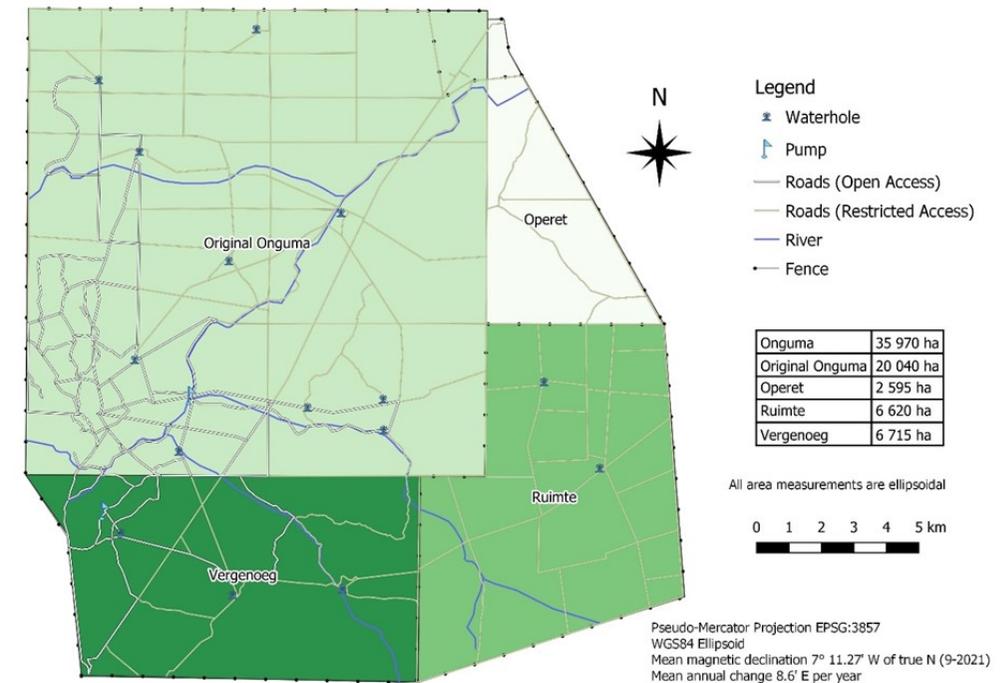


Figure 1: The study area. General map of Onguma Nature Reserve indicating the extent of the original farms. The internal fence about the south-eastern farm is of importance as it excludes big game. Etosha National Park borders the area in the west and in the north. The Etosha pan starts where the southern riverbed reaches the western fence. Drawn with QGIS 3.16 (QGIS Development Team, 2020).

Grid system in QGIS and extraction of indices with R

The dataset was imported to QGIS 3.16 (QGIS Development Team, 2020) (Figure 2). A grid of numbered square cells of 1 km² each was laid over the data, of which the individual cell number was assigned to

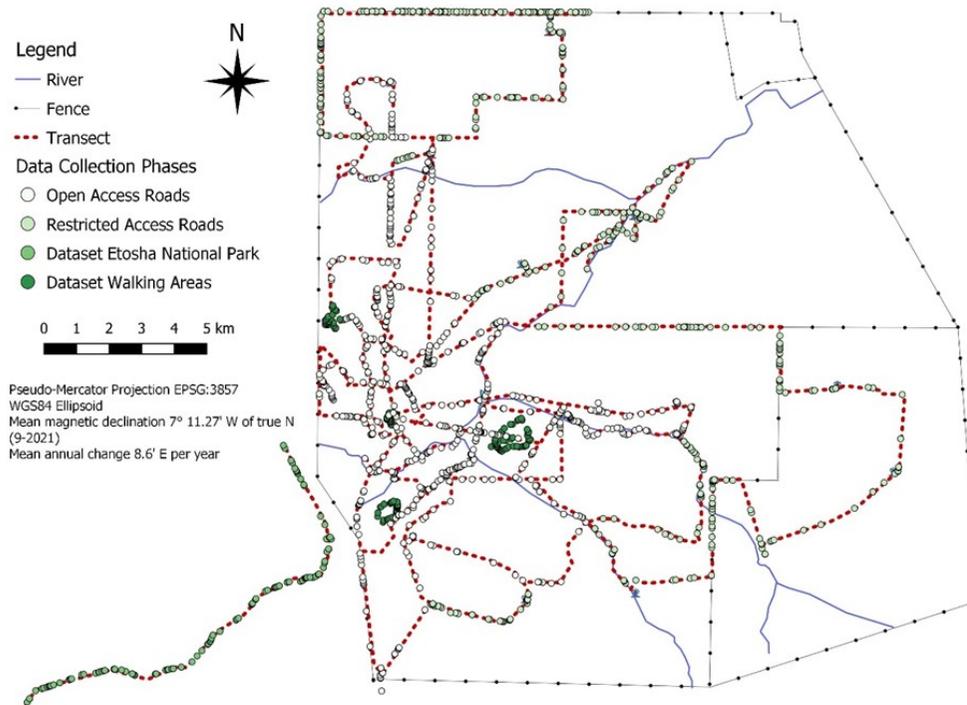


Figure 2: Transects along which birds were recorded. Each of the approximately 2000 datapoint stands for one encounter with one or more birds of the same species. The control dataset was collected in Etosha National Park in the immediate vicinity of Onguma’s western border. Drawn with QGIS 3.16 (QGIS Development Team, 2020).

every datapoint, as well as the total transect length in the cell, thus creating 193 sub-communities. This helped to assign the values of diversity and abundance indicators to every datapoint.

