

# **Kent Academic Repository**

Zielonka, Natalia B., Arellano, Eduardo, Crowther, Liam P., Ferreira, Vinina, Muñoz-Sáez, Andrés, Oliveira-Rebouças, Patricia, da Silva, Fabiana Oliveira, Butler, Simon J. and Dicks, Lynn V. (2024) *Distinct bird communities in forests and fruit farms of Caatinga landscapes*. Ibis, 166 (3). pp. 1081-1091. ISSN 0019-1019.

# **Downloaded from**

https://kar.kent.ac.uk/108188/ The University of Kent's Academic Repository KAR

The version of record is available from

https://doi.org/10.1111/ibi.13311

This document version

Publisher pdf

**DOI** for this version

Licence for this version UNSPECIFIED

**Additional information** 

### Versions of research works

#### Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

# **Author Accepted Manuscripts**

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in *Title* of *Journal*, Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

# **Enquiries**

If you have questions about this document contact <a href="ResearchSupport@kent.ac.uk">ResearchSupport@kent.ac.uk</a>. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our <a href="Take Down policy">Take Down policy</a> (available from <a href="https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies">https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies</a>).

## **Short Communication**

international journal of avian science

# Distinct bird communities in forests and fruit farms of Caatinga landscapes

NATALIA B. ZIELONKA.\*1 EDUARDO ARELLANO, 2,3 LIAM P. CROWTHER,4 VININA FERREIRA, 5 ANDRÉS MUÑOZ-SÁEZ, 6 (D) PATRICIA OLIVEIRA-REBOUÇAS, FABIANA OLIVEIRA DA SÍLVA,8 SIMON J. BUTLER1 (D) & LYNN V. DICKS1,9 (D) <sup>1</sup>School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK <sup>2</sup>Instituto para el Desarrollo Sustentable & Facultad de Agronomía y Sistemas Naturales, Pontificia Universidad Católica de Chile, Santiago, 7830436, Chile <sup>3</sup>Center of Applied Ecology and Sustainability (CAPES), Santiago, 7820244, Chile <sup>4</sup>School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK <sup>5</sup>UNIVASF, Ūniversidade Federal do Vale do São Francisco, Petrolina, PE, 56300-990, Brazil <sup>6</sup>Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago, 8820808, Chile <sup>7</sup>Departamento de Tecnologia e Ciências Sociais, Universidade do Estado da Bahia - Campus III (UNEB), Juazeiro, 48904-711, Brazil <sup>8</sup>National Institute of Science and Technology in Interdisciplinary and Transdisciplinary Studies in Ecology and Evolution - INCT-IN-TREE, Universidade Federal de Sergipe, Nossa Senhora da Glória, 49680-000, Sergipe, Brazil <sup>9</sup>Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, UK

Agricultural expansion and intensification drive changes in bird assemblages and contribute to the homogenization of communities. By working across the semi-arid biome of the Caatinga in northeastern Brazil, this study is the first to compare the bird communities found in intensively managed fruit farms with those in remnant Caatinga forest patches. We show that fruit farm patches host 56% lower bird abundance and 61% lower

\*Corresponding author.

Email: natalia\_b\_zielonka@outlook.com

Twitter: Nat B Zielonka

Simon J. Butler and Lynn V. Dicks are joint last authors.

species richness compared with the remnant Caatinga forest fragments. Bird communities within the fruit farms were distinct from those within the forest patches, and they were characterized by species with broader niches, including two non-native species.

**Keywords:** agricultural expansion, bird assemblages, endemics, intensification, non-natives.

Agricultural landscapes occupy the largest part of the world's terrestrial surface (Foley et al. 2005), and land use change due to agricultural expansion and intensification is a major cause of biodiversity loss globally (Newbold et al. 2016, Jaureguiberry et al. 2022). Agriculture is still expanding rapidly in parts of the world, a trend that is predicted to persist over the coming decades (Godfray et al. 2010). The highest rates of agricultural expansion are predicted in the southern hemisphere, including South America (Zabel et al. 2019), and threaten many of the world's biodiversity hotspots (Molotoks et al. 2018). The responses of biodiversity to agriculture in these regions remain largely unstudied (van der Meer et al. 2020).

Intensively managed agricultural landscapes are frequently homogeneous and experience high levels of anthropogenic disturbance, so that only species able to adapt to these conditions persist (Tscharntke et al. 2012, Newbold et al. 2013, Da Silva et al. 2021). Habitat and diet generalists and migratory and short-lived species do better within human-modified habitats, at the expense of species with narrower niches (Blackburn et al. 2009, Newbold et al. 2013, Val et al. 2018, Smith et al. 2019). This can lead to homogenization of assemblages within agricultural landscapes and could result in the wider homogenization of global biodiversity under agricultural expansion and intensification scenarios et al. 2012). Retaining habitat heterogeneity across agricultural landscapes can counteract this by supporting more diverse communities (Benton et al. 2003, Martin et al. 2019, Sasaki et al. 2020). Within fragmented agricultural landscapes, edge habitats are particularly important because they harbour more biodiversity (Martin et al. 2019, Sasaki et al. 2020), and retaining high edge density has been shown to improve connectivity and promote more diverse assemblages (Boesing et al. 2018, Silva et al. 2020). This, in turn, increases the resilience of agricultural habitats to change and supports the provision of ecosystem services (Tscharntke et al. 2005, Karp et al. 2018, Redhead et al. 2020).

Human-modified and disturbed habitats facilitate the spread and establishment of non-native species, a pattern that is well documented in mammals (Doherty et al. 2016, Hradsky et al. 2017), birds (Bonter et al. 2010, Colléony & Shwartz 2020, Shivambu et al. 2020) and

1082 N. B. Zielonka et al.

plants (Taylor & Irwin 2004). Traits that predict occurrence in human-modified landscapes are common among non-native species (e.g. large body size, low level of specialism; Blackburn *et al.* 2009), and so the proportion of communities that non-native species make up increases with intensity of land-use (Sofaer *et al.* 2020). This is of conservation concern as invasive species threaten native species through competition, predation and disease spread, and can drive native populations to extinction (Bellard *et al.* 2016, Blackburn *et al.* 2019).

