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Bird diversity in the forests and coconut farms of Sulawesi, Indonesia

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Abstract Coconut farming contributes to the livelihoods of millions of people in tropical countries but is less frequently considered as a threat to biodiversity compared to other palm commodities such as oil palm. The expansion of coconut farming alongside other smallholder agriculture in Sulawesi, Indonesia, is of potential concern as the region is a centre of species endemism. We studied bird diversity and community structure in forests, coconut palm plantations and mixed farmland in Gorontalo Province, northern Sulawesi. Forest and non-forest sites supported similar numbers of species overall, but compared to agricultural areas, forest sites had communities that were more diverse and more even (i.e. different species were present at similar abundances). We found far fewer endemic species in agricultural areas compared to forests, and the communities in palm plantations and mixed farmland sites were dominated by generalist birds, with few indicator taxa. Nevertheless, there was a higher number of endemic species in coconut palm plantations than in mixed farmland sites. These findings mirror patterns of biotic homogenization documented elsewhere in the Wallacea centre of endemism, and imply that coconut palm plantations have comparable biodiversity value to other farmland systems. Increased protection of lowland forests and improved management of coconut farms could be important for supporting the conservation of the endemic birds of Sulawesi in the long term, but this warrants further study.

Keywords Avian biodiversity, birds, coconut palm, deforestation, Southeast Asia, Sulawesi, tropical forest, Wallacea

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Introduction

Tropical forests continue to be cleared for agriculture, resulting in high levels of biodiversity loss (Edwards et al., 2019; Oakley & Bicknell, 2022). For example, more than 68 million ha of forest were converted during 2001–2015 to produce cattle, oil palm, soy, cocoa and coffee (Goldman et al., 2020). Public attention has focused on the land-use impacts of major agricultural commodities such as palm oil, but little attention has been paid to other oil crops such as coconut *Cocos nucifera* (Meijaard et al., 2020).

Coconut is a perennial crop that contributes to the livelihoods of millions of people in tropical and subtropical countries, with the leading producers being Indonesia, the Philippines and India (FAOSTAT, 2020). Although the crop is generally grown at the smallholder scale, the cumulative area of coconut farming is large, amounting to > 12.3 million ha (FAOSTAT, 2020). A preliminary study based on global databases identified coconut as a crop with potentially significant impacts on wildlife because coconut palms are mainly grown on tropical islands and/or in coastal areas with high levels of species diversity and endemism (Meijaard et al., 2020). Although the potential impacts of coconut farming are concerning, there are few biodiversity appraisals that compare the conservation value of coconut palm plantations to forests or other land uses (Henson, 2005; Basheer & Aarif, 2013; Dinanti et al., 2018).

Coconut plantations cover > 3.4 million ha across Indonesia (c. 6% of non-forested land), making it the third largest agricultural commodity in the country in terms of area covered (after oil palm *Elaeis guineensis* and rubber *Hevea brasiliensis* at 14.3 and 3.6 million ha, respectively; Badan Pusat Statistik, 2022). Almost one-third of the area under cultivation is in the Wallacea region, a major centre of species endemism comprising the islands of Sulawesi, Nusa Tenggara and Maluku (Struebig et al., 2022). Sulawesi in particular has a long history of coconut cultivation. By 2021, at least 763,135 ha of coconut farms were estimated to have been planted on the island (c. 8% of

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non-forested land), primarily by smallholders. Although deforestation rates have been much lower on Sulawesi than in other parts of Indonesia, there has been a surge in deforestation in recent years associated with the expansion of farming and mining (Voigt et al., 2021). This deforestation is leading to the gradual loss of specialized and endemic wildlife species and their replacement by widely distributed generalists, as demonstrated by bird surveys across the Wallacea region (Mitchell et al., 2022). Nevertheless, the conservation value of the agricultural matrix surrounding the forests of Wallacea remains poorly documented for oil crops such as coconut.

Areas of open, unshaded and/or homogeneous croplands tend to have impoverished wildlife communities and low biodiversity (Oakley & Bicknell, 2022). Similarly to other palms, the planting of coconut changes the floristic, structural and soil characteristics of the habitat available to wildlife (Young et al., 2010), leaving an open understorey and fewer opportunities for feeding and shelter (Dinanti et al., 2018). However, because coconuts are generally grown by smallholders in small plantations and gardens, the effects of this cultivation on biodiversity could be relatively benign compared to those of other crops that are grown at an industrial scale. For example, bird diversity is significantly lower in rubber plantations than in rubber agroforestry and forests in Sumatra (Beukema et al., 2007), and in Kalimantan, indicator species associated with forests and mixed gardens were absent from nearby oil palm plantations (Simamora et al., 2021). Multiple studies have demonstrated that oil palm plantations support much lower levels of species diversity and abundance, even if forests are nearby (Aratrakorn et al., 2006; Fitzherbert et al., 2008; Edwards et al., 2010).