The resulting data frame was loaded into the R statistical package 4.0.1 (R Core Team, 2020). For every datapoint, three indices were calculated, namely:

- The Shannon index of the community encountered within a cell as a measure for species diversity. To exclude the bias of different transect lengths within a cell, this index was only calculated for cells in which the transect length lies within one standard de-

viation from the mean (average) transect length in all cells. The index was calculated using the vegan package (Oksanen et al., 2020) following the formula (with $p(i)$ the proportion of the entire community made up of the species i):

$$H = \sum p(i) * \ln(p(i))$$

- The species richness of the community within the cell in which the datapoint is situated, standardized against the transect length within that cell.
- The number of individuals (total abundance) recorded per transect kilometer within that cell.

These three indices served later as response variables in three different approaches of model construction.

An estimation of the total species richness was generated using the Chao1 indicator (Gotelli and Colwell, 2011) contained in the rareNMtests package (Gotelli, 2014) based on the formula:

$$S_{Chao1} = Observed\ species + \frac{Species\ recorded\ once^2}{2 * Species\ recorded\ twice}$$

Additionally, a probability of detection was calculated by comparing the datapoint density between vehicle-based sampling and atlasing on foot, while standardizing against the structural complexity of the vegetation present translated in the SAR imagery.

Gathering of anthropogenic data

The reserve management provided the spatial information of past management strategies and land uses. The management strategies include:

- The occurrence of veld fires in 2012, 2017 and 2020 at different spatial extents (Figure 3). Although not deliberately started and often the result of farmers burning their fields, veld fires reach Onguma on a regular basis and have covered large portions of the reserve in the past.

- The aerial spraying of herbicide by the means of a plane and later a helicopter in 2007 and 2008 to halt and reverse the process of bush encroachment (Figure 3).
- The manual removal of the encroacher *Dichrostachys cinerea* (sickle bush) over the last years (Figure 3).

Land uses include:

- Cattle farming: This was the main land use of Onguma until the end of the 20th century (Figure 3).
- Absence of game: Ruimte, one of the four farms that fused to result in today's Onguma, is fenced and holds practically no game (Figure 3).

In this instance, the dataset collected in Etosha National Park was considered the null data. The status as category II protected area prescribes the preservation of its larger-scale ecological processes (IUCN, 2016) and therefore limits the possibilities for anthropogenic impacts as mentioned above. However, unwanted fires do occur inside the park. The sample area showed no sign of recent fires. All fires recorded on Onguma over the past ten years entered the reserve from north, east or south and did not reach the western border. Onguma may therefore serve as buffer, potentially protecting the immediate sample area in the park from fire (Figure 3).

Collection of environmental information

The choice of the environmental variables to consider was largely dictated by the scale at which they occur. Climatic and topographic gradients are almost non-existent within the reserve. Due to the evolutionary history of the Etosha pan, the scale of the edaphic turnover on Onguma is of interest. The vegetation structure influences the bird fauna extensively (Tworek, 2007), interacts with the soil and, in the case of plant removal or grazing for example, reflects the effect of the management strategies and land uses themselves. To describe the study area from these perspectives, an additional three layers were added to the model:

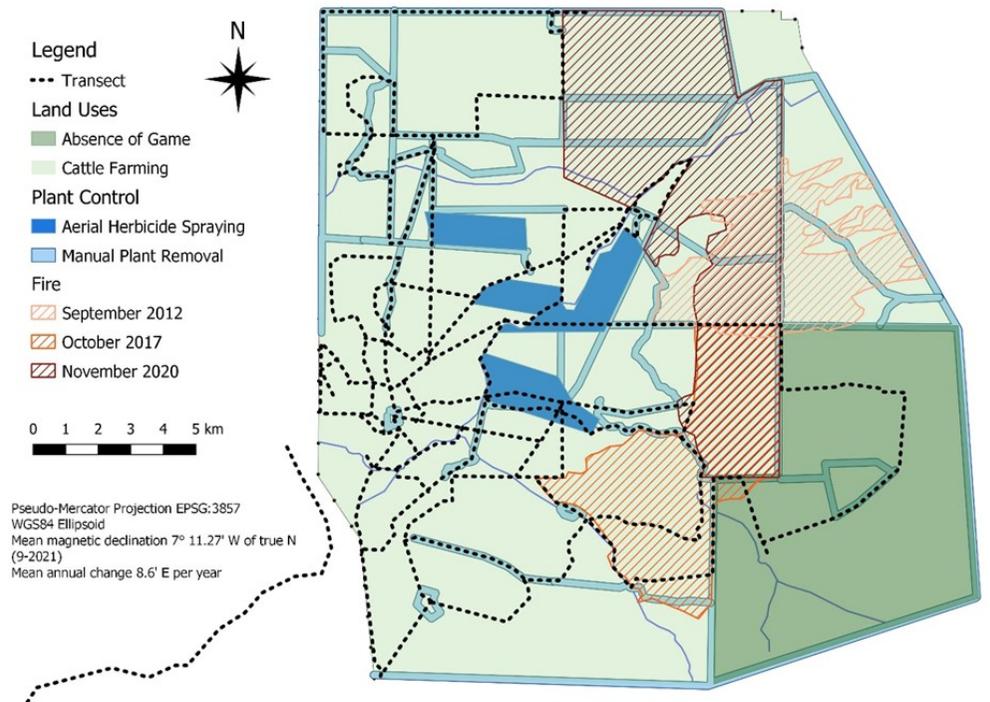


Figure 3: Spatial configuration of the anthropogenic variables. The shades of green stand for the presence or absence of game and cattle over time. The shades of blue show where plant removal occurred. The shades of red outline the spatial extent of veld fires since 2010. The hashed lines are the transects from which birds have been at-lasped. Drawn with QGIS 3.16 (QGIS Development Team, 2020).

