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To cite this article: Robby B Butarbutar *et al* 2026 *Environ. Res.: Ecology* **5** 025010

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ENVIRONMENTAL RESEARCH ECOLOGY

PAPER

Sustaining biodiversity in coconut-dominated agroecosystems: insights from passive acoustic monitoring

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Keywords: coconut, agroforestry, avian, passive acoustic monitoring, bioacoustics, sustainability, landscape ecology

Supplementary material for this article is available [online](#)

RECEIVED
13 October 2025

REVISED
1 May 2026

ACCEPTED FOR PUBLICATION
2 June 2026

PUBLISHED
1 July 2026

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Abstract

Coconut cultivation is concentrated in coastal and island regions that harbor high species diversity and are particularly vulnerable to disturbance. Yet, coconut sustainability standards lack clear biodiversity safeguards despite rising global demand. We assessed how different coconut production systems influence biodiversity in North Sulawesi, Indonesia, using an acoustic index as a validated proxy for acoustic diversity. Across 56 sites and 2410 recording hours, we compared forests, coconut monocultures, and coconut agroforestry systems, and evaluated the influence of local vegetation and landscape variables on temporal acoustic dynamics. Forests supported the highest acoustic index values, while monocultures were lowest, with pronounced divergence at dawn and dusk. Coconut agroforests buffered these extremes: acoustic diversity remained relatively stable across the day and occasionally approached or exceeded forest levels, suggesting that mixed farming systems can sustain more vocally diverse animal communities than monocultures. Within farms, the density of small trees (primarily cocoa intercrops) was positively associated with acoustic diversity during afternoon period, whereas larger orchard trees exerted weaker influence. At the landscape scale, the proportion of forest cover around a locality was the strongest predictor of acoustic diversity, highlighting the role of forest vegetation in maintaining biodiversity across production landscapes. Our findings confirm that natural forests are irreplaceable for biodiversity, but coconut agroforestry can provide meaningful ecological benefits when embedded in forested landscapes. These insights underscore the need for emerging sustainability frameworks to incorporate explicit biodiversity criteria, including forest retention, intercrop diversity, and vertical structure, and to align with cross-commodity standards such as those in cocoa, given that coconut and cocoa are frequently intercropped.

1. Introduction

Agriculture is a primary driver of land-use change, accounting for more than 90% of tropical forest deforestation (Pendrill *et al* 2022). The threat to biodiversity is substantial, largely due to the degradation of primary forests driven by rapid crop expansion and intensification, particularly from open perennial crops such as oil palm (Gibson *et al* 2011, Oakley and Bicknell 2022). Industrial-scale oil palm monocultures are widely recognized for their adverse environmental impacts, while smallholdings are often

perceived as more ecologically benign (Azhar *et al* 2023). Both systems, however, exhibit distinct ecological outcomes depending on management practices involved (Wenzel *et al* 2024). Like oil palm, coconut (*Cocos nucifera*) is a long-established vegetable oil crop and poses a particular threat to rare and endemic species due to its extensive cultivation across tropical island nations (Meijaard *et al* 2020b). Yet recent studies suggest that the biodiversity impacts of coconut farming remain poorly understood (Meijaard *et al* 2020a, Winarni *et al* 2023, Burnett *et al* 2024).

Coconut is a major perennial crop thriving in warm, well-aerated lowland environments (Osman 2019). Frequently referred to as the 'tree of life', coconut is valued for its multifunctionality: nearly every part can be used for food (e.g. coconut water, flesh, milk, sap for sugar), materials (e.g. husk/coir fiber, shell, leaves, trunk wood), or commerce (copra and oil, desiccated coconut, activated charcoal) (Alouw and Wulandari 2020). Copra, the dried kernel of coconut, is mainly utilized for coconut oil extraction, which is one of the key coconut derivatives in international trade (Osman 2019). However, demand for other products such as virgin coconut oil is rapidly increasing, driven by health trends and a growing preference for natural products (Pratama *et al* 2024).