The Caatinga biome in Brazil is the largest semi-arid tropical forest globally and is one of the world's most biodiverse tropical drylands, harbouring over 2000 species of plants and vertebrates (Da Silva et al. 2017, de Araujo et al. 2022). The Caatinga has a rich bird assemblage of 548 species, representing almost 29% of Brazilian species, with 67 species that are endemic or nearendemic to the Caatinga (Araujo & Da Silva 2017, de Araujo et al. 2022). Endemic birds in the Caatinga have already been shown to be vulnerable to climate change (Gonçalves et al. 2023), as many are diet and habitat specialists (Araujo & Da Silva 2017, Vale et al. 2018). The Brazilian Caatinga is undergoing a faster rate of deforestation than tropical rainforests (Miles et al. 2006, Dias et al. 2016) and has experienced high levels of anthropogenic disturbance (Teixeira et al. 2021). The Caatinga is Brazil's second most degraded biome, with half of its original area already lost and only 1% of the remaining Caatinga under strict legal protection (Antongiovanni et al. 2020, Teixeira et al. 2021). Over the past three decades, much of the disturbance and land-use change has resulted from irrigated fruit farming. which is concentrated around the São Francisco River

Valley (de Espindola et al. 2021, Salazar et al. 2021, Jardim et al. 2022).

We studied the bird communities inhabiting table grape and mango farms around Petrolina, in the São Francisco River Valley. Our objectives were to provide the first description of bird communities across these fruit farms, comparing the communities inhabiting the fruit farms and nearby remnant Caatinga forest fragments. We predicted that (1) bird assemblages would be more diverse within Caatinga forest habitat patches, and (2) a higher proportion of the fruit farm communities would be made up of habitat generalists, while species with narrower niches would be limited to the Caatinga forest.

#### **METHODS**

#### Study area

We studied bird communities across 10 irrigated fruit farms (three grape and mango, seven grape-only) in northeastern Brazil (9.41° S, 40.50° W; Fig. 1). Farms were at least 5 km apart (maximum 84 km) and they varied in size of production area (mean 198.7 ha, range 13.55–520.3 ha). All farms were intensively managed for export agriculture and relied heavily on agrochemicals.

The study area is characterized by the semi-arid biome of Caatinga, which has a stable but hot climate and distinct dry (May–December) and wet (January–April, >70% annual rainfall; Jardim *et al.* 2022) seasons. The native vegetation of the Caatinga biome is a mosaic of dry arboreal and shrub forests, and open, rocky areas

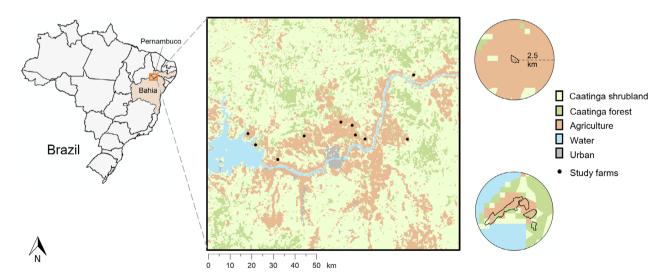


Figure 1. Study area in the states of Pernambuco and Bahia in the Caatinga, northeastern Brazil, the 10 grape and mango farms (black dots) at which bird communities were related to the landscape in the surrounding 2.5-km-radius buffer, and the most homogeneous (top) and most heterogeneous (bottom) landscapes within these buffers.

Caatinga bird communities

(Leal et al. 2005, Da Silva et al. 2017). In the dry seasons, forests and shrubs are mostly bare; green foliage is limited to the wet season (Leal et al. 2005). As a result of ongoing habitat degradation, particularly around agricultural areas, Caatinga is becoming increasingly less dense with more open areas (Ribeiro et al. 2015, Antongiovanni et al. 2020).

#### **Bird surveys**

We used 10-min point counts to survey birds during the wet season between January and March 2020. We performed surveys in two habitat types, 'Caatinga forest' and 'fruit farms', with the latter being either table grape or mango farm parcels. Depending on farm size and Caatinga availability, we conducted surveys at one to three locations per habitat type per farm, totalling 56 survey locations (n = 26 fruit farm locations across 10 farms, of which 17 were in grape and nine in mango parcels; and n = 20 Caatinga forest locations across seven farms). Survey locations were selected randomly but ensuring that all survey sites were at least 50 m from the edge of the surveyed habitat patch and any roads, at least 150 m from other survey locations within the same habitat patch (mean within a farm: 312 m; range: 152-583 m) and at least 250 m from survey locations in the other habitat patch (mean within a farm: 457 m; 257-891 m). All surveys within a farm were performed on the same day, and we surveyed each location twice during the wet season (mean: 11.8 days between surveys; range: 10-14 days). Surveys were conducted by one observer between 6:00 AM and 11:00 AM, only in fair weather conditions, and all species seen and heard within a 50-m radius were recorded, excluding birds that were flying over. We expected detectability to be broadly similar across the two habitats as both are structurally complex and detections were primarily aural.

#### **Variables**

Our sites spanned a landscape complexity gradient (Fig. 1), and we quantified landscape composition within a 2.5-km radius buffer around the central coordinates of each study farm. Within each buffer, we calculated the proportion cover by: Caatinga forest, agriculture, urban areas and water (30-m vector land cover maps; MapBiomas 2018), using ArcGIS 10.6 (ESRI 2018). We also quantified the total edge length using FRAGSTATS 4.2 (McGarigal 1995). We checked the predictors for collinearity, and found a strong, negative correlation between Caatinga cover and Agriculture cover (Spearman's  $\rho = 0.789$ , df = 9, t value = 8.756, P < 0.001), and therefore proceeded to use only Caatinga cover in analyses. We did not consider cover by water and urban

areas in our analyses because these occurred in no more than two landscapes.