- A soil map was produced, based on the integration of an existing soil map for Etosha National Park (Beugler-Bell and Buch, 1997), the FAO Soil Map of the World (FAO, 1961) as well as field observations (Figure 4).
- Synthetic aperture RADAR imagery (SAR) collected by Copernicus's Sentinel-1 satellite constellation of the area of interest on the 2nd of October 2020 were obtained from the Copernicus Open Access Hub (Copernicus Sentinel-1 data 2020, processed by ESA). The imagery was processed and classified into different vegetation types using QGIS 3.16 (QGIS Development

Team, 2020) while using supervised classification by inferring a rule from a set of training observations. This process was based on literature (De Cáceres and Wiser, 2012; Frison and Lardeux, 2017). Existing vegetation classifications were considered (Le Roux et al., 1988; Mayaux et al., 2004). The resulting map was ground truthed extensively to ensure accurate classification.

- The normalized difference vegetation index (NDVI) was generated by processing Sentinel-2 RGB-imagery from the 28th of October 2021 obtained from the Copernicus Open Access Hub (Copernicus Sentinel-2 data 2021, processed by ESA) in QGIS 3.16 (QGIS Development Team, 2020) according to the formula:

$$\frac{\text{Near Infrared Band} - \text{Red Band}}{\text{Near Infrared Band} + \text{Red Band}}$$

- As done in several publications, the NDVI which stands essentially for photosynthetic activity, can be seen as a proxy for vegetation health (e.g. Van Blerk et al., 2021) (Figure 4).

Using both the photosynthetic activity as well as the structural complexity of the vegetation obtained from the SAR-imagery may lead to a more accurate description of the vegetation, as structurally more complex vegetation may not necessarily be photosynthetically more active during the dry winter. In fact, the Pearson correlation coefficient between the NDVI and the VH/VV ratio (vertical transmit – horizontal receive polarization / vertical transmit – vertical receive polarization) equals 0.42 and is thus low enough to avoid variance inflation (Dormann, 2013).

Merging the bird data with the environmental and anthropogenic variables using QGIS

The extraction tools for both raster and vector values in QGIS 3.16 (QGIS Development Team, 2020) were used to assign each data-point of the bird survey the values of every anthropogenic and environmental variable. To prevent any loss of information, the individual raster values of the SAR layer were used, instead of relying on the

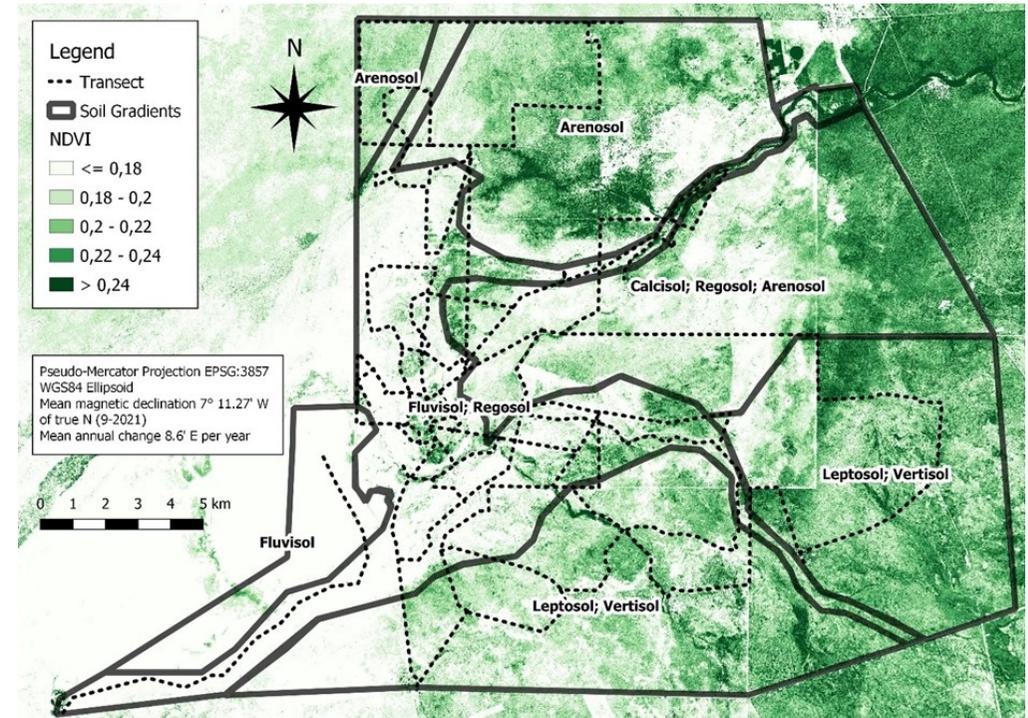


Figure 4: Soil map and NDVI of the study area. The soil layer is based on earlier publications (Beugler-Bell and Buch, 1997; FAO, 1961), the NDVI was calculated from Sentinel-2 imagery (Copernicus Sentinel-2 data 2021, processed by ESA). Together with a measure for the structural complexity of the vegetation obtained from Sentinel-1 imagery (Copernicus Sentinel-1 data 2020, processed by ESA), these two layers account for the variation of the underlying environment in the modelling process. Drawn with QGIS 3.16 (QGIS Development Team, 2020).

classification previously done, as this only served a ground-truthing purpose to guarantee the accuracy of the link between SAR-imagery and vegetation structural complexity. The resulting data frame was opened in the R statistical package 4.0.1 (R Core Team, 2020) and formatted using the dplyr (Wickham et al., 2021) and tidyverse (Wickham and RStudio, 2021) packages.

In all analyses conducted, it was set that the alternative hypothesis was considered proven if the probability that the observed results were in line with the null hypothesis equaled less than 0.05. All plots were produced using ggplot2 (Wickham et al., 2021), ggpubr (Kassambara et al., 2020), patchwork (Pedersen, 2020) and ggrepel (Slowikowski et al., 2021).