Today coconut is most extensively grown in tropical island nations, particularly in low-elevation coastal regions (Descals *et al* 2023). Indonesia, India, and the Philippines together cultivate about 8.75 million hectares of coconut, with Indonesia alone accounting for roughly 2.8 million hectares (FAOSTAT 2023) - this is the third-largest estate crop after oil palm and rubber in the country (Directorate General of Estate Crops 2022). In Indonesia, the largest coconut-producing provinces are Riau (Sumatra), North Sulawesi, and East Java where more than 6.3 million smallholder farmers depend on it for their livelihoods, largely through copra production (Alouw and Wulandari 2020). Farmers producing copra from monoculture practices typically earn a net profit of about USD 500 per hectare per year (Kairupan *et al* 2023), more than half that reported for smallholder oil palm (Yanita *et al* 2019, Astuti *et al* 2020). Despite its economic and cultural significance, coconut remains less competitive than oil palm, primarily due to lower productivity, limited processing capacity, and structural challenges within the industry (Alouw and Wulandari 2020, Pratama *et al* 2024). In addition to addressing systemic issues in the coconut industry, the adoption of sustainability certification is particularly recommended to improve market position in the future (Pratama *et al* 2024). Certification is among the most visible indicators of conservation commitment, yet it remains a notable gap in the coconut sector and in legislation and regulation from coconut-buying countries.

Lessons from oil palm highlight the kinds of biodiversity risks that may also be relevant to coconut, given its predominance in tropical island regions and similar ecological and socioeconomic settings (Meijaard *et al* 2020a). Oil palm expansion has been associated with sharp declines in species diversity and abundance across multiple taxa, particularly forest specialists, while favoring generalists and disturbance-tolerant species (Vijay *et al* 2016). Monoculture plantations reduce habitat heterogeneity, simplify vegetation structure, and fragment landscapes, altering community composition and ecosystem function (Newbold *et al* 2018). Although coconut is often cultivated in smallholdings rather than large industrial estates, historical land conversion and the expansion of monoculture production suggest comparable pressures on biodiversity (Wenzel *et al* 2024). These concerns are amplified by the fact that coconut is predominantly grown in coastal regions and on islands - areas that are often centers of endemism and where biodiversity is especially vulnerable to environmental change (Meijaard *et al* 2020a). Yet, unlike oil palm, the ecological impacts of coconut remain underexplored, representing a critical knowledge gap.

The island of Sulawesi exemplifies the core tension between suitable land for agricultural commodities, mining and tourism, versus the need to conserve endemic-rich ecosystems. Located within the Wallacean biogeographic region, Sulawesi is a globally renowned center for endemism shaped by a complex evolutionary history (Struebig *et al* 2022). The island harbors numerous endemic species including the babirusa (*Babyroussa celebensis*), maleo (*Macrocephalon maleo*) and Sulawesi hornbill (*Rhabdotorrhinus exarhatus*). Historically, deforestation rates in Sulawesi have been lower than in western Indonesia owing to a preponderance of small-holder systems relative to large-scale agriculture and the availability of suitable land for lowland agriculture (Austin *et al* 2019, Voigt *et al* 2021). However, expansion of mining, industrial agriculture, and tourism has recently intensified environmental and social pressures (Supriatna *et al* 2020). Coconut cultivation has historically contributed to deforestation both here and across the Asia-Pacific, replacing primary forests and transforming ecosystems critical for endemic species (Burnett *et al* 2024). Yet, despite evidence that coconut landscapes may threaten biodiversity, our understanding of these effects remains limited. A recent review of coconut by Yin *et al* (2023) found that most studies have focused on food technology, chemistry, and nutrition, with understanding of impacts on ecology being marginal.

Quantifying and monitoring biodiversity in large agricultural landscapes presents a significant logistical challenge. Birds serve as highly effective bioindicators to address this because they respond predictably to environmental change that makes them measurable proxies (Fraixedas *et al* 2020). Passive acoustic monitoring (PAM) offers a powerful approach to capture these avian responses across diverse habitats and spatiotemporal scales (Gibb *et al* 2018). Soundscape analyses using acoustic indices derived from PAM can provide rapid proxies for bird species diversity, particularly in remote or resource-limited settings (Bradfer-Lawrence *et al* 2020, Gaspar *et al* 2023). However, the performance of acoustic indices as proxies for diversity is highly variable across different ecological contexts, therefore validation is necessary (Alcocer *et al* 2022).

Here, we use PAM to characterize bird vocal activity in monoculture coconut plantations and agroforestry systems in North Sulawesi, with forest sites serving as comparative controls. By analyzing acoustic indices and incorporating environmental and anthropogenic factors, we evaluate how different coconut farming plantings support, or limit, vocally active animal communities. Our study aims to identify the key drivers of acoustic diversity in coconut-dominated landscapes and provide insights into the potential role of coconut agroforestry in reconciling agricultural production with biodiversity conservation in hyper-diverse tropical regions.