We collated information on the diet, habitat associations and species' adaptability to human disturbance and habitats for the recorded bird species (see Supplementary Online Information, Table S1). First, we characterized the species by their primary diet (omnivore, insectivore, granivore, carnivore, frugivore, scavenger and nectarivore; Billerman et al. 2022). However, we only recorded one scavenger and one nectarivore species, so excluded these from the trait-based analyses. Secondly, we grouped the species based on their adaptability to anthropogenic habitats and disturbance according to Araujo and da Silva (2017). The three adaptability categories were high adaptability (species commonly present in humanmodified habitats), medium adaptability and low adaptability (species only present in intact and almost undisturbed habitats). These adaptability categories were closely related to the species' habitat use in our study: species with high and medium adaptability were exclusively open-area or generalist species, whereas all low adaptability species were Caatinga forest-dependent species. Lastly, we classified species based on their distribution, either as endemic if the species was exclusively or near-exclusively found in the Caatinga biome (Araujo & Da Silva 2017), or as non-native if the species was not native to Brazil; we classified the remaining species as other.

#### Statistical analyses

We used non-metric multidimensional scaling using Bray–Curtis dissimilarity (following Clarke *et al.* 2014) to compare bird communities between the surveyed habitat patches (mango and grape farms, and Caatinga forest). To compare bird communities between habitat patches, we used permutational analysis of variance (PERMA-NOVA) with 999 permutations (Anderson 2001). This was performed in the VEGAN package (Oksanen 2010).

We calculated total bird abundance, species richness and Shannon diversity per survey and related these to landscape and local habitat predictors in linear mixedeffect models, using the lme4 package (Bates et al. 2015). The predictors were Habitat (two levels after combining mango and grape farms to become fruit farms), Caatinga cover (proportion cover by Caatinga forest within a 2.5-km buffer), Edge density (the total length of edges within 2.5-km buffer) and the Caatinga cover\*Habitat interaction term, with survey ID nested within Farm ID fitted as a random effect. We were unable to fit species as a random effect in the abundance model because many species only occurred in a single habitat, which would result in singularity. We fitted Gaussian models with log link function for abundance and species richness, and inverse link function for Shannon diversity.

1084 N. B. Zielonka et al.

We proceeded with full models, accepting predictor significance when 95% confidence intervals of model estimates excluded zero, and P < 0.05. We inspected the distribution of residuals, dispersion and checked for influential points using the DHARMa package (Hartig 2022). All analyses were performed in R 4.2.0 (R Core Team 2021).

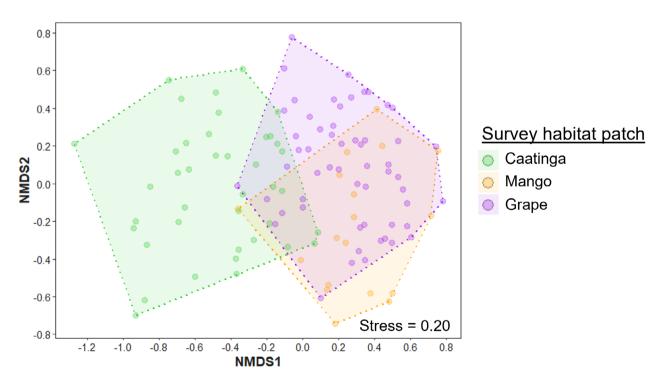
To understand which bird traits affected the likelihood of species occurrence in the surveyed fruit farm and Caatinga forest patches, we used paired t tests to compare (fruit farm versus Caatinga forest) the number of individuals of bird species belonging to each of five dietary groups, three groups defining species' adaptability to human-modified habitats and species that were either endemic or non-native to the Caatinga biome. We were unable to consider individual species because many species had low abundances and only occurred in one of the surveyed habitats. We were only able to perform these tests for seven of the 10 farms (n = 98 surveys), where we surveyed both fruit farm and Caatinga forest habitat patches.

#### **RESULTS**

Across 114 surveys, we recorded 2125 individuals of 78 species (see Supporting Online Information Table S1).

We recorded 66 species in the Caatinga forest (including 27 Caatinga forest-exclusive species; 971 individuals), 28 species in mango farms (two mango farm-exclusive species; 311 individuals) and 47 species in grape farms (six grape farm-exclusive species; 843 individuals). The six most abundant species within the fruit farm patches made up 57% of all individuals recorded within the farms, and were: Picui Ground Dove Columbina picui, White-throated Seedeater Sporophila albogularis (endemic), Blue-black Grassquit Volatinia jacarina, Redcowled Cardinal Paroaria dominicana (endemic), Common Waxbill Estrilda astrild (non-native) and House Sparrow Passer domesticus (non-native). Picui Ground Dove was also the most abundant species within Caatinga forest surveys, followed by Turkey Vulture Cathertes aura, Guira Cuckoo Guira guira, Blue-black Grassquit, Great Kiskadee Pitangus sulphuratus and Eared Dove Zenaida auriculata. Non-metric multidimensional scaling showed that bird communities in the fruit farms differed significantly from those within Caatinga patches (PERMANOVA:  $R^2 = 0.439$ , P < 0.001), but there was little difference in the bird communities between grape and mango farms (Fig. 2), so we combined the fruit farm patch surveys for subsequent analyses.

