Increases in subsistence farming due to land reform have negligible impact on bird communities in Zimbabwe

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Abstract
Habitat alterations resulting from land-use change are major drivers of global biodiversity losses. In Africa, these threats are especially severe. For instance, demand to convert land into agricultural uses is leading to increasing areas of drylands in southern and central Africa being transformed for agriculture. In Zimbabwe, a land reform programme provided an opportunity to study the biodiversity response to abrupt habitat modification in part of a 91,000 ha dryland area of semi-natural savannah used since 1930 for low-level cattle ranching. Small-scale subsistence farms were created during 2001–2002 in 65,000 ha of this area, with ranching continuing in the remaining unchanged area. We measured the compositions of bird communities in farmed and ranched land over 8 years, commencing one decade after subsistence farms were established. Over the study period, repeated counts were made along the same 45 transects to assess species’ population changes that may have resulted from trait-filtering responses to habitat disturbance. In 2012, avian species’ richness was substantially higher (+8.8%) in the farmland bird community than in the unmodified ranched area. Temporal trends over the study period showed increased species’ richness in the ranched area (+12.3%) and farmland (+6.8%). There were increased abundances in birds of most sizes, and in all feeding guilds. New species did not add new functional traits, and no species with distinctive traits were lost in either area. As a result, species’ diversity reduced, and functional redundancy increased by 6.8% in ranched land. By 2020, two decades after part of the ranched savannah was converted into farmland, the compositions of the two bird communities had both changed and became more similar. The broadly benign impact on birds of land conversion into subsistence farms is attributed to the relatively low level of agricultural activity in the farmland and the large regional pool of nonspecialist bird species.

Key words
biodiversity conservation, DPCoA, functional redundancy, functional traits, land-use change, species’ richness

Taxonomy classification
Biodiversity ecology; Conservation ecology; Ecosystem ecology
INTRODUCTION

Habitat modification and land-use change, primarily due to rising human populations and demand for food, are major contributors to biodiversity loss (De Camargo & Currie, 2015; Murphy & Romanuk, 2014). Around a third of all terrestrial land is now used for food production (Diaz et al., 2020) and species’ losses have increased dramatically in recent decades. African ecosystems are particularly exposed to threats posed by land-use change, as the continent is home to a human population that is growing at an estimated annual rate of 2.7% (UN, 2019). The combined pressures of population growth, increased food demand, and land tenure reform are expected to lead to widespread human-driven habitat modification. Small-scale subsistence farming is expected to increase following conversion of marginal drylands, an extensive biome covering nearly 3 million km² in central and southern Africa (Shorrocks, 2007). Drylands, characterised by low and erratic rainfall, are especially vulnerable to biodiversity loss, but the impact of land change on biodiversity in this biome has received little attention (Garcia-Vega & Newbold, 2020).

Intensified land-use and habitat degradation often results in more-specialised species being replaced by generalists, leading to functional homogenisation in changed communities with fewer distinct functional traits (Clavel et al., 2011), and altered ecosystem functioning (Diaz et al., 2007). But this view that land-use intensification inevitably gives rise to species’ loss, leading to a loss of functional traits’ diversity and ecosystem function, is not unchallenged. Mayfield et al. (2010) have argued that research does not support a cascade loss for all natural systems, and that community responses depend upon the intensity and spatial extent of disturbance, species’ traits and pool size, the level of functional redundancy, and environmental filtering effects. There is also evidence that the impact on biodiversity of abrupt land change may not be permanent. Across 5,563 global sites of varying sizes and levels of disturbance (PREDICTS database; Hudson et al., 2017), local species’ richness and abundance in eight taxonomic groups were reduced within 5 years of abrupt land change, but local biodiversity recovered to levels comparable with unchanged sites within a decade (Jung et al., 2019).

The Zimbabwe Fast-Track Land Reform Programme (FTLRP), introduced in 2000 to address historical patterns of inequitable land distribution, resulted in large parts of the country being transformed for subsistence farming. Between 2000 and 2007, over 8 million hectares were converted into farmland by new resettled farmers, many of whom lacked experience, resources, support, and access to training (DeGeorges & Reilly, 2007; Moyo & Matondi, 2008). In one area of Matabeleland, 650 km² of dryland savannah were transformed into farmland during 2001-2002. This savannah landscape of poor soils, used for low-level ranching but otherwise largely unmodified and uninhabited for at least eight decades before 2001, was representative of the ‘natural’ habitat of Matabeleland. The transition into farmland provided an opportunity to study the impact of abrupt land-use change on biodiversity by assessing the trajectory followed by the avian community in the impacted area.

We commenced our study in 2012, counting birds along transects in land modified for farming and also in adjacent unmodified ranched savannah. We used our comparative data for the farmed and ranched area bird communities in 2012 to assess the divergent trend followed by farmland birds over the decade following habitat modification. Then, by using 2012 data as a baseline, our repeated counts of identical transects until 2020 enabled us to measure the extent to which different species and functional groups were affected by habitat change. We hypothesised that: (a) avian taxonomic composition and functional diversity of the farmed and ranched area communities would increasingly diverge, with species’ richness and functional redundancy increasing in farmland as new species with similar traits moved in; and (b) species’ richness and diversity in the ranched area would remain broadly stable, with this area increasingly becoming a refuge for larger birds and those with specialist traits.

METHODS

2.1 Study area and survey methods

The study area in south-central Zimbabwe is a 91,000-ha mosaic of dryland savannah comprising open grassland interspersed with wooded areas of acacia (e.g., *Acacia* spp., *Terminalia* spp.) and miombo (e.g., *Brachystegia* spp., *Julbernardia* spp.) trees varying in height from 3–10 m (Figure 1). This area (centred on 29°34′E, 20°04′S), located on poor Kalahari sands, has long been regarded as unsuitable for commercial agricultural crops, and the entire site was formerly used for low-level cattle ranching. Apart from this activity, these extensive lands were relatively undisturbed as an informally protected area within the private De Beers Shangani Estate (Debshan) since 1930. The FTLRP legislation resulted in a 65,000-ha demarcated section of Debshan being allocated for resettlement farms. During 2001–2002 approximately 3,000 families were moved to 5-ha plots (in total 15,000-ha) distributed across the resettlement area, where they built homesteads, grazed livestock, and established small fields for crops during the summer rainy season. We estimate that, at this time, about 45% (29,000-ha) of the total land demarcated for resettlement was nominally suitable for subsistence crop cultivation, with the remaining area comprising rocky and hilly outcrops, woodland, and small dams. The main crop grown is maize, with smaller quantities of sorghum, finger millet, various pulses (cows peas, ground nuts, round nuts, beans), pumpkins, water melons and cotton. During 2002–2015, a steady influx of new settlers more than doubled the human population in the farmed area (our estimate; there are no official census data). This resulted in all potentially suitable habitat in the resettled farmed area being converted for homesteads, livestock grazing, and crop production. Since 2015, this trend has plateaued and the population has stabilised as a result of drought and movement of younger people back to cities.

We define two land-use types for our study: “farmed,” the newly resettled lands used for subsistence farming; and “ranched,” the remaining untransformed land, which continues, essentially...
unchanged, in private ownership with low-level cattle ranching (about one head of cattle per 6-ha).

Our analysis of Google Earth images from 2011 showed that farmed and ranced lands both contained similar, evenly distributed, mosaics of three fragmented habitat types: open grasslands (48% by area), miombo woodlands 30%, and acacia woodlands 22%. These proportions enabled us to define the number of transects needed in each area and habitat type in order for our surveys to be representative of the entire study site. We did not aim to assess changes in bird communities within each habitat type. A set of linear transects defined by GPS coordinates and with random start points and orientations were identified within each habitat (Figure 1). In total, 45 sites were surveyed: 23 ranced (acacia n = 5, miombo n = 7, open n = 11) and 22 farmed (acacia n = 5, miombo n = 6, open n = 11). These descriptions indicate the dominant habitat in that transect; the proportions of each transect-type match the habitat percentages in each land-use area. To avoid pseudo-replication, transects in ranced and farmed areas of the same habitat type were spaced well apart. Distances (mean, SD, closest) between sites were acacia (16.1; 3.2; 3.5) km; miombo (13.3; 1.8; 3.4) km; open (11.2; 1.1; 3.6) km.