2. Materials and method

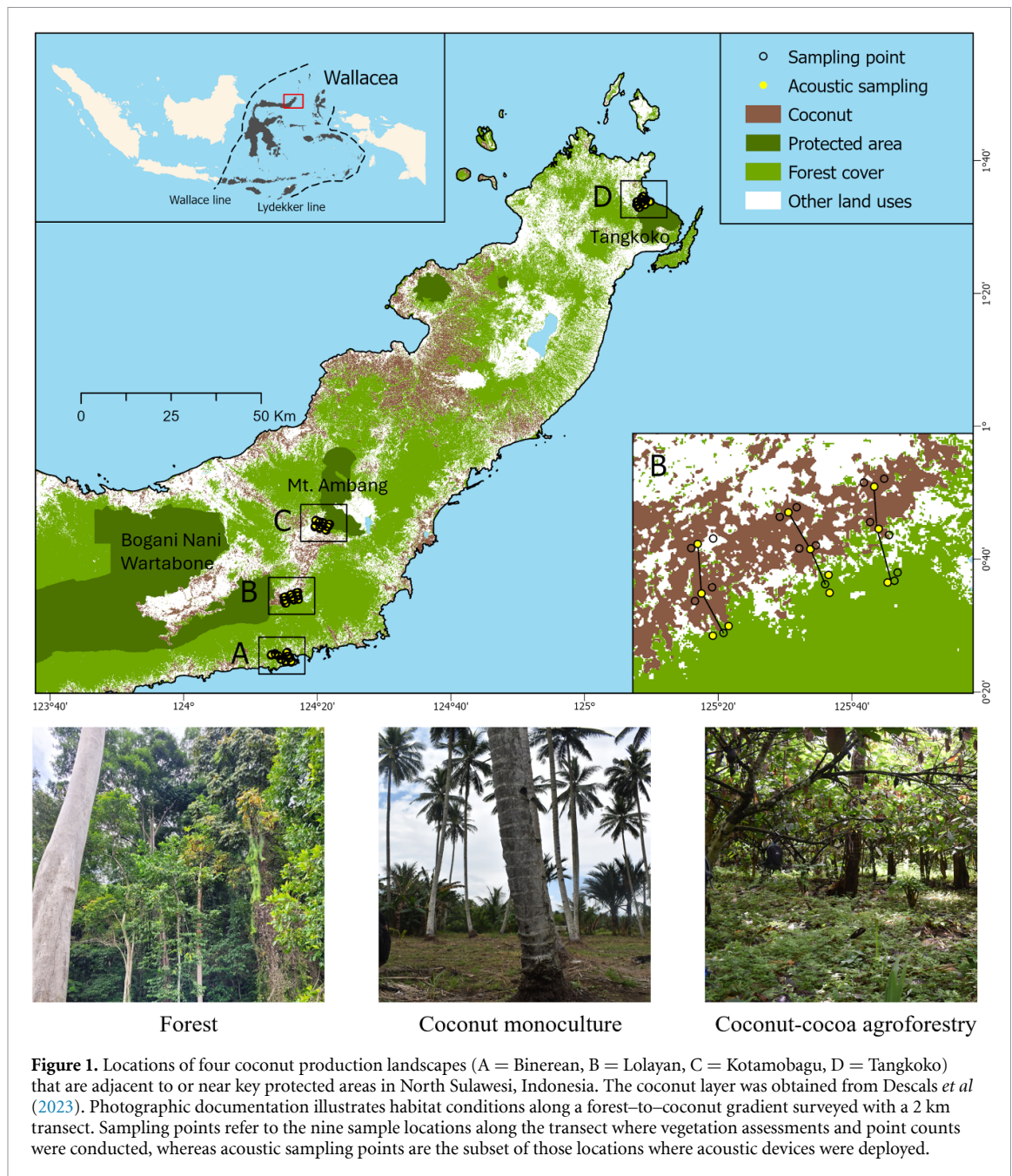
2.1. Study area

Fieldwork was conducted in four landscapes across North Sulawesi province, Indonesia. The province has a tropical climate with a mean annual temperature of $\sim 27^{\circ}\text{C}$ and annual rainfall of ~ 3200 mm (Badan Pusat Statistik 2024). Approximately 40% of the province remains forested (Voigt *et al* 2021), with key protected areas including Bogani Nani Wartabone National Park, Gunung Ambang, Tangkoko and Duasudara Wildlife Reserves. North Sulawesi is also a major coconut-producing region, contributing about 10% of national output (Alouw and Wulandari 2020). The coconut plantations in this region are long-established. The average age of coconut stands across sites was approximately 33 years at the time of study, with some older plantations reaching up to 80 years. Multiple cropping systems are utilized – some coconut is grown as monoculture, while most is intercropped with other commodities. To capture this variation, we selected four landscapes representing a gradient of coconut agroforestry systems and proximity to continuous forest (figure 1). Agroforestry land-holdings are typically polycultural, comprising 2–4 cash crops in addition to coconut, with some including a small number of native forest trees. Smaller trees (diameter < 20 cm) tend to be cocoa, while larger trees (> 20 cm diameter) are more diverse, and include nutmeg (*Myristica fragrans*), clove (*Syzygium aromaticum*), durian (*Durio zibethinus*), banana (*Musa acuminata*), langsung (*Lansium domesticum*), manggo (*Mangifera indica*), candlenut (*Aleurites moluccanus*), matoa (*Pometia pinnata*), rambutan (*Nephelium lappaceum*), and a few native forest trees such as *Swietenia mahagoni*, *Magnolia champaca*, *Palaquium* sp., *Ficus* sp., and *Tectona grandis*.

2.2. PAM and bird point counts

During May and June 2024, we deployed 15 autonomous acoustic recorders (Audiomoth 1.2.0) along a forest-farmland gradient in each landscape. Deployment at one landscape (Lolayan, B) was limited to 11 units due to local constraints. Therefore, 56 recorders were used in total, which included 20 in forest and 36 in coconut farms (14 monocrop and 22 agroforestry) (figure 1). Since Audiomoth microphones are not completely omnidirectional (Lapp *et al* 2023), we mounted recorders on small trees (~ 5 cm diameter) around 2 m above ground to address the lower sensitivity behind the device. Recorders were spaced ≥ 400 m apart in clusters along three 2 km transects per landscape—thus reducing the likelihood of overlapping recordings and ensuring independence between sample points (Alcocer *et al* 2022) (figure 1).