Average bird abundance (Caatinga forest:  $24.3 \pm 1.25$  se, fruit farms:  $15.6 \pm 0.57$  se), species



**Figure 2.** Non-metric multidimensional (NMDS) scaling of the abundance and composition of bird communities considering individual species across fruit farm and remnant Caatinga forest patches. Coloured points represent survey sites (n = 114) in each habitat patch, and the minimum convex polygons group these according to the survey habitat patch.

richness (Caatinga forest:  $11.3 \pm 0.36$  se, fruit farms:  $7.01 \pm 0.25$  se) and Shannon diversity (Caatinga forest:  $2.18 \pm 0.04$  se, fruit farms:  $1.77 \pm 0.04$  se) per point count were significantly higher in the Caatinga forest patches than in fruit farms (Table 1). Bird abundance and diversity were not affected by the proportion of Caatinga cover, nor by edge density in the landscape surrounding the farms (Table 1).

Omnivorous species were most common (40% of species and 61% of total abundance), and were equally likely to occur in the Caatinga forest and fruit farm habitat patches (t(6) = -0.422, P = 0.688; Fig. 3a). The abundance of insectivorous species (n = 27 species; t(6) = 5.605, P = 0.001; Fig. 3b) and frugivorous species (n = 5 species; t(6) = 3.07, t = 0.022; Fig. 3c) was significantly higher in the Caatinga forest than in the fruit farm patches. The abundance of granivorous species (t = 4; t(6) = -1.245, t = 0.259) and carnivorous species (t = 6; t = 0.281, t = 0.788) did not differ between the surveyed habitat patches (Fig. 3d and 3e).

Most of the recorded species (58/78) were classified as having high adaptability to human-modified habitats and accounted for 74% of the total recorded individuals (897 individuals in Caatinga forest and 1128 in fruit farms). Of the other 20 species, 10 were classed as medium adaptability (53 individuals in Caatinga forest, 22 individuals in fruit farms), and 10 were low adaptability (21 individuals in Caatinga forest, 4 individuals in fruit farms). Species of medium (t(6) = 4.032, P = 0.007) and

low adaptability (t(6) = 2.714, P = 0.035) were significantly more abundant within the Caatinga forest patches than in the fruit farms, but the abundance of high-adaptability species did not differ between the habitats (t(6) = -0.181, P = 0.863, Fig. 3f-h).

In total, we recorded 10 endemic (see Supporting Online Information Table S1) and two non-native species in the Caatinga biome. All 10 endemic species were recorded in the Caatinga forest but only six within the fruit farms, though the abundance of endemic species did not vary significantly between the habitat patches (t (6) = -1.002, P = 0.355, Fig. 3i). The two non-native species were Common Waxbill (80 individuals, of which 77 were in fruit farms) and House Sparrow (53 sightings, and only recorded in fruit farms), and the number of individuals of non-native species was significantly higher in fruit farms (130/133, 98%) than Caatinga forest patches (t(6) = -4.785, P = 0.003, Fig. 3j).

#### **DISCUSSION**

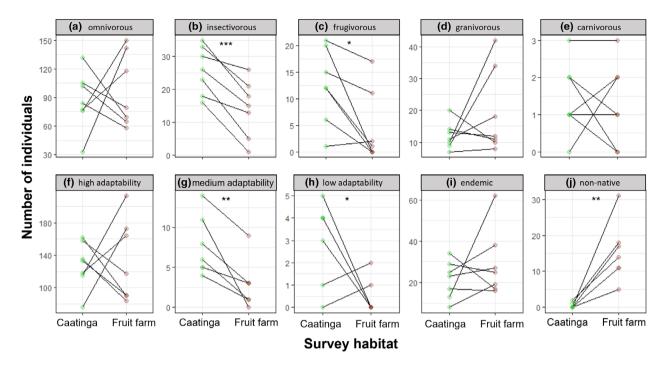
Our study shows that fruit farming in the semi-arid Caatinga biome of northeastern Brazil has a strong effect on native bird communities. Overall, bird abundance, species richness and Shannon diversity within fruit farm patches were significantly lower compared with adjacent patches of remnant Caatinga forest, with a third of all species being only recorded within the forest patches. Fruit farms hosted fewer birds and less diverse

**Table 1.** Model outputs from general linear mixed models testing the effects of survey habitat, proportion of Caatinga cover and edge density in a 2.5-km buffer around study fruit farms on bird abundance, raw species richness and Shannon diversity (n = 114 surveys).

Variable	Estimate (95% CI)	t value	P value	$R^2$	AIC
Abundance					
Intercept (Caatinga forest)	2.061 (-4.759; 8.880)	0.592	0.555	0.316	81.85
Fruit farm	-0.431 (-0.786; -0.076)	-2.374	0.019		
Caatinga cover	0.003 (-0.004; 0.010)	0.903	0.368		
Edge density	0.141 (-0.877; 1.158)	0.271	0.787		
Habitat patch * Caatinga cover	0.0002 (-0.008; 0.008)	0.052	0.959		
Species richness					
Intercept (Caatinga forest)	4.537 (-0.273; 9.198)	1.887	0.062	0.484	145.25
Fruit farm	$-0.440 \; (-0.679; \; -0.198)$	-3.528	< 0.001		
Caatinga cover	0.002 (-0.002; 0.006)	1.042	0.300		
Edge density	-0.327 (-1.025; 0.391)	-0.91	0.365		
Habitat patch * Caatinga cover	-0.0006 (-0.006; 0.005)	-0.203	0.840		
Shannon diversity					
Intercept (Caatinga forest)	4.356 (-1.682; 1.355)	1.383	0.170	0.303	59.187
Fruit farm	-0.456 (0.042; 0.196)	-2.779	0.006		
Caatinga cover	0.0003 (-0.001; 0.001)	0.092	0.927		
Edge density	-0.325 (-0.133; 0.320)	-0.692	0.491		
Habitat patch * Caatinga cover	0.002 (-0.002; 0.001)	0.425	0.672		

Survey ID (n = 57) nested in Farm ID (n = 10) was fitted as a random effect. The model estimates with 95% confidence intervals (CI), t value, P value and model Akaike Information Criterion (AIC) and  $R^2$  values are reported.