Here we explore the conservation value of coconut palm plantations relative to forests and other farmland in Sulawesi. Specifically, we characterize patterns of biodiversity and community structure amongst forest sites, coconut palm plantations and mixed farmland, using birds as a focal taxon. Birds are useful indicators of anthropogenic disturbance as they can be surveyed relatively easily and tend to be sensitive to landscape changes (Schulze et al., 2004; Gardner et al., 2008; Winarni & Jones, 2012). In Sulawesi, forest conversion to cacao agroforests has negatively affected endemic forest birds (Maas et al., 2009), and forest disturbance is an important predictor of occupancy of knobbed hornbills *Rhyticeros cassidix* (Winarni & Jones, 2012). We undertook standardized bird surveys in forests and farmland in the province of Gorontalo and compared species diversity and community structure between landscapes and habitats.

Study area

Gorontalo is located on the Minahasa peninsula of Sulawesi, and is one of the most forested provinces on the island,

with more than 856,000 ha of forest cover (c. 71% of the province) from the coastal lowlands up to an altitude of 2,211 m (Potapov et al., 2022). Key forest trees include rao *Dracontomelon dao*, nantu *Palaquium obovatum* and pangi *Pangium edule* (Macdonald et al., 2011; Rahim, 2015), and these habitats support populations of iconic endemic vertebrates such as the knobbed hornbill, maleo *Macrocephalon maleo*, lowland anoa *Bubalus depressicornis* and Sulawesi babirusa *Babyrousa celebensis*. Although deforestation rates have been lower in Gorontalo than in other parts of Sulawesi, the province is projected to lose 32% of forest cover by the 2050s (Voigt et al., 2021) because of encroachment from small-scale agriculture, namely from coconut, corn and oil palms. Approximately 9% of the province is used to cultivate coconut (Badan Pusat Statistik, 2022). Similarly to other parts of Sulawesi, the landscape is highly heterogeneous because of multiple crops being grown in the region (often in smallholder systems).

Methods

Bird surveys

We undertook bird surveys across forests and farmlands in three landscapes of Gorontalo: Nantu-Tamilo (around Saritani village), Hutamono-Tapaada (Rumbia and Dulangeya) and Bogani-Tinemba (around Lombongo and Tinemba; Fig. 1, Supplementary Table 1). The forest sites included two protected areas: Bogani Nani Wartabone National Park and Nantu Wildlife Reserve. The agricultural areas were dominated by coconut farms, corn fields and mixed farmland, with some smaller areas of oil palm plantations.

We surveyed birds during October–November 2021 by conducting 10-min point counts during periods of peak bird activity (05.40–09.30) in clear weather. On each survey morning, a pair of observers (KY and ZZ/MAWG, or BI and BGA) surveyed a transect of nine points, which were arranged in three clusters of three points each. A distance of c. 1 km separated neighbouring clusters, and the points within a cluster were at least 200 m apart (the recommended distance for avian point counts to ensure spatial independence; Lees & Peres, 2009; Supplementary Fig. 1). We surveyed six transects (two in each landscape), totalling 54 independent points, with four repeat visits to each point conducted on different days. Points were distributed across the three habitat types: forest (16 point count locations), palm (18 coconut farms, with one site also dominated by sugar palm *Arenga pinnata*) and mixed farmland (20 locations; Supplementary Table 1). We sought to survey multiple habitats within each transect (ideally oil palm, coconut palm plantations and mixed farmland in a single morning) and switched the order in which we sampled these points on repeat visits. We defined the configuration