Fitting generalized linear models in R

GLMs (generalized linear models) are the tool of choice to model an output variable based on different predictors (e.g. Bled et al., 2019; Hamza and Hanane, 2021; Lacko et al., 2018). GLMs were fitted in three approaches using the calculated indices that qualify the avifauna as response variables (Shannon index, species richness and abundance).

To satisfactorily center the residuals, the response variables were to be log₁₀- (species richness and abundance) or square-root-transformed (Shannon index).

Although the inclusion of mathematical interactions among the predictors was tested, this did not substantially reduce the AIC (Akaike's Information Criterion) and was therefore considered as unnecessary.

To quantify the contrast of the different treatments with the control dataset, a type III ANOVA (Analysis of variance) using the car package (Fox et al., 2021) was computed after which an emmean post-hoc test was ran over each model (Length et al., 2021).

Species-specific NMDS in R

Based on earlier publications (e.g. Lacko et al., 2018; Mohd-Taib et al., 2020), a non-metric multidimensional scaling (NMDS) ordination using the vegan package (Oksanen et al., 2020) was employed to examine the species assemblages of the sub-communities present in the context of each treatment.

For that purpose, every species was paired with the percentage of records within each treatment, divided by the percentage of the transect length which lies within the treatment. This value, centered around 1, indicated whether a species occurred more within one specific treatment than one would expect from the transect length within an area in which this specific treatment has been applied. Every species was assigned the treatment under which this value was maximized, meaning the treatment under which the species occurs more often than one would expect given the ratio of the transect length within that treatment to the total treatment length. Additionally, the average values of the NDVI and the VH/VV band of the SAR imagery were assigned to each species and standardized against the overall averages at the scale of the dataset. Values equaling zero were replaced by 0.001.

The ordination was computed on two dimensions. A permutational multivariate ANOVA was employed on the resulting pairs of ordination distances. A Tukey HSD (Honestly Significant Difference) post-hoc test was ran on the result to test which of the sub-communities differed significantly.

The NMDS itself was conducted using the anthropogenic treatments only. The NDVI and SAR values were later fitted to the ordination plot.

Results

Impact of the treatments on bird species richness, diversity, and abundance

Figure 5 provides an overview of the findings. The species richness, diversity and abundance of the avifauna encountered is not distributed uniformly across and within treatments. In all three instances, the mean values corresponding to the different treatments aggregate around the control dataset. The removal of game and the spraying of herbicide appear to lower the indices, whereas manual plant control, fire and cattle farming seem to improve the presence and diversity of birds. These hypotheses are tested in three distinct modelling ap-

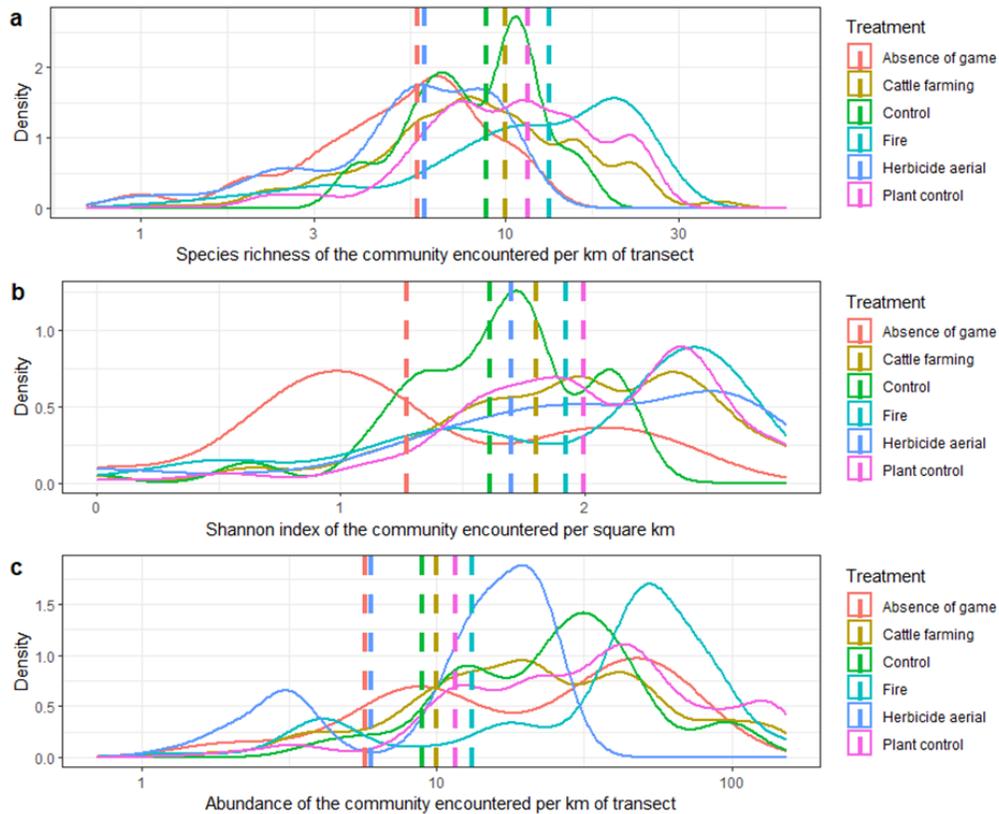


Figure 5: Visualization of the indices. The hashed lines indicate the mean values for each treatment. Graph a plots how many species were encountered per km of transect depending on the treatment. Graph b depicts the Shannon index of the community encountered within one km². Graph c shows the overall bird abundance recorded per km of transect depending on the treatment).

proaches, of which the results are shown in Table 1. The effect of plant control on bird species richness, diversity and abundance seems to depend on the method of implementation. The two management tools included in the models induce a very strong differentiation of the indices: Spraying herbicide from a fixed-wing aircraft affects the environment in a way that birds are less diverse and abundant in the area over ten years after the management intervention. On the other

hand, the more selective, manual removal of encroacher species such as *Dichrostachys cinerea* (Sickle bush) acts diversifying and increases the species richness of birds significantly (Table 1).