Surveys were undertaken during the winters (June–July) of 2012, 2014, 2016, 2018, and 2020 by the same observer team (lead observer NC; recorders MD, SP), along identical transects, and using the same methods. Two 600 m transects, parallel and spaced 300 m apart, were walked at constant slow speed shortly after sunrise (from 05:30), or before sunset (from 16:00), on clear, dry days. Two sites were counted on each day, with sites randomly assigned to morning or afternoon and located as far apart as possible in different habitat types. Birds were only recorded visually, and data collected were distance to the bird(s) using a Leica LRF1200 rangefinder, the number of individuals, and the angle of deviation from the transect. All birds over-flying the transects were disregarded, and great care was taken to avoid double counting. Indications of human activities and the presence of game animals observed at all distances from transects were also recorded: numbers of people, buildings, livestock, dogs, game animals, presence of standing water, and evidence of tree cutting.

2.2 | Data analyses: Input data, species’ richness, and abundances

We ran EstimateS 9.1.0 software (Colwell, 2013) on individual-based count data to evaluate sampling adequacy and calculate Chao1 estimators of species’ richness (SR). Differences in species’ richness between land-uses were assessed in terms of effect size (ES), calculated...
as: $ES = \text{Absolute} \left( SR_{\text{ranched}} - SR_{\text{farmed}} \right) / \text{pooled population standard deviation}$ (Smart et al., 2009). We highlight ES values $>1.0$ as indicators of potentially important ecological changes (Smart et al., 2009).

We used Distance 7.1 software (Thomas et al., 2010), applied separately to transect counts for each year and land-use, to calculate species' abundances corrected for variable probabilities of detection. Records of birds sighted at distances $>100$ m from transect lines were discarded. Conventional Distance Sampling mode was used, with 2 modeling options: half normal functions with Cosine series expansion and uniform functions with simple polynomial series expansion (Buckland et al., 2001). The most parsimonious model solution was chosen using Akaike's Information Criterion (Buckland et al., 2001). In the analyses, every species was grouped into one of 11 classes of perceived detectability ("prominence," Table A1), by which we categorized the conspicuousness and behavior of that species based on our extensive field experience in African ornithology. This method allowed counts of all species, including those rarely observed, to be adjusted for variable detectability and inclusion in subsequent analyses of abundances and population densities (Pringle et al., 2019).

We used counts during 2012–2020 to estimate temporal trends in individual species and in bird communities in ranched and farmed areas. To do so, we used a two-step process involving the R-based software packages "trimr" and "BRC indicators" (R Core Team, 2019). These methods are used to assess trends in annual abundance indices from national bird counts in European countries (PECBMS, 2021). In the first step (trimr), we used species' abundances, corrected for detection probabilities, to calculate population indices and standard errors adjusted for the effects of overdispersion and serial correlation between years (Pannekoek & van Strien, 2005). We used these outputs in a log-linear Poisson regression (BRC indicators) to calculate the slopes and 95% CIs of the population trends. This method applies Monte Carlo procedures to account for sampling errors and generate confidence intervals for multi-species indicators (MSIs) and trends in MSIs. In our model, we ran 5,000 simulations, using 2012 as the base year with MSI value set at 1 and standard error zero. The trend in each species, or group of species, is determined by calculating the multiplicative trend, which reflects changes in terms of the average percentage change per year. The overall population trend is then converted into a trend category based on the multiplicative trend and its 95% confidence interval. There are six categories, ranging from "strong increase" to "steep decline" (Table A2; Soldaat et al., 2017).

### 2.3 Data analyses: Species' traits, diversity, and functional analyses

We compiled a database of traits for every species from standard references (Brown et al., 1982; Fry & Keith, 2004; Fry et al., 1988, 2000; Keith et al., 1992; Urban et al., 1986, 1997). Our database included nine traits per species: five measurements of morphology (average adult body mass; lengths of wing, tail, bill, and tarsus), bill shape (16 categories), primary feeding guild (frugivore, granivore, insectivore, nectarivore, omnivore, or predator), nest type (six categories), and average clutch size (Table A3). These traits were chosen to reflect distinctive aspects of species as well as relating to resource usage that drives ecosystem functions (Şekercioğlu, 2006). Body metrics reflect resource consumption (mass), foraging mode and behavior (bill and tarsus), and flight range for resource access and dispersal (wing and tail). Bill shape and primary feeding guilds are relevant in terms of ecosystem services, population control, resource removal and nutrient recycling. Nest type reflects the role of birds as ecosystem engineers, e.g., in providing structures that host other organisms, or in modifying trees or soil by excavating cavity nests. Temporal changes in the avian communities recorded in ranched and farmed areas were evaluated by combining this traits database with species' abundances in each year.

We follow Pavoine (2020) in defining diversity in the two land-use areas: species' diversity is the number of species present (= species' richness), weighted by the abundance of each species; phylogenetic beta diversity is the difference between communities in positions of species on the abundance-weighted phylogenetic trees. An R-based software package, "div," and associated functions "divparam" and "abgevodivparam" (Pavoine, 2020; R Core Team, 2019) were used to measure species' diversity and phylogenetic beta diversity, together with changes in these indices during 2012–2020. These functions include a parameter ($\eta$) that controls the relative weighting of rare and abundant species, which aids in interpreting trends. Functional redundancy, measured in terms of distances between species in the functional traits dendrogram and weighted by species' abundances, was calculated using the "uniqueness" function. This technique quantifies redundancy by comparing the observed community to one in which traits of all species are maximally dissimilar (Pavoine, 2020).

To analyze temporal trends in the phylogenetic compositions of communities in the two land-use areas, we used a version of double principal coordinate analysis (DPCoA; Pavoine et al., 2013) to include the effects of two crossed factors. The crossed-DPCoA method, available within the package "adiv," uses ordination techniques within a mathematical space in which species' abundances, their traits dissimilarities, and two factors (in our case, land-use type and year) are represented by a set of points. The method allows the interacting effects of the two factors to be decomposed, i.e., the effect of land-use type is separated from the year of survey with regard to variations in phylogenetic composition (Pavoine, 2020).

### 3 RESULTS

Some indications of changes in the farmed area during 2012–2020 are given by our indirect measures of human impact (Table 1). The number of people encountered during our transect counts is not systematic or representative of overall human population size and pressures. However, when compared with transect counts in the ranched area, there are 10–20 times as many people present in
The number of buildings seen from the transects virtually doubled over 8 years in farmland, suggesting an increasing human population. New buildings in the ranched area relate to modified grazing methods, which have also impacted the numbers of cattle seen on ranched transects. Livestock trends in farmland are unclear; after increasing rapidly during 2012–2016, numbers have declined, possibly reflecting drought conditions following low summer rainfall in 2018–2019 (Figure S1). Drought conditions, combined with disease, may have been responsible for the reduced number of dogs. Game animals are now largely restricted to the ranched area.

For each year, habitat, and land-use type, numbers of species recorded approached asymptotes, suggesting that only a few uncommon species were overlooked in each survey set. In 2012, species' richness was 8.8% higher in farmland than in the ranched area, and it continued to be higher throughout the study period, with an effect size >1 in all years except 2014 (Table 2). However, the ranched area species' richness also increased by 12.3% during 2012–2020 as new species colonized that area.

With the possible exception of predators in farmland, abundances of birds in all primary feeding guilds, and in both land-use areas, increased during 2012–2020 (Figure 2). When analyzed by species' average body mass, abundances also increased in most mass ranges (Figure 3). The MSI technique, which corrects for overdispersion and serial correlation between years, confirmed significant moderate or strong increases in abundance of most categories of birds (Table 3; Table A2). These increases occurred in a large number of individual species across a range of feeding guilds (Figure 4), and few species showed moderate or steep declines in either area during 2012–2020 (Table A4). The analyses were restricted to species with total numbers >50 recorded in both areas across all surveys. However, even with this cut-off level, many uncommon species are included, as the limit equates to 5 individuals/year recorded across all transects in each land-use area.

Species' diversity curves, modulated by abundance weighting, show marked differences between bird communities according to land use and year (Figure S5a). In 2012, there was higher species' richness ($q = 0$, representing presence/absence) in farmed areas (105 vs 91 species), but higher species' diversity in the ranched area for $q > 0.7$ as abundance weighing increased. In contrast, the species' diversity curves for 2020 show almost identical species' richness
Compared with 2012, the lower diversity values in 2020 at $q = 3$ indicates that common species were increasingly dominant in both areas. However, even with these species given high weighting, in 2020 the bird community in the rangeland area continued to have higher species’ diversity than in farmland. These trends are reflected in the phylogenetic beta diversity curves, which show that the traits-based dissimilarity between rangeland and farmed area bird communities was lower in 2020 than in 2012 for all values of $q$ (Figure 5b).