1086 N. B. Zielonka et al.



**Figure 3.** Number of individuals of bird species belonging to one of the five dietary groups (a–e), the three groups defining species' adaptability to human-modified habitats (f–h) and species that are endemic to the Caatinga biome (i) or non-native to Brazil (j), recorded in Caatinga forest (n = 40) and fruit farm (n = 58) habitat patches across seven study farms. Significant differences, as tested by paired t tests, are indicated by asterisks: \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.

communities, and were characterized by bird assemblages composed of species with broader niches, including two non-native species.

Habitat type was the strongest driver of bird community structure, with Caatinga forest and fruit farm patches harbouring distinct assemblages. responses to agricultural expansion depend on their traits, such as the level of specialization and dispersal ability (Tscharntke et al. 2012, Newbold et al. 2013, Da Silva et al. 2021) and, in our system, the occurrence of insectivorous and frugivorous species was significantly lower within the fruit farms. A lower abundance of insectivores within farms has been observed in other tropical systems (Sekercioglu 2012), and may be linked to the use of agrochemicals within farms, which probably decreases prey availability. However, the reduction in frugivorous species within fruit farms was unexpected, particularly as farmers frequently report birds feeding on grapes (Herrmann & Anderson 2016, Peisley et al. 2017). Fruit damage caused by birds is often highest at field edges neighbouring native habitats (Peisley et al. 2017, Olimpi et al. 2020), which we did not survey, and we hypothesize that the density of frugivorous species may be higher there, particularly in fields with ripe fruits. We also only surveyed bird communities in the wet season, when there was increased abundance of fruit within the Caatinga forest, and we hypothesize that the abundance of frugivorous species within farms may increase during the dry season when alternative resources are scarcer.

Across our study landscapes, 87% of the species were habitat generalists or open-habitat species, and predominantly omnivorous; five species with these traits made up over half of all bird sightings within the fruit farms, and therefore may have had a strong influence on our findings for overall abundance. This aligns with findings from guava farms in the Caatinga biome, where omnivorous and disturbance-resistant species were most abundant (Da Silva et al. 2021). In our study, species characterized by these traits included two species that are non-native to Brazil: Common Waxbill and House Sparrow. These species occurred predominantly within the fruit farms, the House Sparrow exclusively so, which supports the well-established pattern that human-modified habitats support invasions and the persistence of non-native species (Pyšek et al. 2010, Smith et al. 2019, Colléony & Shwartz 2020, Shivambu et al. 2020). These species may be having a negative impact on native species by restricting their access to resources and breeding areas (Peck et al. 2014, Le Louarn et al. 2016), though as they seem limited to the fruit farm patches, their impact may be less than observed elsewhere (Blackburn et al. 2019).

Population declines resulting from agriculture are often more pronounced among endemic species (Newbold et al. 2013, Smith et al. 2019), though we found mixed patterns across the studied fruit farms. In line with previous literature (Newbold et al. 2013) and our prediction, we found that seven out of the 10 endemic species had specialized diets and these species were exclusively recorded in the Caatinga forest. However, two endemics, the White-throated Seedeater and Redcowled Cardinal, were more abundant in fruit farms than in forest patches. These species use open habitats, and have been observed to forage and breed within guava fruit farms in the Caatinga biome (Da Silva et al. 2021), so they are likely to persist, if not increase in abundance, under agricultural expansion in the region.

Contrary to expectations, Caatinga cover and edge density in the wider landscape did not affect bird abundance and diversity. The importance of semi-natural habitat cover and high edge density for maintaining biodiversity has been well documented within agricultural landscapes (Carrara et al. 2015), including in similar biogeographical regions (Boesing et al. 2017, Muñoz-Sáez et al. 2017, Adorno et al. 2021, Estupiñan-Mojica et al. 2022). Landscape heterogeneity and edge density support species dispersal and spill-over through decreased isolation of habitat patches (Silva et al. 2020, Boesing et al. 2021). Nonetheless, in high-contrast landscapes, limited spill-over across habitats has been noted (Boesing et al. 2021, Alvarez-Alvarez et al. 2022). Our study area is characterized by such high contrast of habitats because the Caatinga forest is seasonally dry and structurally complex, whereas the fruit farms are irrigated, planted in straight rows and experience high levels of disturbance. Furthermore, the area has experienced prolonged disturbance (da Silva et al. 2018) so assemblages may be filtered, with species that are more resilient to human disturbance and less reliant on the native vegetation persisting (Filgueiras et al. 2021).

#### CONCLUSION

Our study has documented the effects of fruit farming on bird assemblages in the highly diverse Caatinga biome, and our findings suggest that continuing agricultural expansion and intensification may result in the homogenization of avian communities. As observed in other regions (Newbold et al. 2013, Smith et al. 2019, Boesing et al. 2021), and within the Caatinga (Da Silva et al. 2021), intensively managed fruit farms harbour more generalist species that are able to adapt to human-modified habitats. The resulting species loss is detrimental to biodiversity more widely, but can also be disadvantageous to production, as some bird species, such as insectivores, can deliver important ecosystem services

including pest control (Barbaro *et al.* 2017, Boesing *et al.* 2017, Martin *et al.* 2019). This calls for conservation measures to be incorporated within farming, which can include retaining Caatinga forest fragments and patches of trees within the farms, to act as stepping stones, and to increase connectivity (Silva *et al.* 2020, Salazar *et al.* 2021). Caatinga harbours diverse communities of endemic species, many of which are habitat specialists and sensitive to habitat loss (Antongiovanni *et al.* 2020, Salazar *et al.* 2021, Estupiñan-Mojica *et al.* 2022), and we argue that increasing the amount of Caatinga that is under strict legal protection in areas that have not experienced past disturbance is crucial to addressing the wider decline of biodiversity across the biome.