Areas that have burnt during the past ten years displayed more species and a more diverse avifauna (Table 1).

The presence of game or a history of cattle farming do not seem to go at the expense of bird species richness, diversity and abundance (Table 1). The overlapping of the areas in which cattle farming and the management tools were implemented makes it however difficult to judge, whether the effect of cattle farming was sufficiently isolated.

The removal of game severely lowers the avifaunal diversity and presence. However, the general abundance of birds is not affected detrimentally (Table 1). Nevertheless, the bird fauna is then likely to be dominated by a few, common species.

Differing species composition of the sub-communities

With a stress value of 0.097, the NMDS provided satisfactory results on a two-dimensional scale. Figure 6 provides an idea of the relative constellation of the sub-communities and the degree of their overlap, depending on the treatments present in any given area.

The two continuous environmental variables were fitted to the ordination plot and are displayed as arrows (Figure 6). They indicate the axis on which the difference between the sub-communities is affected by the state of the environmental variables under which they occur. The spacing between the communities on the plot orthogonally to this axis is thus more important when trying to sieve out the effect of the environmental turnover to isolate the impact of each treatment. However, the prior-implementation choice of the treatment depends on the underlying state of the environment which in turn will be affected by the intervention.

Table 1: Output from the GLMs, ANOVAs and post-hoc tests. The table is divided in the three modelling approaches. The six predictors of interest are listed at the end of each section. The two last columns contain the results from the emmeans post-hoc tests where the contrasts between the control variable and each treatment are computed based on the output of the type III ANOVA. **Bold red** values indicate that the treatment significantly reduces the output of the response variable. **Bold green** values indicate that the treatment significantly increases the response variable.

| Model Structure | Model Type | Estimate | Std Error | p-value From Type III ANOVA | Isolated Absolute Estimate | Emmeans Post-hoc Contrast | Emmeans Post-hoc p-value |
|--|--------------------|----------|-----------|-----------------------------|----------------------------|---------------------------|--------------------------|
| 0. Response variable | | | | | | | |
| Explanatory variable 1 | Distribution | | | | | | |
| Explanatory variable 2 | Transformation AIC | | | | | | |
| 1. Species richness / km | | | | | | | |
| NDVI | GLM | 0.93 | 0.09 | <0.001 | 8.51 | | |
| VH/VV (SAR) | Gaussian | -0.48 | 0.19 | 0.01 | 2.82 | | |
| Soil type | Log base 10 | -0.03 | 0.01 | <0.01 | 7.94 | | |
| - Calcisol/Arenosol | 228.89 | | | | | | |
| - Fluvisol | | -0.05 | 0.03 | 0.04 | 7.59 | | |
| - Fluvisol/Regosol | | -0.16 | 0.08 | 0.03 | 5.89 | | |
| - Leptosol/Vertisol | | -0.02 | 0.02 | 0.3 | 8.13 | | |
| | | -0.08 | 0.02 | <0.01 | 7.08 | | |
| Control | | 0.09 | 0.09 | 0.27 | 10.47 | Compairs | Compairs |
| Absence of game | | -0.13 | 0.04 | <0.01 | 6.31 | -0.26 | <0.001 |
| Cattle farming | | 0.05 | 0.08 | 0.51 | 9.55 | 0.15 | 0.56 |
| Fire | | 0.14 | 0.02 | <0.001 | 11.75 | 0.38 | <0.001 |
| Herbicide aerial | | -0.18 | 0.03 | <0.001 | 5.62 | -0.35 | <0.001 |
| Plant control | | 0.16 | 0.01 | <0.001 | 12.3 | 0.41 | <0.001 |
| 2. Shannon index / km² | | | | | | | |
| NDVI | GLM | 1.31 | 0.09 | <0.001 | 1.72 | | |
| VH/VV (SAR) | Gaussian | -0.26 | 0.18 | 0.15 | 1.1 | | |
| Soil type | Square root | -0.04 | 0.01 | <0.001 | 1.61 | | |
| - Calcisol/Arenosol | -564.2 | | | | | | |
| - Fluvisol | | -0.04 | 0.02 | 0.12 | 1.61 | | |
| - Fluvisol/Regosol | | -0.12 | 0.07 | 0.06 | 1.42 | | |
| - Leptosol/Vertisol | | -0.01 | 0.01 | 0.7 | 1.69 | | |
| | | 0.05 | 0.02 | 0.01 | 1.85 | | |
| Control | | 0.02 | 0.09 | 0.86 | 1.77 | Compairs | Compairs |
| Absence of game | | -0.22 | 0.04 | <0.001 | 1.19 | -0.27 | <0.001 |
| Cattle farming | | 0.11 | 0.09 | 0.25 | 2.02 | 0.48 | 0.1 |
| Fire | | 0.03 | 0.02 | <0.001 | 1.8 | 0.37 | <0.001 |
| Herbicide aerial | | -0.25 | 0.05 | <0.001 | 1.12 | -0.32 | <0.001 |
| Plant control | | 0.1 | 0.1 | <0.001 | 1.99 | 0.45 | <0.001 |
| 3. Bird abundance / km | | | | | | | |
| NDVI | GLM | 1.21 | 0.13 | <0.001 | 16.22 | | |
| VH/VV (SAR) | Gaussian | -0.19 | 0.29 | 0.52 | 10.47 | | |
| Soil type | Log base 10 | -0.07 | 0.02 | <0.001 | 13.8 | | |
| - Calcisol/Arenosol | 1667.78 | | | | | | |
| - Fluvisol | | -0.06 | 0.04 | 0.12 | 14.13 | | |
| - Fluvisol/Regosol | | 0.11 | 0.11 | 0.34 | 20.89 | | |
| - Leptosol/Vertisol | | 0.01 | 0.03 | 0.6 | 16.6 | | |
| | | -0.17 | 0.04 | <0.001 | 10.96 | | |
| Control | | 0.21 | 0.13 | 0.1 | 26.3 | Compairs | Compairs |
| Absence of game | | 0.15 | 0.06 | 0.02 | 22.91 | -0.21 | 0.35 |
| Cattle farming | | 0.12 | 0.12 | 0.31 | 21.38 | -0.29 | 0.63 |
| Fire | | 0.24 | 0.03 | <0.001 | 28.18 | 0.22 | 0.39 |
| Herbicide aerial | | -0.27 | 0.05 | <0.001 | 8.71 | -1.63 | <0.001 |
| Plant control | | 0.28 | 0.02 | <0.001 | 30.9 | 0.4 | 0.13 |