Linear regressions show unchanged functional redundancy during 2012–2020 in the farmland bird community ($\text{Slope} = -0.0011 \pm 0.0093$ with $R^2 = 0.005$; $F(1,3) = 0.134; p = .914$), but a significant redundancy increase among those species present in the rangeland area ($\text{Slope} = 0.0080 \pm 0.0024$ with $R^2 = .782$; $F(1,3) = 10.740; p = .047$) (Figure 6a).

The first stage of crossed-DPCoA analysis of species’ abundances and functional traits, with land-use type (A) and year (B) as factors, generated an ordination plot showing the positions of communities around the first two axes (Figure 6b). The principal (X) and secondary (Y) axes expressed 40% and 32%, respectively, of the variance in the position of the levels of factor A. Along the X-axis, communities in rangeland areas are clearly separated on the positive side of the origin from those in farmland on the negative side. The sequences of transect counts in rangeland and farmed areas show a converging pattern during 2012–2020, with the greatest changes occurring in the rangeland area community. The close proximity of the

![Figure 2](image-url)

**Figure 2** Birds in virtually all primary feeding guilds and land-use areas were increasingly abundant over the study period (farmland trend: predators uncertain). Data points (red: farm; blue: ranch) are log-transformed densities of every species recorded during biennial counts of identical winter transects from 2012 to 2020. Species’ counts are corrected for detection probability; each species is then assigned to its primary feeding guild. Lines are linear regressions, with shading indicating 95% CIs. The significance of these trends is assessed using packages “rtrim” and “BRC indicators,” which calculate population indices and standard errors adjusted for the effects of overdispersion and serial correlation between years (Table 3).
2020 points indicates that the two communities were the most similar in that year.

Trends in the proportions of individual species in each land-use area during 2012–2020 are shown in Figure 7. The central dendrogram shows functional traits dissimilarities between species. The differences between bird communities were mostly due to the higher proportion of small granivores (e.g., waxbills, canaries, and doves) and larger insectivores (e.g., rollers, starlings, and thrushes) in farmland in 2012–2016, during which time the ranned area held higher proportions of small insectivores (e.g., cisticolas, eremomelas) and ground-dwelling birds such as lapwings and spurfowl. In 2016 and 2018, some of the earlier trends in species’ abundances were changing, or even reversing. For example, in 2016, small granivorous birds (e.g., waxbills, weavers, and canaries) strongly increased in abundance in the ranned area. The ranned area also gained more rollers, starlings, and thrushes in 2018.

4 | DISCUSSION

For many decades prior to 2001, the entire study area was uninhabited savannah used for low-level cattle ranching. In 2001–2002, abrupt human settlement, accompanied by building of homesteads and commencement of subsistence farming, resulted in widespread
habitat modification in a part of this area. This resulted in a matrix of subsistence farms, interspersed with areas of uncropped grassland and woodland patches, replacing the former contiguous savannah. Although the resettled farming households are now well established, their reliance on farming in unproductive shallow sandy soils leads to a tenuous existence. Droughts and socioeconomic instability have meant that many younger people leave the farms to work in urban areas, thereby limiting growth in the community (pers. obs.).

The immediate impact of rapid land conversion during 2001–2002 on bird species’ richness and abundance in the farmed part of

### TABLE 3 Population trends of species grouped by primary feeding guild and by average body mass

| Community trend during 2012–2020 | Ranched area | Farmed area |
|---------------------------------|-------------|-------------|
| **Trend ± SE**                  | **Category**| **Trend ± SE** | **Category** |
| **Guild**                      |             |             |
| Frugivore                      | 1.151 ± 0.018 | Strong increase | 1.188 ± 0.016 | Strong increase |
| Granivore                      | 1.267 ± 0.020 | Strong increase | 1.179 ± 0.009 | Strong increase |
| Insectivore                    | 1.048 ± 0.010 | Moderate increase | 1.099 ± 0.009 | Strong increase |
| Nectarivore                    | 1.434 ± 0.051 | Strong increase | 1.198 ± 0.034 | Strong increase |
| Omnivore                       | 1.198 ± 0.016 | Strong increase | 1.117 ± 0.012 | Strong increase |
| Predator                       | 1.207 ± 0.065 | Strong increase | 1.098 ± 0.055 | Uncertain |
| All guilds                     | 1.162 ± 0.007 | Strong increase | 1.143 ± 0.005 | Strong increase |
| **Mass**                       |             |             |
| 1–12 g                         | 1.316 ± 0.017 | Strong increase | 1.122 ± 0.009 | Strong increase |
| 13–25 g                        | 1.118 ± 0.040 | Moderate increase | 1.119 ± 0.010 | Strong increase |
| 26–50 g                        | 1.021 ± 0.014 | Stable | 1.050 ± 0.012 | Moderate increase |
| 51–100 g                       | 1.190 ± 0.016 | Strong increase | 1.201 ± 0.013 | Strong increase |
| 101–300 g                      | 1.151 ± 0.017 | Strong increase | 1.125 ± 0.015 | Strong increase |
| >300 g                         | 0.988 ± 0.200 | Uncertain | 1.243 ± 0.075 | Strong increase |
| All masses                     | 1.162 ± 0.007 | Strong increase | 1.143 ± 0.005 | Strong increase |

Note: The trends are generated using the multispecies indicator function “msi” in the BRC indicators package (Soldaat et al., 2017). The significance of trends and their classification are as defined in Table A2.
our study area is unknown. However, our 2012 results show that, by then, these indices were similar to (or exceeded) levels in rangeland. This is consistent with the >10-year biodiversity recovery period from abrupt land change estimated by Jung et al. (2019). Our further surveys to 2020 show that, after a time-lag well in excess of 10 years from abrupt disruption, the bird community in farmed land restructured in a way that increased species’ richness with loss of diversity. In the adjacent rangeland, a similar trajectory was followed, but with an additional time lag. Although some other studies of land conversion in Africa (e.g., Baudron et al., 2019; Coetzee & Chown, 2016; Marcacci et al., 2020; Mulwa et al., 2012; Norfolk et al., 2017) have identified benefits for certain bird groups, our results suggest an overall benign impact on the entire bird community in this specific case. The increased species’ richness that we recorded in the rangeland area was unexpected, as the habitat in this area has remained unchanged.

Bird population densities increased considerably over the survey period, with moderate to strong increases across a wide range of species in all feeding guilds. Some guilds (e.g., granivores) are expected to benefit from land conversion to agriculture, but it is surprising that, in our study area, abundances increased in all guilds, and in all areas. Abundances appear to be unrelated to average adult...

**FIGURE 5** (a) Avian species’ diversity curves differed between farmed and rangeland areas, and shifted between 2012 and 2020. The parameter $q$ controls the sensitivity of species’ diversity to abundance-weighting of each species. At $q = 0$, species’ abundances are disregarded and reflect presence/absence, thus the $y$-intercept is the observed species’ richness for the community. In effect, at $q = 0$, rare species are given higher weighting than common species. For $q > 0$, species’ diversity increasingly accounts for abundance until at $q = 3$, abundant species are given high weight and rare species low weight; (b) phylogenetic beta diversity between rangeland and farmed bird communities decreased from 2012 (blue) to 2020 (brown). As in (a), parameter $q$ controls the sensitivity of this diversity index to the abundance weighting of each species. In 2012, phylogenetic differences between birds in different land-use types were highest for more abundant species, whereas differences reduced and were confined to rarer species (low $q$ values) in 2020.