We thank our study farms and farm managers for access to field sites and support with in-field logistics. We thank Gilson Amorim and Danilo Soares De Souza for their assistance with fieldwork. We thank Professor Zhijun Ma and an anonymous reviewer for their comments on the manuscript. N.B.Z. was supported by UKRI Biotechnology and the Biological Sciences Research Council Norwich Research Park Biosciences Doctoral Training Partnership [Grant number BB/M011216/1], and other co-authors were funded through the Nexus project initiative from the Newton Fund/BBSRC (BB/R016429/1) and ANID project NEXUS (BB/R0164291), and the Center of Applied Ecology and Sustainability (CAPES) (PIA/BASAL FB0002).

#### **AUTHOR CONTRIBUTIONS**

Natalia B. Zielonka: Conceptualization; methodology; formal analysis; investigation; data curation; writing – original draft; writing – review and editing; visualization. Eduardo Arellano: Writing – review and editing; project administration; resources. Liam P. Crowther: Methodology; writing – review and editing. Vinina Ferreira: Resources; writing – review and editing. Andrés Muñoz-Sáez: Methodology; writing – review and editing; investigation. Patricia Oliveira-Rebouças: Resources; writing – review and editing. Fabiana Oliveira da Silva: Resources; writing – review and editing; investigation. Simon J. Butler: Conceptualization; methodology; supervision; writing – review and editing; formal analysis. Lynn V. Dicks: Conceptualization; methodology; supervision; writing – review and editing; funding acquisition; project administration.

#### **FUNDING**

Biotechnology and Biological Sciences Research Council.

#### **ETHICS STATEMENT**

None.

#### CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

#### **Data Availability Statement**

Species-level data used in this study are available in Supporting Online Information Table S1 and more detailed data can be obtained from the corresponding author upon reasonable request.

#### REFERENCES

- Adorno, B.F.C.B., Barros, F.M., Cezar Ribeiro, M., da Silva, V.X. & Hasui, É. 2021. Landscape heterogeneity shapes bird phylogenetic responses at forest-matrix interfaces in Atlantic Forest, Brazil. *Biotropica* **53**: 409–421.
- Alvarez-Alvarez, E.A., Almazán-Núñez, R.C., Corcuera, P., González-García, F., Brito-Millán, M. & Alvarado-Castro, V.M. 2022. Land use cover changes the bird distribution and functional groups at the local and landscape level in a Mexican shaded-coffee agroforestry system. Agric. Ecosyst. Environ. 330: 107882.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26: 32–46.
- Antongiovanni, M., Venticinque, E.M., Matsumoto, M. & Fonseca, C.R. 2020. Chronic anthropogenic disturbance on Caatinga dry forest fragments. J. Appl. Ecol. 57: 2064–2074.
- Araujo, H. & da Silva, J.M. 2017. The avifauna of the Caatinga: biogeography, ecology, and conservation. In da Silva, J.M.C., Leal, I.R. & Tabarelli, M. (eds) Caatinga: The Largest Tropical Dry Forest Region in South America: 181– 210. Cham: Springer Nature.
- de Araujo, H.F.P., Garda, A.A., de Girão e Silva, W.A., do Nascimento, N.F.F., Mariano, E.F. & da Silva, J.M.C. 2022. The Caatinga region is a system and not an aggregate. *J. Arid Environ.* 203: 104778.
- Barbaro, L., Rusch, A., Muiruri, E.W., Gravellier, B., Thiery, D. & Castagneyrol, B. 2017. Avian pest control in vineyards is driven by interactions between bird functional diversity and landscape heterogeneity. J. Appl. Ecol. 54: 500–508.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using Ime4. *J. Stat. Softw.* 67: 1–48
- Bellard, C., Cassey, P. & Blackburn, T.M. 2016. Alien species as a driver of recent extinctions. *Biol. Lett.* 12: 20150623.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18: 182–188.
- Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. 2022. *Birds of the World.* Ithaca, NY: Cornell Laboratory of Ornithology.
- Blackburn, T.M., Cassey, P. & Lockwood, J.L. 2009. The role of species traits in the establishment success of exotic birds. *Glob. Chang. Biol.* **15**: 2852–2860.
- **Blackburn, T.M., Bellard, C. & Ricciardi, A.** 2019. Alien versus native species as drivers of recent extinctions. *Front. Ecol. Environ.* **17**: 203–207.