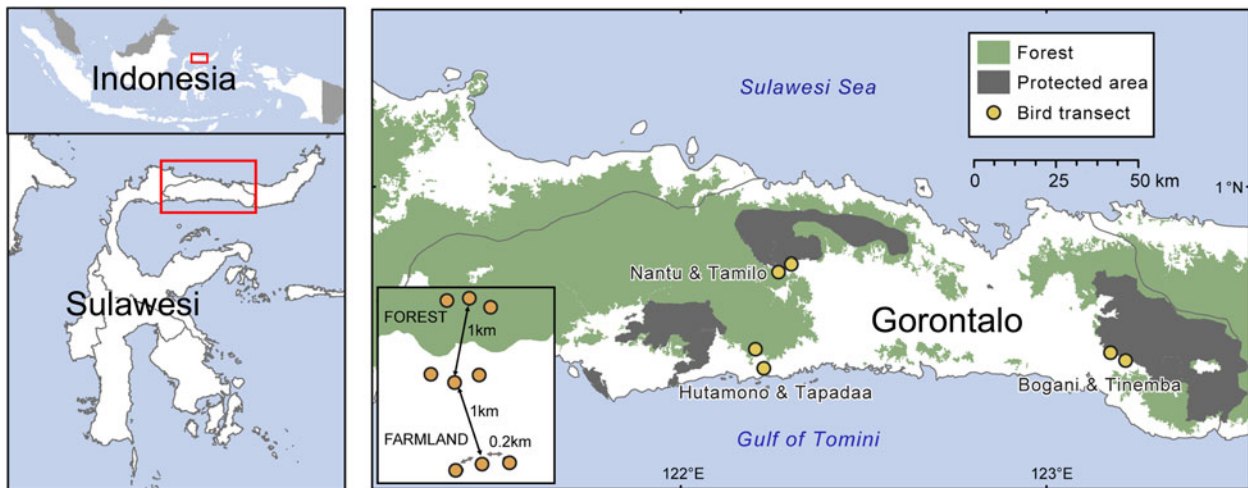


Fig. 1 Study sites in Gorontalo Province, Sulawesi, Indonesia. An overview of the spatial configuration of point count locations within each survey transect is shown in the inset.

in advance of the survey using *Google Earth* imagery (Google, Mountain View, USA) to avoid location bias in the field.

For each point count, observers recorded the number and identity of individual birds that were identified based on their vocalizations or direct observations. We made audio recordings of most counts, and a second observer verified these (using recordings shared on *xeno-canto* if needed; Xeno-canto Foundation, 2021) at a later date. We included birds observed in flight in these counts. We followed the taxonomy used by Eaton et al. (2016) and BirdLife International (2023) and classified species as endemic based on available checklists (Lepage & Warnier, 2014).

Analysis

To compare species accumulation between landscapes and habitats, we constructed sample-based rarefaction curves based on the point count data using the package *iNEXT* in R 3.5.2 (Hsieh et al., 2016; R Core Team, 2019). The rarefaction analyses used the Hill number framework to generate three measures of diversity: species richness (i.e. effective species numbers), Shannon index (i.e. the exponent of Shannon entropy, with high values representing a high level of uncertainty in species identity and thus high diversity) and Simpson index (i.e. the inverse of the Simpson concentration, with high values indicating greater evenness in the species abundance distribution and thus high diversity; Magurran, 2004). We extrapolated bird detections to a common upper sample size of 1,000 individuals for standardized comparisons, and we generated 84% confidence intervals for the curves. Comparisons of the curves are deemed statistically significant when these confidence intervals do not overlap, which is equivalent to a P-value of 0.05 (MacGregor-Fors & Payton, 2013).

We used ordinations to explore variations in bird community compositions between landscapes and habitats. We first standardized the species-point data matrix by maximum values (a Wisconsin double standardization) to facilitate the detection of community patterns, before calculating pairwise Bray–Curtis dissimilarity coefficients between point-count inventories. We generated a non-metric multi-dimensional scaling ordination using the R package *vegan* (Oksanen et al., 2022) to visualize patterns of bird community composition across forests, mixed farmland and palm plantations. We applied permutational multivariate analysis of variance to examine compositional differences amongst habitats using the *ADONIS* function in *vegan*. We also identified indicator species for each habitat type using the multi-level pattern analysis in the *Indicspecies* package in R (Dufrene & Legendre, 1997; Cáceres & Legendre, 2009). Species indicator values combine information on the relative abundance and relative frequency of occurrence of species in the defined habitats to narrow down a large number of species to a few species of interest that are the most characteristic species of the groups. We implemented the analysis predefining the three habitats as ‘groups’ and calculated indicator values with 999 permutations as a measure of statistical significance. Thus, the detections of species with significant indicator values are strongly associated with particular habitat types.

Results

We recorded 100 bird species during 162 visits to the 54 point-count localities (Supplementary Table 1). Of these, 62 species were observed in forests, 75 in coconut palm plantations and 75 in mixed farmland. Species accumulation curves for each habitat type approached an asymptote, indicating sufficient survey effort (Fig. 2). Although