**FIGURE 6** Bird communities in farmed and rangeland areas became increasingly similar between 2012 and 2020. (a) Functional redundancy increased in the rangeland area (blue) bird community, approaching the level of farmland birds (red). Redundancy values are calculated using distances between species in the functional traits dendrogram, weighted by species’ abundances. Dotted lines are linear regressions, which show unchanged functional redundancy during 2012–2020 in the farmland bird community (Slope = $-0.0011 \pm 0.0093$ with $R^2 = .005$; $F(1, 3) = 0.014; p = .914$), but a significant redundancy increase among those species present in the rangeland area (Slope = $0.0080 \pm 0.0024$ with $R^2 = .782; F(1,3) = 10.740; p = .047$). (b) Differences in the composition of bird communities decreased over time (as indicated by converging count year arrow sequences) and were smallest in 2020. Over the period 2012–2020, the greatest changes (arrow length and direction) occurred in the rangeland area community. The communities in each year are represented by points derived from nonmetric ordination, which distils the main patterns of species’ richness, abundance, and traits present in each land-use onto two principal axes. Increasingly similar communities result in more closely clustered points.
There were proportionately more small granivores and large insectivores in farmland in 2012–2016, while the ranched area held more small insectivores and ground-dwelling birds. However, this pattern changed from 2016 as new species colonized the ranched area. This DPCoA analysis shows trends in the phylogenetic composition of bird communities in each land-use area, with the central dendrogram showing functional traits’ dissimilarities between species. Interpretation of this figure is in two stages. In the first stage, consider the (primary) X-axis of Figure 6b, which shows that all bird communities in the ranched area lie on the positive side of that axis, with all farmland communities on the negative side. In this figure, the color-coded scale (+1 to −1) relates to the ± axes values in Figure 6b. The colored ring labeled “X-axis” displays the relative proportion of each species in each area. Species forming a higher proportion of the ranched area community are shaded yellow-brown, indicating distance (increasing proportion) along the positive X-axis. In the same way, shades of blue (negative X-axis) indicate a higher proportion in farmland, while green shading indicates equal proportions in communities of both land-use areas. In the second stage, consider the (secondary) Y-axis of Figure 6b and again apply the colour-coding convention. The pattern of point distribution here is more complex and harder to interpret as the survey years for ranched and farmed area communities are not clearly separated relative to the Y-axis origin. However, points furthest from the Y-axis origin carry the greatest weight and dominate trends reflected in this figure, i.e., changes in the ranched area community (positive in 2018, negative in 2016). This suggests that, in these years, some of the trends observed on the X-axis were changing, or even reversing. For example, the proportion of small, predominantly granivorous species (e.g., waxbills, weavers, and canaries) strongly increased in the ranched area in 2016. This area also gained more rollers, starlings, and thrushes in 2018.
body mass, with stability or increasing populations in all mass ranges, with the possible exception of ranched area birds with mass >300 g. Although the reasons for these increasing abundances are unclear, nationwide surveys in grassland, savannah, and woodland habitats in neighboring Botswana recorded a strong increase in bird populations during 2010–2015. In Botswana, 49% of recorded species showed significant increases, and common species fared best outside protected areas (Wotton et al., 2017). A similar pattern is observed in our data, which shows increased abundances in 56%–64% of those species recorded in sufficient numbers to permit analysis (Table A4).

The differing profiles of species’ diversity curves for bird populations indicate that, although species’ richness was higher in farmland in 2012, species’ diversity was higher in the ranched area when abundances were taken into account. By 2020, species’ diversity profiles had shifted as some species that were only in farmland in 2012 spread into the ranched area, increasing richness in that area, but leaving it unchanged in farmland. The changed composition of the populations is also reflected in the phylogenetic beta diversity curves for 2012 and 2020, which show marked differences in the dissimilarity profiles between the ranched and farmed communities. In 2012, phylogenetic differences between birds in different land-use types were highest for more abundant species, whereas differences reduced and were confined to rarer species in 2020.

These diversity trends are confirmed by changes in other indices. Trends in functional redundancy, a measure of the abundance of species with similar traits, differed according to land use. In the farmed area, it was relatively stable, while increasing redundancy was recorded in the ranched area bird community. Communities impacted by land-use change may follow a number of different trajectories as they adapt and restructure following disturbance (Mayfield et al., 2010). In our study, the trends should reflect the environmental filtering effects of subsistence farming on the bird community that was initially present in the unmodified dryland savannah. At the start of our study in 2012, species’ richness and functional redundancy were higher in farmland than in the ranched area, suggesting that additional species from the regional species’ pool had colonized farmland after land-use change in 2002, but had added few new traits. This pattern is expected in tropical areas, where species’ pools are large (Mayfield et al., 2010). During 2012–2020, further new species colonizing the farmland added no new traits as functional redundancy remained largely unchanged. In contrast, in the untransformed ranched land, functional redundancy increased during 2012–2020. If species’ richness in this area had declined or remained constant, this would have suggested that some species with diverse traits were lost, then partly or fully replaced by an influx of new species with similar traits. However, ranched area species’ richness increased, and no loss of bird species was apparent over the survey period. It appears that the composition of the bird communities in the two land-use areas started to converge, with new species becoming increasingly abundant, initially in farmland, and later in the ranched land, but contributing few new functional traits.

Our DPCoA analysis reveals the major changes that occurred in the phylogenetic composition of bird communities during our 8-year study. Throughout the study period, about 50% of species maintained broadly similar proportions of the communities present in each land-use area. Some differences we recorded in functional groups (e.g., a higher proportion of granivores in farmland) were to be expected on the basis of other research in Africa (e.g., Gove et al., 2013; Greve et al., 2011; Sinclair et al., 2002). The availability of suitable food in the vicinity of crops and homesteads is likely to have benefitted over 25 species of doves, pigeons, seedeaters, waxbills, and buntings in the farmland. Several of these species (e.g., Jameson’s Firefinch, Common Waxbill) were not recorded in the ranched area in 2012 and appear to have been early colonizers of the farmland. Other trends in farmland, such as proportionately more medium-sized frugivores, insectivores, and omnivores (e.g., rollers, starlings, thrushes, go-away birds), suggest that they too benefitted from habitat change. The trends in the above functional groups in farmland led to lower proportions of some other functional groups such as ground-dwelling birds (e.g., lapwings, spurfowl) compared with the ranched area community. By 2016 and 2018, some earlier trends in phylogenetic composition were changing, or even reversing. For example, in 2016, small granivorous birds (e.g., waxbills, weavers, and canaries) strongly increased in the ranched area. The ranched area also gained more rollers, starlings, and thrushes in 2018. The converging sequence of points in the ordination plot provides further evidence of the two bird communities becoming more similar with increased time since the habitat was transformed in the farmed area.

All of the bird species in this study have a wide distribution in southern Africa. Of the 187 species we recorded, all except nine are classed as Least Concern (IUCN, 2021). The birds of conservation concern include three vulture species and three eagles. Of the vulture species in the study area, White-backed Vultures Gyps africanaus (Critically Endangered) have established a growing breeding colony in the ranched area (but outside our transects). Although numbers were small, the Secretarybird Sagittarius serpentarius (Endangered) was more often recorded in the farmed area, rather than ranched land. In South Africa, this species has adapted to transformed areas in South Africa, but declined inside the protected Kruger National Park (Hofmeyr et al., 2014). Grey Crowned Cranes Balearica regulorum (Endangered) occurred only in the farmed area, and Kori Bustards Ardeotis kori (Near Threatened) were restricted to ranched land; numbers of both species were low.

This study supports growing evidence that, where interspersed with intact natural habitat, subsistence farming in Africa can support an abundant and richly diverse avian community. Recent research findings from Kenya (Norfolk et al., 2017) and Ethiopia (Baudron et al., 2019; Marcacci et al., 2020) suggest that, for taxa such as birds, a multifunctional landscape that includes small-scale agriculture can play an important role in biodiversity conservation. Common factors that link these studies are the presence of a wide range of habitat-generalist species, and the heterogeneous habitat mosaics in which low-level farming activities are embedded. Harsh environmental conditions in this newly farmed area of Zimbabwe...
placed natural constraints on farming activities and human impact over the past two decades, and the modified landscape retained much of the original habitat within the agricultural matrix. Our study provides a unique insight into the initial impact of, and subsequent recovery from, an abrupt land-use change event in an understudied dryland biome.

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CONFLICT OF INTEREST
The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS
Stephen Pringle: Data curation (supporting); formal analysis (lead); investigation (supporting); methodology (equal); writing – original draft (lead); writing – review and editing (equal). Ngoni Chiweshe: Conceptualization (equal); data curation (lead); investigation (lead); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). Martin Dallimer: Conceptualization (equal); data curation (supporting); investigation (supporting); methodology (equal); writing – original draft (supporting); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT
Data used in the analyses are accessible from the Research Data Leeds Repository (http://archive.researchdata.leeds.ac.uk/) under citation: Pringle (2022).