- Boesing, A.L., Nichols, E. & Metzger, J.P. 2017. Effects of landscape structure on avian-mediated insect pest control services; a review. *Landsc. Ecol.* 32: 931–944.
- Boesing, A.L., Nichols, E. & Metzger, J.P. 2018. Land use type, forest cover and forest edges modulate avian crosshabitat spillover. *J. Appl. Ecol.* **55**: 1252–1264.
- Boesing, A.L., Marques, T.S., Martinelli, L.A., Nichols, E., Siqueira, P.R., Beier, C., de Camargo, P.B. & Metzger, J.P. 2021. Conservation implications of a limited avian cross-habitat spillover in pasture lands. *Biol. Conserv.* 253: 108898.
- Bonter, D.N., Zuckerberg, B. & Dickinson, J.L. 2010. Invasive birds in a novel landscape: habitat associations and effects on established species. *Ecography* **33**: 494–502.
- Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M. & Fahrig, L. 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biol. Conserv.* 184: 117–126.
- Clarke, K.R., Gorley, R.N., Somerfield, P.J. & Warwick, R.M. 2014. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 3rd edn. Plymouth: Primer-E Ltd.
- Colléony, A. & Shwartz, A. 2020. When the winners are the losers: invasive alien bird species outcompete the native winners in the biotic homogenization process. *Biol. Conserv.* 241: 108314.
- Da Silva, C., Ruiz-Esparza, J., da Silva, F.O., de Azevedo, C.S. & Ribeiro, A.S. 2021. Can guava monocultures (*Psidium guajava* L.) function as refuge for bird conservation? *Neotrop. Biol. Conserv.* 16: 475–491.
- Dias, L.C.P., Pimenta, F.M., Santos, A.B., Costa, M.H. & Ladle, R.J. 2016. Patterns of land use, extensification, and intensification of Brazilian agriculture. *Glob. Chang. Biol.* 22: 2887–2903.
- Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G. & Dickman, C.R. 2016. Invasive predators and global biodiversity loss. *Proc. Natl Acad. Sci. USA* 113: 11261–11265.
- de Espindola, G.M., de Silva Figueredo, E., Picanço Júnior, P. & dos Reis Filho, A.A. 2021. Cropland expansion as a driver of land-use change: the case of Cerrado-Caatinga transition zone in Brazil. *Environ. Dev. Sustain.* 23: 17146–17160.
- **ESRI** 2018. *ArcGIS*. Redlands, CA: Environmental Systems Research Institute.
- Estupiñan-Mojica, A., Portela-Salomão, R., Liberal, C.N., Santos, B.A., Machado, C.C.C., de Araujo, H.F.P., Von Thaden, J. & Alvarado, F. 2022. Landscape attributes shape dung beetle diversity at multiple spatial scales in agricultural drylands. *Basic Appl. Ecol.* 63: 139–151.
- Filgueiras, B.K.C., Peres, C.A., Melo, F.P.L., Leal, I.R. & Tabarelli, M. 2021. Winner-loser species replacements in human-modified landscapes. *Trends Ecol. Evol.* 36: 545–555.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. 2005. Global consequences of land use. *Science* 309: 570–574.

- Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M. & Toulmin, C. 2010. Food security: the challenge of feeding 9 billion people. Science 327: 812–818.
- Gonçalves, G.S.R., Cerqueira, P.V., Silva, D.P., Gomes, L.B., Leão, C.F., Andrade, A.F.A.d. & Santos, M.P.D. 2023. Multi-temporal ecological niche modeling for bird conservation in the face of climate change scenarios in Caatinga, Brazil. *PeerJ* 11: e14882.
- Hartig, F. 2022. DHARMa: Residual diagnostics for hierarchical (Multi-level/Mixed) regression models. R package version 0.4.5.
- Herrmann, E. & Anderson, M.D. 2016. Foraging behaviour of damage-causing birds in table grape vineyards in the Orange River valley, South Africa. South African J. Enol. Vitic. 28, (2007): 150–154. Available at: https://doi.org/10.21548/28-2-1468
- Hradsky, B.A., Robley, A., Alexander, R., Ritchie, E.G., York, A. & Di Stefano, J. 2017. Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes. Sci. Rep.* **7**: 12291.
- Jardim, A.M.R.F., Araújo Júnior, G.N., da Silva, M.V., dos Santos, A., da Silva, J.L.B., Pandorfi, H., de Oliveira-Júnior, J.F., Teixeira, A.H.C., de Teodoro, P.E., Lima, J.L.M.P., da Silva Junior, C.A., de Souza, L.S.B., Silva, E.A. & da Silva, T.G.F. 2022. Using remote sensing to quantify the joint effects of climate and land use/land cover changes on the Caatinga biome of northeast Brazilian. *Remote Sens.* 14: 1911.
- Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z. & Purvis, A. 2022. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. 8: eabm9982.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tscharntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Ćetković, A., Henri, D.C., Chabert, A., Costamagna, A.C., de la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseth, A.S., Inclán, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, Molina-Montenegro, M.A., O'Neal, Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö.,

- Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plećaš, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A. & Zou, Y. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc. Natl Acad. Sci. USA 115: E7863-E7870.
- Le Louarn, M., Couillens, B., Deschamps-Cottin, M. & Clergeau, P. 2016. Interference competition between an invasive parakeet and native bird species at feeding sites. *J. Ethol.* 34: 291–298.
- Leal, I.R., da Silva, J.M.C., Tabarelli, M. & Lacher, T.E. Jr. 2005. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. *Conserv. Biol.* 19: 701–706.
- MapBiomas. 2018. Project MapBiomas Collection v.4.1 of Brazilian Land Cover & Use Map Series. Available at: https://mapbiomas.org (accessed March 2020).
- Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Hassan, D.A., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M.V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Féon, V.L., Marshall, J., Moonen, A.-C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M. & Steffan-Dewenter, I. 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22: 1083-1094.
- McGarigal, K. 1995. FRAGSTATS: Spatial Pattern Analysis
  Program for Quantifying Landscape Structure. Portland, OR:
  U.S. Department of Agriculture, Forest Service, Pacific
  Northwest Research Station.
- van der Meer, M., Kay, S., Lüscher, G. & Jeanneret, P. 2020. What evidence exists on the impact of agricultural practices in fruit orchards on biodiversity? A systematic map. *Environ. Evid.* 9: 2.
- Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V. & Gordon, J.E. 2006. A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* 33: 491–505.
- Molotoks, A., Stehfest, E., Doelman, J., Albanito, F., Fitton, N., Dawson, T.P. & Smith, P. 2018. Global projections of