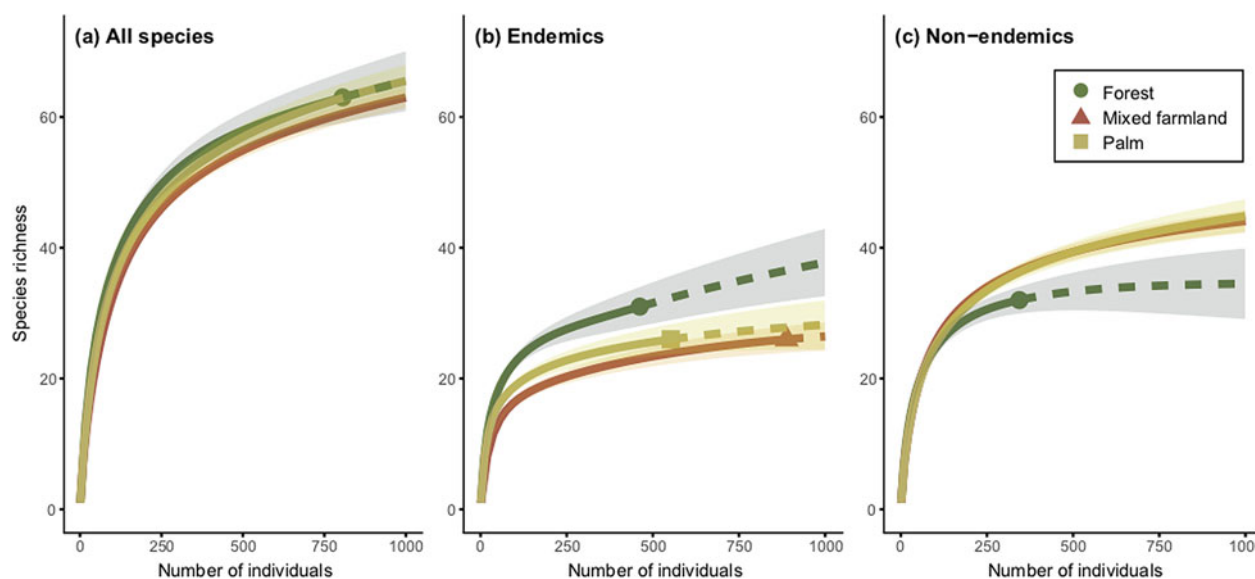


FIG. 2 Rarefied species accumulation curves for bird communities in the forests, coconut palm plantations and mixed farmland of Gorontalo Province, Sulawesi, Indonesia (Fig. 1). We conducted analyses separately for (a) all species, (b) taxa endemic to Sulawesi and the surrounding islands and (c) non-endemic species. We extrapolated the curves (dashed lines) to 1,000 individuals to ensure a consistent sample size for each comparison. We set the confidence intervals (shaded areas) at 84%, which has been demonstrated to be equivalent to a P-value of 0.05 for significant differences (MacGregor-Fors & Payton, 2013).

there were no significant differences in the numbers of bird species between forests, coconut palm plantations and mixed farmland, forests supported more even bird communities (i.e. species were present at similar abundances), as indicated by significantly higher Shannon and Simpson diversity (Fig. 3). Palm plantations supported intermediate levels of diversity compared to forests and mixed farmland. Forests also supported more endemic bird species and fewer non-endemics than palm plantations and mixed farmland (Fig. 3, Supplementary Fig. 1).

The non-metric multidimensional scaling ordinations robustly reflected the variation in bird community structure amongst sites according to stress values (all < 0.157), and showed substantial overlap in community composition between forests, coconut palm plantations and mixed farmland. Nevertheless, permutational multivariate analysis of variance comparisons revealed subtle and significant differences between the bird communities across all three habitats ($R^2 = 0.11$, $P < 0.001$), as well as between individual locations within the same habitat type ($R^2 = 0.06$ – 0.11 , $P < 0.002$). This pattern persisted when we repeated the analyses for endemic ($R^2 = 0.10$, $P < 0.001$) and non-endemic ($R^2 = 0.10$, $P < 0.001$) species. Notably, there was much more variation in the identity and abundance of non-endemic species between different forest sites than between agricultural sites; the latter tended to be much more homogeneous in their bird community compositions (Fig. 4).

Indicator species analysis revealed eight species that were significantly associated with forest habitat, four with coconut palm plantations and five with mixed farmland

(Table 1). Amongst the forest indicator species, six were endemic: the Sulawesi dwarf kingfisher *Ceyx fallax*, ashy woodpecker *Dryocopus fulvus*, Oberholser's fruit dove *Ptilinopus gularis*, Sulawesi babbler *Pellorneum celebensis*, ornate lorikeet *Saudareos ornata* and pale-blue monarch *Hypothymis puella*. There were no endemics amongst the indicator species of palm plantations, and only one endemic was identified for mixed farmland (the grosbeak myna *Scissirostrum dubium*). A further two species were prominent in forests and coconut palm plantations (the Sulawesi cuckoo dove *Macropygia albicapilla* and white-eyed spangled drongo *Dicrurus leucops*), and three were indicators of mixed farmland and coconut palm plantations. No indicator species overlapped between forests and mixed farmland.