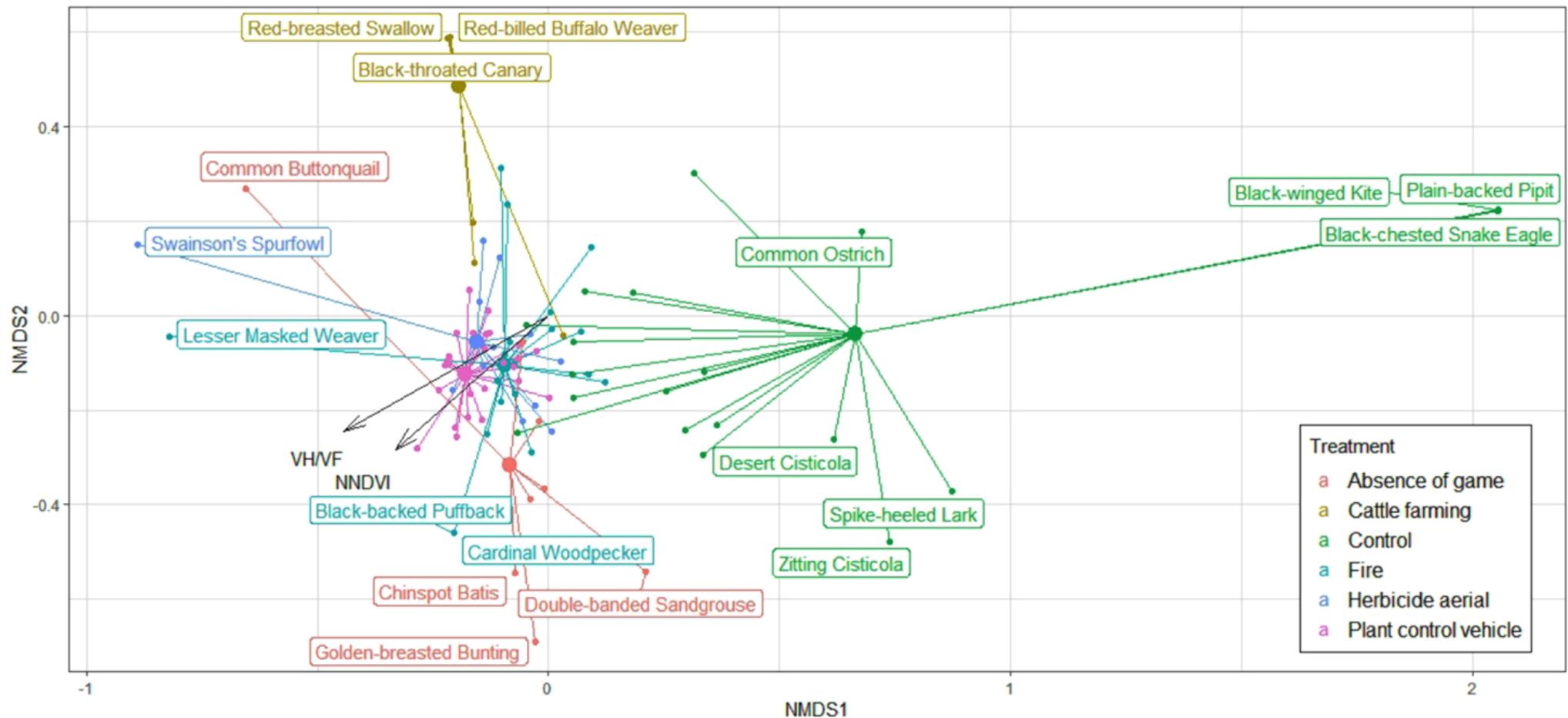


Figure 6: NMDS ordination plot. Each point stands for one species. The position of each species on the ordination scale indicates under which treatment and in which combination the species are likely to occur. Every species is color-coded according to the treatment under which the species occurs the most unexpectedly by controlling for the transect length covered within each treatment. The isolated points on the edge of the plot can be considered as indicator species for the relative treatment.

The two continuous environmental variables were fitted to the ordination plot and are displayed as arrows. They indicate the axis on which the difference between the sub-communities is affected by the state of the environmental variables under which they occur.

A permutational multivariate ANOVA (analysis of variance) confirmed that the differences of species composition between the treatments were significant (Table 2). The results of a Tukey HSD post-hoc test suggest that the predominant land use influences the species composition of the individual sub-community stronger than does the implementation of a management tool (Table 2). In fact, all three land uses contrasted significantly with at least one other land use, whereas only areas that burnt or where herbicide was applied contrasted with any of the land uses. The sub-communities encountered in the context of the different management tools did not contrast significantly among each other.

Discussion

The major findings align well with existing literature: Herbicide treatment has a negative effect while manual plant removal increases bird species richness and diversity (Easton and Martin, 1998). Fire can act diversifying (Lindenmayer et al., 2008). The overall game numbers of Onguma seem healthy as the removal of the latter did cause a decline in the avifauna. In fact, the effect of herbivores is compatible with a healthy bird fauna when held at low enough stocking rates (Ogada et al., 2008).