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### APPENDIX A

#### TABLE A1  Categories and definitions of prominence codes assigned to bird species recorded across all habitats in farmed and ranched areas of the study site

| Code | Description | Examples |
|------|-------------|----------|
| cry  | Cryptic or secretive | Nightjars, owls, bitterns, coursers, thick-knees, quails, cuckooshrikes |
| fli  | Aerial feeders | Swifts, swallows, martins, bee-eaters |
| flo  | Flocking birds | Queleas, weavers, waxbills, mannikins, bishops, widowbirds, whydahs |
| lbb  | Large bush birds | Hornbills, turacos, pigeons, large doves, rollers, coucals |
| lgr  | Large ground dwellers | Lapwings, guineafowl, spurfowl, francolins |
| lob  | Large birds; birds of prey | Bustards, herons, crows, ravens, hamerkops, vultures, eagles, buzzards, kestrels, falcons |
| mbb  | Medium bush birds | Drongos, small doves, thrushes, starlings, cuckoos, orioles, honeyguides, babblers |
| sbb  | Small bush birds | Robins, chats, bulbul, shrikes, seedeaters, canaries, sparrows, flycatchers |
| sgr  | Small ground dwellers | Larks, pipits, wagtails, longclaws, bunting, wheatears, sparrow larks, hoopoes |
| tbb  | Tiny bush birds | Tits, eremomelas, camaropteras, white-eyes, warblers, crombecs, prinias, cisticolas, sunbirds |
| tre  | Tree specialists | Woodpeckers, barbets, parrots, kingfishers, wood hoopoes, scimitarbills |

#### Table A.2  Categories of trends in populations based on the slope and 95% CI output of software packages "rtrim" and "BRC indicators" (Soldaat et al., 2017)