Discussion

Community structure and composition amongst forests and agricultural habitats

Sulawesi is a rugged and geologically complex region, with much of the island being mountainous and only a small proportion of forest in the lowlands (Whitten et al., 2002). In Gorontalo, pressures from logging, transmigration and estate crop plantation are high because of this limited extent of lowland forests (FWI/GFW, 2002; Supriatna et al., 2020). There have not been many studies conducted on the use of commodity plantations by birds in Indonesia and Southeast Asia more broadly. Bird surveys in the forests, rubber plantations and agroforest systems of jungle rubber, damar

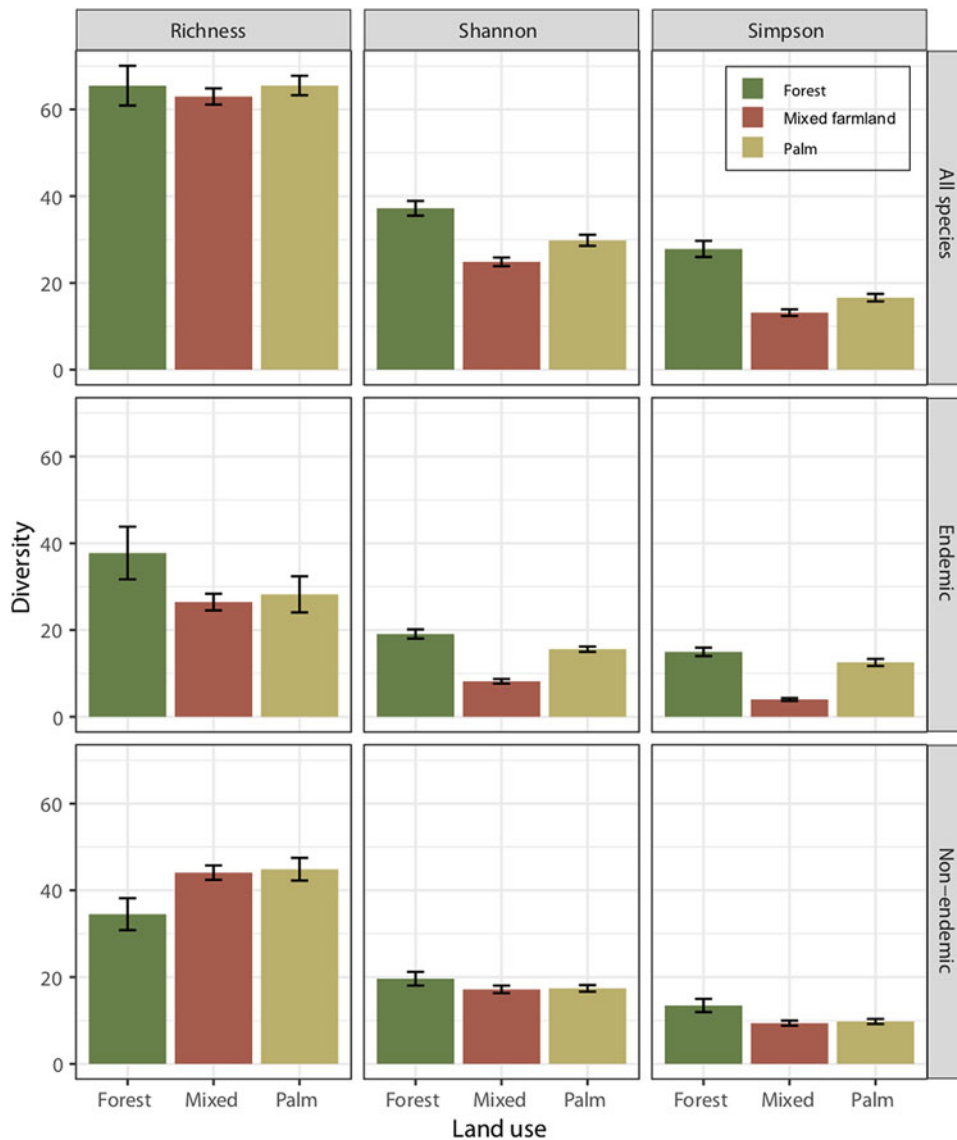


FIG. 3 Standardized comparisons (at 1,000 individuals) of richness, Shannon–Weiner diversity and Simpson diversity of bird species amongst forest, coconut palm plantations and mixed farmland sites in Gorontalo Province, Sulawesi, Indonesia. Analyses are shown for the whole bird community and for endemic and non-endemic species. Error bars represent 84% confidence intervals (for rationale, see MacGregor-Fors & Payton, 2013).