Contextualizing the findings

Surprisingly, the species richness, diversity and abundance of the avifauna were all negatively correlated with the structural complexity of the vegetation (Table 1). As this variable was only included to control for the variation of the underlying environment, this question does not have to be addressed. However it is very likely that this may be linked to a lower probability of detection in denser vegetation as most publications state that structurally more complex vegetation acts diversifying and enables more species to co-exist (e.g. Lindenmayer, 2008).

Although many passerines move around in parties (Kajiki et al., 2018), using a vehicle for bird atlassing is likely to lower the overall probability of detection. By comparing the main dataset to the data

Table 2: Results from the ANOVA and the Tukey HSD post-hoc test.

The permutational ANOVA was computed from the ordination assigned to the species, and thus their position on the ordination scale relative to the different treatments. The ANOVA concluded that the treatments are associated with significantly different species assemblages. A Tukey HSD post-hoc test clarified which treatments contrasted significantly with each other.

| Permutational multivariate ANOVA Number of permutations: 999 | Sum squares | Mean squares | F-value | P-value |
|---|-------------|---------------------------|---------------------------|------------------|
| Treatments | 1.56 | 0.39 | 17.38 | 0.001 |
| Residuals | 2.74 | 0.02 | | |
| Tukey HSD post-hoc test | Difference | Lower confidence interval | Upper confidence interval | P-value |
| Land uses | | | | |
| Cattle farming – Absence of game | -0.16 | -0.32 | -0.01 | 0.03 |
| Control – Absence of game | 0.12 | -0.05 | 0.28 | 0.29 |
| Control – Cattle farming | 0.28 | 0.19 | 0.38 | <0.001 |
| Land use – Management tool | | | | |
| Absence of game – Fire | -0.04 | -0.21 | 0.13 | 0.97 |
| Absence of game – Herbicide aerial | -0.01 | -0.2 | 0.18 | 1 |
| Cattle farming – Fire | 0.13 | 0.03 | 0.23 | 0.01 |
| Cattle farming – Herbicide aerial | 0.15 | 0.02 | 0.29 | 0.01 |
| | - | - | | |
| Control – Fire | 0.16 | 0.27 | -0.04 | <0.01 |
| Control – Herbicide aerial | -0.13 | -0.27 | 0.01 | 0.1 |

collected on foot, it was possible to estimate that vehicle-based atlassing only detects 59% of all datapoints than would be gathered on foot. This can be explained by the reduced audible detectability due to the soundscape produced by the vehicle's engine, as well as the slightly faster speed at which the sampling takes place along the transect. As the main dataset was collected from a vehicle, the transects were restricted to the roads, potentially favoring the encounter of species that can endure habitat fragmentation.

Although the bird survey was extensive, it is unlikely that all species were recorded. Using the Chao1 index, a non-parametric species

richness estimator based on abundance data (Gotelli and Colwell, 2011), the total species richness of the bird community on Onguma during winter can be estimated at 142 species, with a 95% probability that the actual number is between 132 and 173. This proved to be fairly accurate: During the atlassing, 129 species were encountered, while a total of 138 species were recorded on the reserve during the months in which sampling took place.

Choice of the variables

The avifauna on Onguma is influenced by a wide array of factors that operate at different scales in space and time. Additional unconsidered drivers would have possibly improved the modeling approach. For instance, research has shown that there is a positive impact of *Macrotermes* termites – of which Onguma holds numerous colonies – on bird abundance and diversity in African savannas (Moe et al., 2017).

The aim of the present experiment was to isolate the effect of the main anthropogenic activities that have taken place on Onguma nature reserve during its written history. Literature lacks a consensus about which anthropogenic disturbances can be detrimental to birds. A global meta-analysis found that it is mostly habitat isolation, logging and urbanization that exhibit a consistent negative effect on the functional diversity of birds, while habitat loss and agriculture had no effect in most cases (Matuoka et al., 2021). Although it is likely that the grasp on the human influence on Onguma over the past decades has been well described with the variables included, birds may be influenced by variables operating beyond Onguma's borders, including some of the examples mentioned above. Additionally, the temporal difference between the implementation of a certain treatment and the sampling may, in some cases, blur the effect of the actual treatment on birds. In the case of the veld fires, it may have been useful to differ between different post-fire ages. Nevertheless, all treatments influenced at least one of the indices for bird diversity and abundance significantly.

Understanding the mechanisms behind differing sub-communities

As discussed above, the overall shape of the ordination plot is characterized by more than just the treatment in question. This paragraph will examine the different drivers that can affect the segregation of the spectrum of species into different sub-communities, by focusing on the difference between the community encountered in Etosha compared to the bird fauna of Onguma as an example. While the species typically encountered in the context of the treatments linked to Onguma appear to aggregate on the scale, the species that are indicators for the control dataset collected in Etosha National Park differ significantly, with several species exclusively recorded in the park such as the plain-backed pipit (*Anthus leucophrys*) and the black-chested snake eagle (*Circaetus pectoralis*).

Environmental gradients

Environmental gradients can bias the results of a differentiation based on land uses and treatments. For example, the comparatively large ordination distances of the species in Figure 6 that are characteristic for the control dataset and that seemingly don't or only rarely occur under other treatments, are linked to the variation of the environment. In fact, the study area in which the control dataset was collected is situated between Onguma and the Etosha pan and is characterized by a less complex vegetation structure.

In all contexts, some species might benefit from the prevailing conditions (Ludwig et al., 2009). Local environmental turnover and species-specific habitat occupancy is synonymous with beta diversity and suggests that conservation and management strategies should be implemented at a regional spatial scale and focus on the conservation of this mosaic. (Signor and Pinho, 2011).