| Trend category     | Trend slope ($S$) | 95% CI lower limit (L) | 95% CI upper limit (U) |
|--------------------|-------------------|------------------------|------------------------|
| Strong increase    | $S > 1.05$        | $L > 1.05$              | None                   |
| Moderate increase  | $1.00 < S \leq 1.05$ | $1.00 < L < 1.05$       | None                   |
| Stable             | Any               | $0.95 \leq L$          | $U \leq 1.05$          |
| Uncertain          | Any               | Either $0.95 > L$ or $U > 1.05$ |                       |
| Moderate decline   | $0.95 \leq S < 1.0$ | None                   | $0.95 < U < 1.00$      |
| Steep decline      | $S < 0.95$        | None                   | $U < 0.95$             |
| Standard IOC Name       | Scientific Name              | Guild | Mass | Wing | Tail | Culmen | Tarsus | Bill | Nest | Clutch |
|-------------------------|------------------------------|-------|------|------|------|--------|--------|------|------|--------|
| Acacia Pied Barbet      | Tricholaema leucomas         | f     | 30   | 82   | 49   | 20     | 19     | ser  | hol  | 2.9    |
| African Fish Eagle      | Haliæetus vocifer           | p     | 2,820| 559  | 252  | 41     | 85     | hoo  | plt  | 2.0    |
| African Goshawk         | Accipiter tachiro           | p     | 356  | 230  | 198  | 17     | 63     | hoo  | plt  | 2.5    |
| African Green Pigeon     | Treron calvus                | f     | 231  | 171  | 99   | 13     | 22     | sle  | plt  | 1.5    |
| African Grey Hornbill    | Tockus nasutus              | m     | 208  | 215  | 192  | 88     | 36     | cas  | hol  | 4.0    |
| African Hawk-Eagle       | Hieraaetus spilogaster      | p     | 1,420| 440  | 272  | 31     | 95     | hoo  | plt  | 1.6    |
| African Hoopoe           | Upupa africana              | i     | 53   | 137  | 92   | 49     | 19     | dec  | hol  | 3.4    |
| African Jacana           | Actophilornis africanus     | i     | 182  | 156  | 45   | 52     | 65     | pro  | gnd  | 3.6    |
| African Pipit            | Anthus cinnamomeus          | i     | 27   | 87   | 64   | 14     | 26     | sli  | gnd  | 2.7    |
| African Scops Owl        | Otus senegalensis           | i     | 69   | 137  | 65   | 11     | 22     | hoo  | hol  | 2.7    |
| African Stonechat        | Saxicola torquatus          | i     | 15   | 72   | 52   | 16     | 23     | sli  | cup  | 3.2    |
| African Wattled Lapwing  | Vanellus senegalus          | i     | 224  | 232  | 99   | 34     | 85     | pro  | gnd  | 3.6    |
| African Wood Owl         | Strix woodfordii            | p     | 299  | 249  | 153  | 30     | 46     | hoo  | hol  | 2.0    |
| African Yellow White-eye | Zosterops senegalensis      | i     | 11   | 59   | 40   | 10     | 15     | sho  | cup  | 2.8    |
| Amethyst Sunbird         | Chalcomitra amethystina     | n     | 11   | 64   | 41   | 24     | 16     | dec  | ovl  | 1.8    |
| Arrow-marked Babbler     | Turdoides jardineii         | i     | 72   | 110  | 108  | 24     | 32     | sle  | cup  | 2.8    |
| Bar-throated Apalis      | Apalis thoracica            | i     | 11   | 52   | 55   | 13     | 20     | sho  | ovl  | 2.7    |
| Bateleur                 | Terathopis ecaudatus        | p     | 2,242| 527  | 109  | 36     | 73     | hoo  | plt  | 1.0    |
| Bearded Scrub Robin      | Cercotrichas quadricularata | i     | 26   | 80   | 73   | 18     | 26     | sli  | cup  | 2.8    |
| Bearded Woodpecker       | Dendropicos namaquis        | i     | 83   | 132  | 67   | 31     | 19     | chi  | hol  | 3.0    |
| Black Crane              | Amaurornis flavirostra      | m     | 94   | 103  | 42   | 25     | 40     | pro  | gnd  | 4.0    |
| Black Cuckoo-Shrike      | Campephaga flava            | i     | 34   | 104  | 100  | 15     | 19     | sle  | cup  | 1.9    |
| Black-backed Puffback    | Dryoscopus cubla            | i     | 27   | 80   | 71   | 19     | 22     | hoo  | cup  | 2.7    |
| Black-bellied Bustard    | Lissotis melanogaster       | i     | 1,966| 353  | 186  | 44     | 131    | pro  | gnd  | 1.5    |
| Black-chested Snake Eagle| Circaetus pectoralis        | p     | 1,962| 510  | 272  | 34     | 87     | hoo  | plt  | 1.0    |
| Black-collared Barbet    | Lybius torquatus            | m     | 59   | 92   | 57   | 23     | 21     | ser  | hol  | 3.3    |
| Black-crowned Tchagra    | Tchagra senegalus           | i     | 51   | 86   | 101  | 23     | 28     | hoo  | cup  | 2.5    |
| Black-eared Seedeeater   | Serinus mennelli            | g     | 15   | 81   | 52   | 11     | 13     | con  | cup  | 3.0    |
| Black-headed Heron       | Ardea melanopechala        | p     | 1,078| 401  | 157  | 100    | 136    | poi  | plt  | 2.8    |
| Black-headed Oriole      | Oriolus larvatus           | m     | 65   | 137  | 97   | 28     | 22     | sle  | cup  | 2.4    |
| Blacksmith Lapwing       | Vanellus armatus           | i     | 156  | 211  | 88   | 28     | 73     | pro  | gnd  | 3.4    |
| Black-throated Canary    | Serinus arrocularis        | m     | 11   | 71   | 43   | 9      | 12     | con  | cup  | 3.0    |
| Black-winged Kite        | Elanus caeruleus           | p     | 248  | 272  | 122  | 17     | 36     | hoo  | plt  | 3.5    |
| Blue Waxbill             | Uraeginthus angolensis      | g     | 11   | 52   | 54   | 10     | 14     | con  | ovl  | 3.5    |
| Bronze Mannikin          | Lonchura cucullata         | g     | 9    | 49   | 30   | 10     | 14     | con  | ovl  | 2.7    |
| Broad-billed Roller      | Eurystomus glaucurus       | i     | 105  | 176  | 98   | 22     | 17     | sle  | hol  | 4.9    |
| Brown Snake Eagle        | Circaetus cinereus         | p     | 2,048| 514  | 270  | 43     | 100    | hoo  | plt  | 1.0    |
| Brown-crowned Tchagra    | Tchagra australis          | i     | 33   | 76   | 94   | 18     | 24     | hoo  | cup  | 2.4    |
| Brown-hooded Kingfisher  | Halcyon albiventris        | p     | 64   | 107  | 66   | 49     | 16     | poi  | hol  | 3.7    |
| Brubru                   | Nilsa afer                 | i     | 24   | 84   | 57   | 16     | 22     | hoo  | cup  | 2.0    |
| Burnt-necked Eremomela   | Eremomela isticollis       | i     | 9    | 55   | 43   | 12     | 20     | sho  | cup  | 2.6    |
| Bushveld Pipit           | Anthus caffer              | i     | 16   | 72   | 53   | 11     | 17     | sli  | gnd  | 2.5    |
| Cape Starling            | Lamproptornis nitens       | i     | 88   | 132  | 90   | 23     | 34     | sle  | hol  | 2.8    |
| Cape Wagtail             | Motacilla capensis         | i     | 21   | 82   | 84   | 14     | 23     | sli  | cup  | 2.8    |
| Capped Wheatear          | Oenanthe pileata           | i     | 33   | 94   | 59   | 15     | 31     | sli  | hol  | 3.0    |
| Standard IOC Name | Scientific Name | Guild | Mass | Wing | Tail | Culmen | Tarsus | Bill | Nest | Clutch |
|-------------------|------------------|-------|------|------|------|--------|--------|------|------|--------|
| Cardinal Woodpecker | Dendrocolus fuscens | i     | 31   | 94   | 47   | 19     | 16     | chi  | hol  | 2.4    |
| Chestnut-backed Sparrow Lark | Eremopterus leucotis | g     | 13   | 83   | 46   | 11     | 16     | con  | gnd  | 1.9    |
| Chestnut-vented Warbler | Sylvia subcereolata | i     | 15   | 66   | 68   | 12     | 21     | sho  | cup  | 2.5    |
| Chinspot Batis | Batis molitor | i     | 12   | 60   | 47   | 13     | 18     | sho  | cup  | 1.7    |
| Cinnamon-breasted Bunting | Emberiza tahapisi | g     | 14   | 77   | 60   | 10     | 16     | con  | cup  | 3.0    |
| Common Buttonquail | Turnix sylvestris | m     | 45   | 81   | 32   | 11     | 19     | sto  | gnd  | 6.6    |
| Common Quail | Coturnix coturnix | m     | 96   | 105  | 36   | 13     | 24     | sto  | gnd  | 6.6    |
| Common Scimitarbill | Rhinopomastus cyanomelas | i     | 37   | 108  | 125  | 42     | 19     | dec  | hol  | 2.7    |
| Common Waxbill | Estrilda astrild | g     | 8    | 49   | 56   | 9      | 15     | con  | ovl  | 4.9    |
| Coqui Francolin | Peliperdix coqui | m     | 261  | 132  | 75   | 22     | 37     | sto  | gnd  | 5.0    |
| Crested Barbet | Trachyphonus vaillantii | m     | 71   | 102  | 86   | 23     | 26     | ser  | hol  | 2.9    |
| Crested Francolin | Dendrocolus sephaena | m     | 342  | 151  | 95   | 22     | 44     | sto  | gnd  | 6.5    |
| Crimson-breasted Shrike | Lanius atrorococineus | i     | 48   | 99   | 100  | 23     | 32     | hoo  | cup  | 2.7    |
| Croaking Cisticola | Cisticola natalensis | i     | 21   | 66   | 59   | 14     | 28     | sho  | ovl  | 3.3    |
| Crowned Lapwing | Vanellus coronatus | m     | 155  | 202  | 91   | 31     | 68     | pro  | gnd  | 2.7    |
| Dark-capped Bulbul | Pygornotus barbatus | f     | 39   | 97   | 87   | 17     | 21     | sli  | cup  | 2.6    |
| Emerald-spotted Wood Dove | Turtur chalcospilos | g     | 64   | 111  | 84   | 18     | 18     | sle  | plt  | 2.0    |
| Fiery-necked Nightjar | Caprimulgus pectoralis | i     | 55   | 161  | 120  | 12     | 16     | wid  | gnd  | 3.1    |
| Familiar Chat | Oenanthe familiaris | i     | 21   | 85   | 62   | 16     | 24     | sli  | hol  | 1.9    |
| Flappet Lark | Mirafra rufocinamomea | i     | 26   | 81   | 55   | 14     | 22     | con  | gnd  | 2.2    |
| Fork-tailed Drongo | Dicrurus adsimilis | i     | 51   | 134  | 119  | 21     | 22     | sle  | cup  | 2.8    |
| Freckled Nightjar | Caprimulgus tristigma | i     | 79   | 190  | 132  | 13     | 19     | wid  | gnd  | 2.0    |
| Gabar Goshawk | Micronis gabar | p     | 155  | 195  | 163  | 13     | 45     | hoo  | plt  | 2.3    |
| Giant Kingfisher | Megaceryle maxima | p     | 364  | 206  | 117  | 87     | 16     | poi  | hol  | 3.5    |
| Golden-breasted Bunting | Emberiza flaviventris | g     | 18   | 82   | 69   | 13     | 17     | con  | cup  | 2.4    |
| Golden-tailed Woodpecker | Campethera abingoni | i     | 68   | 118  | 65   | 27     | 17     | chi  | hol  | 2.9    |
| Greater Blue-eared Starling | Lamprotornis chalybaeus | f     | 86   | 131  | 90   | 19     | 32     | sle  | hol  | 3.5    |
| Greater Honeyguide | Indicator indicator | i     | 48   | 109  | 70   | 14     | 15     | sto  | par  | 3.0    |
| Green Wood Hoopoe | Phoeniculus purpureus | i     | 71   | 154  | 236  | 51     | 22     | dec  | hol  | 3.0    |
| Green-capped Eremomela | Eremomela scotops | i     | 9    | 57   | 47   | 11     | 18     | sho  | cup  | 2.5    |
| Green-winged Pytilia | Pytilia melba | m     | 15   | 59   | 49   | 13     | 15     | con  | ovl  | 3.8    |
| Grey Crowned Crane | Balearica regulorum | m     | 3772 | 565  | 239  | 62     | 207    | pro  | gnd  | 2.6    |
| Grey Go-away-bird | Corythaixoides concolor | f     | 268  | 220  | 245  | 24     | 40     | sto  | plt  | 2.6    |
| Grey Penduline Tit | Anthoscopus caroli | i     | 6    | 51   | 27   | 8      | 13     | sho  | ovl  | 4.4    |
| Grey Tit-Flycatcher | Myioparus plumbeus | i     | 13   | 66   | 58   | 14     | 18     | sho  | hol  | 2.5    |
| Grey-backed Camaroptera | Camaroptera brevicaudata | i     | 11   | 54   | 39   | 12     | 21     | sho  | ovl  | 2.8    |
| Grey-headed Bush-Shrike | Malacopterus blanchoti | i     | 77   | 114  | 111  | 28     | 32     | hoo  | cup  | 2.9    |
| Grey-rumped Swallow | Pseudhirundo griseopygia | i     | 10   | 97   | 73   | 5      | 11     | wid  | hol  | 3.3    |
| Groundscraper Thrush | Psophocichla lititsirupa | i     | 76   | 128  | 69   | 27     | 33     | sle  | cup  | 2.7    |
| Hadada Libus | Bostrychia hagedash | i     | 1,262 | 353  | 154  | 134    | 68     | ben  | plt  | 2.7    |
| Hamerkop | Scopus umbretta | p     | 422  | 305  | 156  | 82     | 70     | com  | ovl  | 3.3    |
| Standard IOC Name          | Scientific Name                  | Guild | Mass | Wing | Tail | Culmen | Tarsus | Bill | Nest | Clutch |
|---------------------------|----------------------------------|-------|------|------|------|--------|--------|------|------|--------|
| Helmeted Guineafowl       | Numida meleagris                 | m     | 1,480| 265  | 171  | 25     | 81     | sto  | gnd  | 12.5   |
| Jameson's Firefinch       | Lagonosticta rhodopoearia        | g     | 9    | 48   | 41   | 10     | 13     | con  | ovl  | 3.6    |
| Kori Bustard              | Ardeotis kori                    | m     | 16,250| 678  | 370  | 98     | 206    | pro  | gnd  | 2.0    |
| Kurrichane Thrush         | Turdus libyanus                  | i     | 60   | 116  | 97   | 22     | 29     | sle  | cup  | 2.9    |
| Lappet-faced Vulture      | Torgos tracheliotus              | p     | 6600 | 776  | 351  | 70     | 143    | hoo  | plt  | 1.0    |
| Laughing Dove             | Streptopelia senegalensis        | g     | 103  | 138  | 110  | 16     | 23     | sle  | plt  | 2.0    |
| Lesser Grey Shrike         | Lanius minor                     | i     | 46   | 116  | 89   | 17     | 24     | hoo  | cup  | 3.5    |
| Lesser Honeyguide         | Indicator minor                  | i     | 26   | 88   | 55   | 10     | 14     | sto  | par  | 3.0    |
| Lesser Jacana             | Microparra capensis              | i     | 41   | 88   | 29   | 17     | 34     | pro  | gnd  | 3.3    |
| Lesser Striped Swallow    | Cercopis abyssinica              | i     | 18   | 112  | 100  | 6      | 10     | wid  | hol  | 3.0    |
| Levaillant's Cisticola    | Cisticola tinniens               | i     | 12   | 51   | 55   | 11     | 19     | sho  | ovl  | 3.5    |
| Lilac-breasted Roller     | Coracias caudatus               | i     | 106  | 166  | 187  | 33     | 22     | sle  | hol  | 2.8    |
| Little Bee-eater          | Merops pulillus                  | i     | 14   | 80   | 65   | 27     | 8      | dec  | hol  | 4.0    |
| Little Grebe              | Tachybaptus ruficollis           | p     | 147  | 101  | 15   | 20     | 27     | poi  | gnd  | 3.2    |
| Little Sparrowhawk        | Accipiter minullus               | p     | 90   | 150  | 117  | 10     | 42     | hoo  | plt  | 2.0    |
| Lizard Buzzard            | Kaupifalco monogrammicus        | p     | 294  | 226  | 140  | 17     | 53     | hoo  | plt  | 1.9    |
| Long-billed Crombec       | Sylvietta rufescens              | i     | 12   | 61   | 28   | 15     | 19     | sli  | cup  | 1.8    |
| Magpie Shrike             | Urolestes melanoleucus           | i     | 82   | 134  | 282  | 18     | 33     | hoo  | cup  | 3.3    |
| Malachite Kingfisher      | Alcedo cristata                 | p     | 15   | 57   | 27   | 34     | 7      | poi  | hol  | 3.7    |
| Marico Flycatcher         | Bradornis mariquensis           | i     | 25   | 85   | 76   | 13     | 21     | sho  | cup  | 2.9    |
| Martial Eagle             | Polemaetus bellicosus           | p     | 3965 | 612  | 288  | 45     | 114    | hoo  | plt  | 1.0    |
| Meyer's Parrot            | Pocephalus meyeri               | f     | 117  | 152  | 67   | 20     | 17     | hoo  | hol  | 2.7    |
| Mombio Double-collared Sunbird | Cinnyris manoensis            | n     | 9    | 63   | 46   | 24     | 17     | dec  | ovl  | 1.9    |
| Mocking Cliff Chat        | Thammolaea cinnamomeiventris    | m     | 48   | 112  | 95   | 20     | 29     | sli  | hol  | 2.8    |
| Namaqua Dove              | Oena capensis                   | g     | 40   | 105  | 140  | 14     | 15     | sle  | plt  | 2.0    |
| Natal Spurfowl            | Pternistis natalensis           | m     | 458  | 165  | 96   | 19     | 47     | sto  | gnd  | 6.5    |
| Nedicky                   | Cisticola fulvicapilla          | i     | 8    | 48   | 42   | 11     | 17     | sho  | ovl  | 3.3    |
| Orange-breasted Bush-Shrike | Telophorus sulphureopectus      | i     | 27   | 88   | 88   | 16     | 26     | hoo  | cup  | 1.8    |
| Orange-breasted Waxbill   | Amanda subflava                 | g     | 8    | 45   | 30   | 9      | 12     | con  | ovl  | 5.0    |
| Pearl-spotted Owl         | Glaucidium perlatum             | p     | 82   | 107  | 76   | 11     | 21     | hoo  | hol  | 3.0    |
| Pied Crow                 | Corvus albus                    | m     | 519  | 354  | 187  | 59     | 61     | com  | cup  | 4.1    |
| Purple Roller             | Coracias naevius                | i     | 168  | 189  | 143  | 41     | 24     | sle  | hol  | 3.3    |
| Qualifinich               | Ortygospiza fuscoscissa         | m     | 11   | 55   | 28   | 9      | 14     | con  | ovl  | 4.2    |
| Rattling Cisticola        | Cisticola chiniana              | i     | 16   | 61   | 60   | 13     | 21     | sho  | ovl  | 3.1    |
| Red-billed Buffalo-Weaver | Bubalornis niger                | i     | 81   | 119  | 104  | 23     | 30     | con  | ovl  | 3.3    |
| Red-billed Firefinch      | Lagonosticta senegala           | g     | 9    | 48   | 36   | 9      | 12     | con  | ovl  | 3.4    |
| Red-billed Quelea         | Quelea quelea                   | g     | 19   | 66   | 37   | 14     | 18     | con  | ovl  | 2.0    |
| Red-billed Teal           | Anas erythrorrhyncha            | m     | 568  | 217  | 81   | 44     | 35     | dep  | gnd  | 10.0   |
| Red-breasted Swallow      | Cecropis semirufa               | i     | 30   | 130  | 118  | 7      | 14     | wid  | hol  | 3.0    |
| Red-capped Lark           | Calandrella cinerea             | i     | 24   | 91   | 62   | 13     | 20     | con  | gnd  | 2.1    |
| Red-crested Korhaan       | Lophotis ruficrista             | m     | 680  | 259  | 133  | 33     | 78     | pro  | gnd  | 2.0    |
| Red-eyed Dove             | Streptopelia semitorquata       | g     | 235  | 189  | 125  | 22     | 25     | sle  | plt  | 2.0    |