- future cropland expansion to 2050 and direct impacts on biodiversity and carbon storage. *Glob. Chang. Biol.* **24**: 5895–5908.
- Muñoz-Sáez, A., Perez-Quezada, J.F. & Estades, C.F. 2017.
  Agricultural landscapes as habitat for birds in central Chile.
  Rev. Chil. Hist. Nat. 90: 3.
- Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioğlu, C.H., Alkemade, R., Booth, H. & Purves, D.W. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B* 280: 20122131.
- Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., de Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W. & Purvis, A. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353: 288–291.
- Oksanen, J. 2010. Vegan: community ecology package. Available at: http://vegan.r-forge.r-project.org/Available at: https://cir.nii.ac.jp/crid/1570291225091856896 (accessed November 2020).
- Olimpi, E.M., Garcia, K., Gonthier, D.J., De Master, K.T., Echeverri, A., Kremen, C., Sciligo, A.R., Snyder, W.E., Wilson-Rankin, E.E. & Karp, D.S. 2020. Shifts in species interactions and farming contexts mediate net effects of birds in agroecosystems. *Ecol. Appl.* 30: e02115.
- Peck, H.L., Pringle, H.E., Marshall, H.H., Owens, I.P.F. & Lord, A.M. 2014. Experimental evidence of impacts of an invasive parakeet on foraging behavior of native birds. Behav. Ecol. 25: 582–590.
- Peisley, R.K., Saunders, M.E. & Luck, G.W. 2017. Providing perches for predatory and aggressive birds appears to reduce the negative impact of frugivorous birds in vineyards. *Wildl. Res.* 44: 9.
- Pereira, H.M., Navarro, L.M. & Martins, I.S. 2012. Global biodiversity change: the bad, the good, and the unknown. *Annu. Rev. Environ. Resour.* 37: 25–50.
- Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., Gassó, N., Kenis, M., Lambdon, P.W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M. & Hulme, P.E. 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Glob. Ecol. Biogeogr.* 19: 317–331.
- R Core Team. 2021. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/
- Redhead, J.W., Oliver, T.H., Woodcock, B.A. & Pywell, R.F. 2020. The influence of landscape composition and configuration on crop yield resilience. J. Appl. Ecol. 57: 2180–2190.
- Ribeiro, E.M.S., Arroyo-Rodríguez, V., Santos, B.A., Tabarelli, M. & Leal, I.R. 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *J. Appl. Ecol.* **52**: 611–620.
- Salazar, A.A., Arellano, E.C., Muñoz-Sáez, A., Miranda, M.D.,
   Oliveira da Silva, F., Zielonka, N.B., Crowther, L.P., Silva-Ferreira, V., Oliveira-Reboucas, P. & Dicks, L.V. 2021.
   Restoration and conservation of priority areas of Caatinga's

- semi-arid Forest remnants can support connectivity within an agricultural landscape. *Landarzt* **10**: 550.
- Sasaki, K., Hotes, S., Kadoya, T., Yoshioka, A. & Wolters, V. 2020. Landscape associations of farmland bird diversity in Germany and Japan. *Glob. Ecol. Conserv.* 21: e00891.
- Sekercioglu, C.H. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.* **153**: 153–161.
- Shivambu, T.C., Shivambu, N. & Downs, C.T. 2020. Impact assessment of seven alien invasive bird species already introduced to South Africa. *Biol. Invasions* 22: 1829–1847.
- da Silva, J.M., Leal, I. & Tabarelli, M. 2017. Caatinga: The Largest Tropical Dry Forest Region in South America. Cham: Springer Nature.
- da Silva, J.M.C., de Souza, M.A., Ribeiro, V. & Machado, R.B. 2018. Niche expansion of the common waxbill (*Estrilda astrild*) in its non-native range in Brazil. *Biol. Invasions* 20: 2635–2646.
- Silva, C.M., Pereira, J.A.C., Gusmões, J.D.S.P., Mendes, B.E.P., Valente, H., Morgan, A.P., Goulart, D. & Hasui, É. 2020. Birds' gap-crossing in open matrices depends on landscape structure, tree size, and predation risk. *Perspect. Ecol. Conserv.* 18: 73–82.
- Smith, O.M., Kennedy, C.M., Owen, J.P., Northfield, T.D., Latimer, C.E. & Snyder, W.E. 2019. Highly diversified crop-livestock farming systems reshape wild bird communities. *Ecol. Appl.* 30: e02031.
- Sofaer, H.R., Flather, C.H., Jarnevich, C.S., Davis, K.P. & Pejchar, L. 2020. Human-associated species dominate passerine communities across the United States. *Glob. Ecol. Biogeogr.* **29**: 885–895.
- Taylor, B.W. & Irwin, R.E. 2004. Linking economic activities to the distribution of exotic plants. *Proc. Natl Acad. Sci. USA* 101: 17725–17730.
- Teixeira, L.P., Lughadha, E.N., Silva, M.V.C.d. & Moro, M.F. 2021. How much of the Caatinga is legally protected? An analysis of temporal and geographical coverage of protected areas in the Brazilian semiarid region. *Acta Bot. Bras.* 35: 473–485.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity Ecosystem service management. *Ecol. Lett.* 8: 857–874.
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151: 53–59.
- Val, J., Eldridge, D.J., Travers, S.K. & Oliver, I. 2018. Livestock grazing reinforces the competitive exclusion of small-bodied birds by large aggressive birds. *J. Appl. Ecol.* 55: 1919–1929.
- Vale, M.M., Tourinho, L., Lorini, M.L., Rajão, H. & Figueiredo, M.S.L. 2018. Endemic birds of the Atlantic Forest: traits, conservation status, and patterns of biodiversity. J. Field Ornithol. 89: 193–206.
- Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W. & Václavík, T. 2019. Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. Nat. Commun. 10: 2844.

Caatinga bird communities

Received 20 October 2023; Revision 8 January 2024; revision accepted 17 January 2024. Associate Editor: Zhijun Ma.

#### **SUPPORTING INFORMATION**

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

Table S1. List of bird species recorded across fruit farm and Caatinga forest patches in north eastern Brazil. For each species, the number of individuals recorded per habitat patch is given, along with the species' diet, habitat association, adaptive ability and conservation status in the Caatinga (see main text for details).