Rating species composition

Although the community encountered in the park does not necessarily appear to hold more species or to be more diverse than the bird fau-

na of Onguma, it is possible that the protected area status has, over time, encouraged the presence of rare species. Additionally, Onguma directly serves as spatial buffer for the park and may cushion some of the anthropogenic drivers that act beyond its borders. This aligns well with existing literature, according to which protected areas don't necessarily hold more abundant and diverse bird communities, but usually more specialists. Thus unprotected areas can significantly contribute to conservation efforts (Asefa et al., 2017).

Predominating effects of certain treatments

As cattle farming occurred everywhere within today's Onguma and thus includes all other treatments spatially, it remains difficult to segregate the effect of the latter from other treatments. This will be further discussed below. Additionally, it is not the actual presence of cattle but its stocking rate that will cause the effect (Ogada et al., 2008). Different vegetation communities are differently suited and vulnerable to grazing and will thus react in a variety of ways. Many of the species recorded in Etosha are singletons, species recorded only once throughout the dataset. This is particularly true for grassland birds such as *Cisticola juncidis* (Zitting cisticola) or *Chersomanes albofasciata* (Spike-heeled lark) (Figure 6), suggesting that the cattle stocking rates on Onguma were indeed too high and that habitat-specific degradation has taken place.

Spatial inter-dependence of the variables

The difficulty of spatially separating the treatments is outlined in Figure 6. The species composition of the sub-communities present in the context of the management tools that were implemented where cattle farming occurred overlap considerably with each other (Figure 6). This is further confirmed in the results from the Tukey HSD post-hoc test (Table 2), according to which the sub-communities associated with the land uses contrast stronger than the sub-communities that characterize the management tools.

This contrasts with the finding that manual plant control acts diversifying, while aerial herbicide spraying reduces bird abundance and di-

versity considerably. Additionally, findings from other studies could not be confirmed, according to which the effect of different degrees of plant removal from the environment on birds appears to be guild-specific (Basile et al., 2019).

The problem for the lack of control for the treatment "cattle farming" is further illustrated by the position of the common buttonquail (*Turnix sylvaticus*) on the ordination scale (Figure 6), according to which the species could be considered as indicator for cattle farming. However, it is assigned the red color of the community where there is no game, a treatment that is spatially restricted to a larger area in which there was cattle farming. In the area that holds game and where cattle farming was also a past land use, buttonquails were recorded twice. This is the reason that, despite the relatively high encounter rate of buttonquails in the game-free area, the species has been placed closer to the community assigned to cattle farming on the ordination scale.

The state of the environment mediates the relationship between treatments and birds

The approach of trying to filter out the environmental variables to obtain the isolated effect of each treatment can be considered as deterministic approach, as it does not seek to understand what the exact effect of the treatment is on the environment, which in turn will influence the birds. For instance, the exclusion of megaherbivores keeps the canopy intact and does not reduce the biomass of ground-dwelling arthropods (Ogada et al., 2008). This directly provides shelter and food for the birds. The approach of this study is simplified by directly examining the effect of a specific treatment on the avifauna and not how the environment is altered by the treatment.

The attempt of building a mechanistic model would complicate the process considerably, as it is very difficult to separate environment and treatment. The pre-implementation choice of a treatment depends on the state of the environment, while the outcome influences the environment. Birds are solemnly indicators of the state in which the treatment transforms the environment, for instance of the structural complexity of the vegetation which results from the treatment. In

fact, the impact of grazing on birds – as an example – occurs mostly indirect through the alteration of the vegetation structure and can become negative when the grazing pressure is too high (Bleho et al., 2014).

It is thus possible to rate whether a management tool has reached its purpose (given that the purpose of a management tool is to increase biodiversity) and whether a land use has been implemented in the right way.

Conclusion

Management recommendations

Given that maintaining biodiversity is the central aim of Onguma's management strategies, the following implications may be considered.

Plant removal

Spraying herbicide from an aircraft severely affects the environment negatively and is thus not recommendable as management strategy for the future.

The removal of encroacher species such as *Dichrostachys cinerea* (Sickle bush) is to be encouraged, as the positive, diversifying effect on the indicator taxon is highly significant.

Land uses

It is reasonable to think that cattle stocking rates were locally too high on Onguma. Especially the grassland areas of the reserve appear to have not yet recovered from this land use. Restoring existing grassland habitat on Onguma can thus benefit biodiversity.

The overall game numbers appear to be healthy on Onguma. The environment is in better condition in areas where game is present. This does not take into consideration the recent flux of the African savanna elephant (*Loxodonta africana*) from Etosha to Onguma. Nevertheless it seems advisable to remove the fence separating game-free Ruimte from the rest of Onguma.

Fire

The occurrence of fire in the context of the current regime has had a positive impact on the indicator taxon. At the current frequency, fire should be encouraged and regarded as management tool.

Further research

Surveying the vegetation can provide further insight as it reduces the relative distance between the taxon of interest and the treatment generated by the mediating environment.

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Biodiversity and Development Institute*

Biodiversity Observations

The scope of Biodiversity Observations includes papers describing observations about biodiversity in general, including animals, plants, algae and fungi. This includes observations of behaviour, breeding and flowering patterns, distributions and range extensions, foraging, food, movement, measurements, habitat and colouration/plumage variations. Biotic interactions such as pollination, fruit dispersal, herbivory and predation fall within the scope, as well as the use of indigenous and exotic species by humans. Observations of naturalised plants and animals will also be considered. Biodiversity Observations will also publish a variety of other interesting or relevant biodiversity material: reports of projects and conferences, annotated checklists for a site or region, specialist bibliographies, book reviews and any other appropriate material. Further details and guidelines to authors are on the journal website (<https://journals.uct.ac.za/index.php/BO/>).

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