(Continues)
| Standard IOC Name                  | Scientific Name          | Guild | Mass | Wing | Tail | Culmen | Tarsus | Bill | Nest | Clutch |
|-----------------------------------|--------------------------|-------|------|------|------|--------|--------|------|------|--------|
| Red-faced Mousebird               | Urococlis indicus        | f     | 56   | 96   | 210  | 14     | 18     | sto  | cup  | 2.6    |
| Red-headed Weaver                 | Anaplectes rubriceps     | i     | 22   | 80   | 51   | 17     | 19     | con  | ovl  | 2.5    |
| Red-winged Starling               | Onychognathus morio      | m     | 139  | 149  | 126  | 28     | 33     | slo  | cup  | 3.1    |
| Retz's Helmetshrike               | Prionops retzii          | i     | 48   | 130  | 92   | 24     | 22     | hoo  | cup  | 3.2    |
| Ring-necked Dove                  | Streptopelia capirola    | g     | 153  | 157  | 101  | 13     | 20     | sle  | plt  | 2.0    |
| Rosy-throated Longclaw            | Macronyx amelaei         | i     | 33   | 89   | 79   | 15     | 30     | sle  | gnd  | 2.7    |
| Rufous-naped Lark                 | Mirafra africana         | i     | 42   | 95   | 64   | 20     | 29     | con  | gnd  | 2.4    |
| Scaly-feathered Weaver            | Sporopipes squamifrons   | g     | 12   | 57   | 37   | 9      | 15     | con  | ovl  | 4.1    |
| Scarlet-chested Sunbird           | Chalcomitra squamifrons  | n     | 13   | 78   | 43   | 29     | 16     | slo  | cup  | 3.1    |
| Secretary Bird                    | Sagittarius serpentarius| p     | 4052 | 644  | 700  | 49     | 307    | hoo  | ovl  | 1.9    |
| Senegal Coucal                    | Centropus senegalensis   | p     | 170  | 172  | 205  | 28     | 38     | sto  | ovl  | 3.5    |
| Shelley's Franolin                | Scleroptila shelleyi     | m     | 438  | 161  | 79   | 25     | 41     | slo  | gnd  | 4.8    |
| Shikra                            | Accipiter badius         | p     | 123  | 182  | 137  | 11     | 44     | hoo  | ovl  | 2.5    |
| Southern Black Flycatcher         | Melaenornis pemalaina    | i     | 30   | 104  | 93   | 14     | 19     | sho  | cup  | 2.6    |
| Southern Black Tit                | Parus niger              | i     | 22   | 82   | 71   | 11     | 9      | sho  | hol  | 3.6    |
| Southern Fiscal                   | Lanius collaris          | i     | 39   | 99   | 106  | 20     | 27     | hoo  | cup  | 3.5    |
| Southern Grey-headed Sparrow      | Passer diffusus          | m     | 24   | 81   | 61   | 13     | 18     | con  | hol  | 3.3    |
| Southern Masked Weaver            | Ploceus velatus          | m     | 26   | 76   | 51   | 16     | 21     | con  | ovl  | 2.6    |
| Southern Red Bishop               | Euplectes oix            | g     | 23   | 71   | 40   | 15     | 21     | con  | ovl  | 2.7    |
| Southern White-crowned Shrike     | Eurocephalus anguitimens | i     | 69   | 136  | 108  | 17     | 24     | hoo  | cup  | 3.3    |
| Southern White-faced Owl          | Ptilopsis granti         | p     | 198  | 196  | 93   | 17     | 25     | hoo  | ovl  | 2.4    |
| Southern Yellow-billed Hornbill   | Tockus leucomelas        | m     | 190  | 198  | 208  | 64     | 38     | cas  | hol  | 3.7    |
| Speckled Pigeon                   | Columba guinea           | g     | 352  | 226  | 114  | 23     | 34     | slo  | plt  | 2.0    |
| Spotted Eagle-Owl                 | Bubo africanus           | p     | 666  | 336  | 197  | 39     | 73     | hoo  | gnd  | 2.4    |
| Spotted Thick-knee                | Burhinus capensis        | i     | 453  | 231  | 123  | 37     | 95     | pro  | gnd  | 2.0    |
| Stierling's Wren-Warbler          | Calamastes stierlingi    | i     | 13   | 60   | 45   | 13     | 21     | sho  | ovl  | 2.5    |
| Striped Kingfisher                | Halcyon chelicti         | i     | 38   | 83   | 45   | 32     | 11     | poi  | hol  | 3.4    |
| Swainson's Spurfowl               | Pternistis swainsonii    | m     | 621  | 183  | 84   | 21     | 56     | sto  | gnd  | 6.2    |
| Swallow-tailed Bee-eater          | Merops hirundineus       | i     | 22   | 95   | 103  | 29     | 9      | dec  | hol  | 3.5    |
| Tawny Eagle                       | Aquila rapax             | p     | 2,351| 523  | 270  | 40     | 86     | hoo  | ovl  | 1.7    |
| Tawny-flanked Prinia              | Prinia subflava          | i     | 9    | 49   | 61   | 11     | 20     | sho  | ovl  | 3.1    |
| Temminck's Couiser                | Cursorius temminckii     | i     | 67   | 124  | 46   | 20     | 40     | pro  | gnd  | 1.8    |
| Terrestrial Brownbul              | Phyllostomus terrestris  | m     | 31   | 90   | 96   | 21     | 25     | sli  | cup  | 2.1    |
| Three-banded Couiser              | Rhinoptilus cinctus      | i     | 125  | 163  | 83   | 20     | 72     | pro  | gnd  | 2.0    |
| Tropical Boubou                   | Laniarius aethiopicus    | i     | 50   | 95   | 98   | 23     | 34     | hoo  | cup  | 2.6    |
| Village Indigobird                | Vidua chalybeata         | g     | 12   | 67   | 36   | 8      | 14     | con  | par  | 3.0    |
| Village Weaver                    | Ploceus cucculatus       | i     | 37   | 85   | 54   | 20     | 21     | con  | ovl  | 2.6    |
| Violet-backed Starling            | Cinnyricinclus leucogaster| f   | 45   | 107  | 60   | 15     | 20     | slo  | hol  | 2.6    |
| Violet-eared Waxbill              | Uraeginthus granatarius  | g     | 12   | 57   | 66   | 11     | 16     | con  | ovl  | 4.5    |
| White-backed Vulture              | Gyps africanus           | p     | 5380 | 610  | 258  | 48     | 104    | hoo  | ovl  | 1.0    |
| White-bellied Sunbird             | Cinnyris talatala        | n     | 7    | 52   | 33   | 20     | 16     | dec  | ovl  | 1.9    |
| White-breasted Cuckoo-Shrike      | Coracina pectoralis      | i     | 58   | 141  | 112  | 19     | 23     | slo  | cup  | 1.5    |
| Standard IOC Name                  | Scientific Name          | Guild | Mass | Wing | Tail | Culmen | Tarsus | Bill | Nest | Clutch |
|-----------------------------------|--------------------------|-------|------|------|------|--------|--------|------|------|--------|
| White-browed Robin-Chat           | Cossypha heuglini        | i     | 35   | 98   | 87   | 20     | 30     | sli  | cup  | 2.7    |
| White-browed Scrub Robin          | Cercotrichas leucophrys  | i     | 17   | 68   | 65   | 15     | 24     | sli  | cup  | 2.7    |
| White-browed Sparrow-Weaver       | Plocepasser mahali       | m     | 41   | 103  | 63   | 17     | 26     | con  | ovl  | 2.0    |
| White-crested Helmetshrike        | Prionops plumatus       | i     | 33   | 107  | 85   | 20     | 21     | hoo  | cup  | 3.8    |
| White-headed Vulture              | Trigonocetes occipitalis| p     | 4700 | 627  | 280  | 51     | 102    | hoo  | plt  | 1.0    |
| White-necked Raven                | Corvus albicollis       | p     | 911  | 403  | 182  | 63     | 75     | com  | gnd  | 3.4    |
| White-throated Robin-Chat         | Cossypha humeralis       | i     | 21   | 78   | 70   | 16     | 27     | sli  | cup  | 2.7    |
| White-winged Widowbird            | Euplectes albonotatus    | g     | 21   | 71   | 61   | 14     | 19     | con  | ovl  | 2.6    |
| Wire-tailed Swallow               | Hirundo smithii         | i     | 12   | 107  | 67   | 8      | 7      | wid  | cup  | 2.9    |
| Yellow Bishop                     | Euplectes capensis       | g     | 19   | 73   | 55   | 19     | 25     | con  | ovl  | 2.7    |
| Yellow-bellied Eremomela          | Eremomela icteropygialis| i     | 7    | 60   | 36   | 11     | 18     | sho  | cup  | 2.3    |
| Yellow-bellied Greenbul           | Chlorocichla flaviventris| m   | 39   | 101  | 96   | 19     | 23     | sli  | cup  | 2.1    |
| Yellow-fronted Canary             | Crithagra mozambica      | m     | 11   | 69   | 41   | 9      | 13     | con  | cup  | 3.2    |
| Yellow-fronted Tinkerbird         | Pogoniulus chrysoconus   | m     | 13   | 62   | 34   | 13     | 13     | ser  | hol  | 2.5    |
| Yellow-throated Longclaw          | Macronyx croceus         | i     | 48   | 101  | 76   | 18     | 35     | sle  | gnd  | 3.0    |
| Yellow-throated Petronia          | Petronia supercilialis   | m     | 25   | 91   | 57   | 14     | 19     | con  | hol  | 3.1    |
| Zitting Cisticola                 | Cisticola juncidis       | i     | 9    | 51   | 38   | 10     | 18     | sho  | ovl  | 3.3    |