Shorea javanica and durian *Durio zibethinus* of Sumatra revealed higher species richness in the agroforest rubber tree systems than damar and durian systems, with the lowest diversity occurring in the durian areas (Thiollay, 1995; Beukema et al., 2007). The bird diversity in the forest-like conditions of jungle rubber sites tended to be most similar to that recorded in forest sites (Beukema et al., 2007). Bird diversity is known to be significantly reduced in oil palm plantations, although this reduction is less severe in small-holder farms, especially those with higher yields (Razak et al., 2020). In Sulawesi, bird taxa are able to persist in shade-grown cacao farms, including ornate lorikeets that are endemic to the island and crimson sunbirds *Aethopyga siparaja* (Siebert, 2002), two species confirmed as indicators of forest habitat in our study.

Our surveys in the northern region of Sulawesi demonstrate that overall bird diversity levels are similar between

forests, mixed farmland and palm/coconut plantations, yet the agricultural habitats lacked many of the endemic species characteristic of forests and instead were dominated by generalist, non-endemic species. This pattern of biotic homogenization is being reported increasingly around the world (McKinney, 2006; Devictor et al., 2008; Ibarra & Martin, 2015; Kormann et al., 2018), including in Sulawesi (Maas et al., 2009). Across six Wallacean islands, conversion from forest to agricultural landscapes was associated with the replacement of more specialized, range-restricted species by a shared cohort of generalists and human commensals with wider global ranges (Mitchell et al., 2022).

The modest differences in the bird communities were reflected in the differences in bird diversities between forests, mixed farmland and palm/coconut plantations. Forest sites supported the highest levels of bird diversity compared to

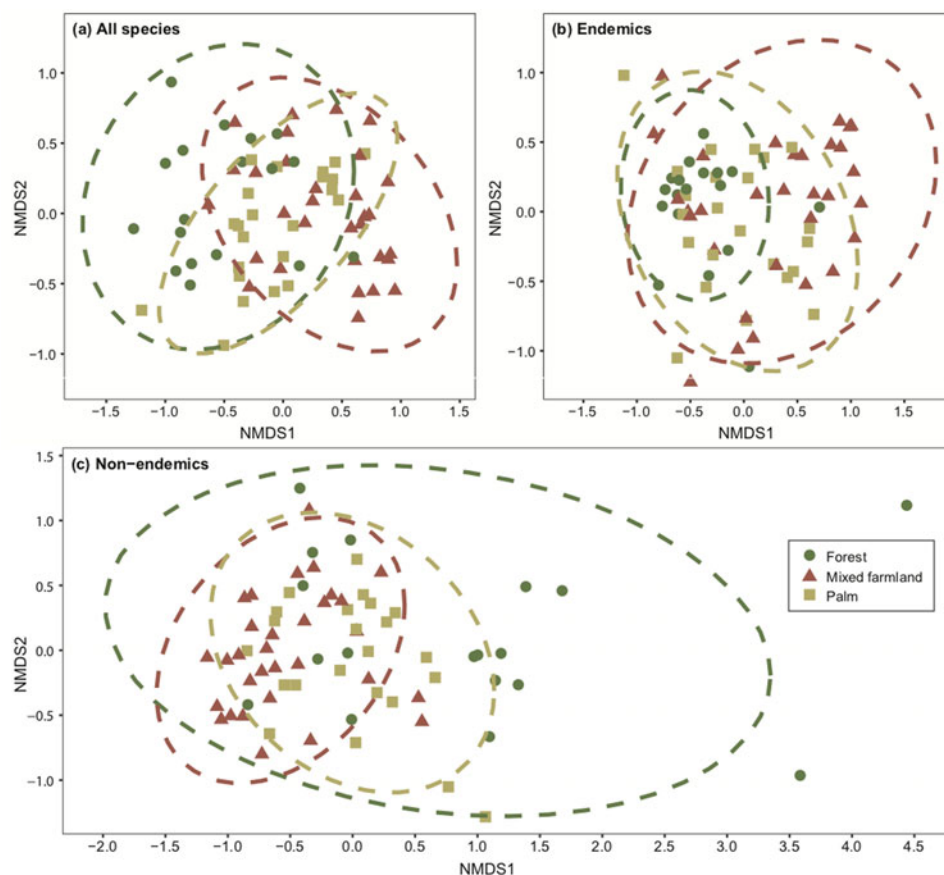


FIG. 4 Non-metric multidimensional scaling (NMDS) ordinations showing variation in bird community structure across forest, coconut palm plantation and mixed farmland sites in Gorontalo Province, Sulawesi, Indonesia. We undertook ordinations separately for (a) all species, (b) endemic species only and (c) non-endemic species.