Note: The naming convention used is the IOC World Bird List v 7.3.

**TABLE A4** Species’ abundance trends generated by Wild Bird Indices modeling using the multispecies indicator function "msi" in the BRC indicators package (Soldaat et al., 2017)

| No. species with >50 individuals | Ranched | Farmed |
|----------------------------------|---------|--------|
|                                  | 61      | 76     |
| Strong increase                  | 49.2%   | 46.1%  |
| Moderate increase                | 14.8%   | 10.5%  |
| Stable                           | 6.6%    | 17.1%  |
| Uncertain                        | 21.2%   | 15.8%  |
| Moderate decline                 | 4.9%    | 3.9%   |
| Steep decline                    | 3.3%    | 6.6%   |

Note: Species included in this analysis were those for which the total number of individuals recorded during the period 2012–2020 in one land-use area was >50. Trend classifications are as defined in Table A2.
| No. species with > 50 individuals | Ranched | Farmed |
|----------------------------------|---------|--------|
| Strong increase                  | 49.2%   | 46.1%  |
| Moderate increase                | 14.8%   | 10.5%  |
| Stable                           | 6.6%    | 17.1%  |
| Uncertain                        | 21.2%   | 15.8%  |
| Moderate decline                 | 4.9%    | 3.9%   |
| Steep decline                    | 3.3%    | 6.6%   |

**FIGURE A1** Annual rainfall recorded in the study area during 2001–2020

**Species' trends**

- Strong increase
- Moderate increase
- Stable
- Uncertain
- Moderate decline
- Steep decline

**FIGURE A1** Annual rainfall recorded in the study area during 2001–2020