sites in coconut plantations or mixed farmland. It has been suggested previously that agroforest is an environment in which small frugivores, foliage insectivores and nectarivores can thrive (Thiollay, 1995). Our indicator species analyses for Gorontalo revealed that frugivores and insectivores tended to flourish in forests, whereas there were more aerial insectivores (barn swallow *Hirundo rustica*) and granivores (Eurasian tree sparrow *Passer montanus*) in mixed farmland. The coconut plantations may act as an intermediate habitat between forests and the much more open mixed farmland as smallholder coconut plantations are usually intercropped with other plants. This provides an intermediate vegetation structure that is more complex than mixed farmland (Kumar & Kunhamu, 2022) and thus offers potential habitat features for nectarivores and insectivores. Similar species compositions were also indicated in the coconut farms in West Java, where the lesser coucal *Centropus bengalensis* was dominant (Dinanti et al., 2018). Recent research on oil palm plantations in Indonesia found no indicator bird species in these plantations (Simamora et al., 2021). Further studies comparing bird diversity in coconut vs oil palm plantations are needed to investigate whether this apparent lack of indicator species reflects any significant differences in the communities supported by these crops.

Deforestation leads to increased forest fragmentation and edge effects, changing the community structure of birds, and increases the distribution of common, introduced species (Leven & Corlett, 2004; Waltert et al., 2005; Maas et al., 2009; Sodhi et al., 2011). The latter pattern is characteristic of biotic homogenization, in which native, specialized and endemic species are replaced by widely distributed, common, generalist species (Devictor et al., 2008; Mitchell et al., 2022). Sooty-headed bulbuls *Pycnonotus aurigaster*, Java sparrows *Padda oryzivora* and zebra doves *Geopelia striata* are becoming widely distributed in the Minahasa peninsula, from North Sulawesi to Bogani Nani Wartabone National Park in Gorontalo (Fitzsimons et al., 2011). Over 10 years of observations in Lore Lindu, Central Sulawesi, endemic birds decreased in abundance and were replaced by more generalist species (Maas et al., 2009). An earlier study in that region demonstrated clearer differences in the bird fauna between forest and agroforest habitats than we describe in Gorontalo (Waltert et al., 2004), implying that biotic homogenization is an ongoing process and could be at a more advanced stage in the farming systems in the north of Sulawesi. In our study we recorded the more generalist species such as sooty-headed bulbuls in all habitat types, including the forest, and we only recorded the zebra dove in mixed farmland

TABLE 1 Bird indicator species for forests, mixed farmland and coconut palm plantations in Sulawesi, Indonesia (Fig. 1), as well as indicator species for forest and coconut palm plantations, and those for mixed farmland and coconut palm plantations.

Species (by habitat type)	Species indicator value	P-value
Forest		
Sulawesi dwarf kingfisher <i>Ceyx fallax</i>	0.424	0.0008***
Black-crowned white-eye <i>Zosterops atrifrons</i>	0.394	0.0015**
Ashy woodpecker <i>Dryocopus fulvus</i>	0.343	0.0027**
Oberholser's fruit dove <i>Ptilinopus gularis</i>	0.327	0.0087**
Sulawesi babbler <i>Pellorneum celebensis</i>	0.323	0.0178*
Ornate lorikeet <i>Saudareos ornatus</i>	0.316	0.0133*
Pale-blue monarch <i>Hypothymis puella</i>	0.302	0.0320*
Crimson sunbird <i>Aethopyga siparaja</i>	0.291	0.0374*
Mixed farmland		
Grosbeak myna <i>Scissirostrum dubium</i>	0.386	0.0014**
Barn swallow <i>Hirundo rustica</i>	0.381	0.0023**
Black-faced munia <i>Lonchura molucca</i>	0.306	0.0219*
Purple heron <i>Ardea purpurea</i>	0.300	0.0234*
Eurasian tree sparrow <i>Passer montanus</i>	0.295	0.0294*
Coconut palm plantations		
Brown-throated sunbird <i>Anthreptes malacensis</i>	0.483	0.0003***
Lesser coucal <i>Centropus bengalensis</i>	0.462	0.0001***
Sahul sunbird <i>Cinnyris clementiae</i>	0.400	0.0022**
Black-naped oriole <i>Oriolus chinensis</i>	0.377	0.0029**
Forest & coconut palm plantations		
Sulawesi cuckoo dove <i>Macropygia albicapilla</i>	0.352	0.0084**
White-eyed spangled drongo <i>Dicrurus leucops</i>	0.309	0.0269*
Mixed farmland & coconut palm plantations		
Collared kingfisher <i>Todiramphus chloris</i>	0.452	0.0004***
Golden-bellied gerygone <i>Gerygone sulphurea</i>	0.316	0.0195*
Spotted dove <i>Spilopelia chinensis</i>	0.314	0.0198*

*P < 0.5, **P < 0.01, ***P < 0.001.

and palm plantations. Birds such as sooty-headed bulbuls were amongst the first species to colonize Krakatau 25 years after its eruption, suggesting that they are pioneers

that are able to utilize human-disturbed areas and secondary forests (Thornton et al., 1990; Corlett & Hau, 2000; Winarni & Wijoyo, 2014; Winarni et al., 2019). Although these birds have been reported in South Sulawesi since the 1990s (MacKinnon & Phillipps, 1993; Coates et al., 1997), their presence in the North Sulawesi and Gorontalo provinces is probably a result of caged birds having escaped there, rather than an expansion of the population from South Sulawesi (Fitzsimons et al., 2011).

Implications for endemic birds

There is a growing literature on the changes to ecological communities because of agriculture, including the replacement of native bird species with widely distributed, often invasive, taxa (Maas et al., 2009; Peh, 2010; de Solar et al., 2015; Newbold et al., 2018). Forests accommodate more endemic species, whereas non-endemic species thrive in palm plantations and mixed farmland. We recorded birds originally from Southeast Asia such as zebra doves and sooty-headed bulbuls in mixed farmland and palm plantations. The invasion of these species could have a significant effect on native species through competition, leading to their local extirpation. Invasive bird species could also become agricultural pests and carry diseases that harm native flora and fauna (Mack et al., 2000; Sodhi et al., 2011). We recorded the sooty-headed bulbul (an introduced Javan and Indochinese species) during our surveys, which has been suggested as a potential competitor to native, endemic birds in Wallacea (Peh, 2010).

Coconut is cultivated and produced in all 34 provinces in Indonesia (Alouw & Wulandari, 2020). Over decades, this cultivation has expanded from lowland coastal areas to include some hilly areas (Sondakh & Kaligis, 1991). Intercropping with corn, rice, soybeans, groundnuts, cassava or sweet potatoes occurs in coconut farming, which could support greater biodiversity (Godoy & Bennett, 1991; Sondakh & Kaligis, 1991; McLaughlin & Mineau, 1995; Manoppo & Yusron, 2021). Birds may be able to use palm trees for nesting and foraging in agricultural environments where native plants are lacking. Birds particularly utilize the crowns of live palm trees in the upper layer of the canopy for nesting, as well as dead trunks in the middle layer of the canopy (Basheer & Aarif, 2013; Dinanti et al., 2018).

The expansion of coconut farmland is likely to lead to negative consequences for biodiversity across tropical and subtropical regions because much of the area left for cultivation is on small islands that support disproportionately large numbers of endemic species. For example, the newly described Wangi-wangi white-eye *Zosterops paruhbesar* is restricted to a single island of 155 km² where coconut farming is extensive (Irham et al., 2022). Although we recorded one endemic bird (the grosbeak myna) as being associated

with mixed farmland, many endemic birds are highly or moderately dependent on forests (Buchanan et al., 2008). Forests remain important habitats for endemic Sulawesi birds, particularly forest dwellers such as the Sulawesi dwarf kingfisher and ashy woodpecker (Coates et al., 1997). Therefore, the continuing expansion of croplands in Gorontalo is worthy of attention.

The decline of endemic species in Sulawesi is unlikely to be driven by agricultural expansion alone. For biodiversity monitoring on Buton Island, Southeast Sulawesi, the knobbed hornbill is used as an indicator of anthropogenic disturbance because of its sensitivity to human-induced habitat alteration. Although these birds are able to utilize different habitats, their presence or absence is explained by habitat disturbance and forest condition, because they require large trees for nesting and figs as a food resource (Kinnaird & O'Brien, 2007; Winarni, 2009; Winarni & Jones, 2012). In our study knobbed hornbills were rarely recorded within the forests, mixed farmland or palm plantations, suggesting that the nearby forests may have experienced some degradation. Forest degradation and fragmentation are generally linked with agricultural expansion in Wallacea (Voigt et al., 2021), and exploring which incentives drive the trajectories of forest conversion in these systems should be a research priority in this region. The designation of additional protected areas alone may not be adequate to protect some endemic species, because protected area status does not necessarily reduce forest loss (Curran et al., 2004; Hassan et al., 2005). Safeguarding the endemic avifauna of Sulawesi is likely to require additional legislative enforcement of forest protections as well as a shift towards policies and management strategies that reduce the environmental impacts of agricultural activities.

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Conflicts of interest None.

Ethical standards This research abided by the Oryx guidelines on ethical standards and followed ethical research standards in Indonesia, including appropriate field protocols and research permissions. Bird surveys were based on field observations, without

collection or handling of specimens, and were conducted with permission from the landowners.

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