The units were configured to record the dawn (05:00–09:30) and dusk choruses (15:10–19:00) when bird activity is typically highest. Each was scheduled to operate in 5 min increments (295 s on and 5 s off) for up to seven days, with a sampling rate of 32 kHz to capture bird vocalizations typically within the 2–12 kHz frequency range (Zhao *et al* 2019). To validate the recordings and acoustic indices against direct observations of birds, we conducted 10 min bird point counts during the dawn chorus (05:20–09:30) at nine sampling points per transect on the same days that the Audiomoths were operating. Each point count survey was repeated on three occasions at different times by randomizing the order of transects, habitat clusters, and sampling points visited on successive days. To mitigate noise generated during point counts, surveyors minimized disturbances and conducted counts 10–15 m away from the audio recorders. We also excluded the first and last 10 min of each recording to remove sound associated with deployment and retrieval.



2.3. Acoustic processing and indices

As we were interested in bird vocalizations, audio files were filtered to minimize the influence of rainfall and other non-target sounds (i.e. insects, anthropophony, and geophony). We band-pass filtered recordings to 187–6437 Hz, a range that contained 90% of bird vocalizations with minimum masking by non-target sounds, estimated from 120 min of annotated sample recordings (refer to SI section 6 for more information). We calculated five commonly used acoustic indices that quantify biological, geological and anthropogenic sounds in the environment, following established protocols (Truskinger *et al* 2014, Burivalova *et al* 2019). We then assessed the relationships of acoustic indices with bird richness using a poisson generalized linear mixed model, comparing results with two datasets: (i) bird richness from point-count observations and (ii) richness derived from 120 min of manually annotated sample recordings (refer to SI section 6.3 for more information). We did this because the performance of acoustic indices depends on habitat, environmental conditions, recording devices and the choice of indices used, making ground-truthing and context specific validation essential (Gibb *et al* 2018). The Bioacoustic Index, defined as the sum of the normalized energy values across a selected frequency bin, weighted by the frequency resolution (Boelman *et al* 2007), showed the strongest positive association and precision with bird richness across datasets and so was selected to track relative trends in bird diversity across habitats and

Table 1. Plot and landscape level variables used in the linear mixed-effects models to determine how the local and broader environment influenced the Bioacoustic Index along a forest to coconut farming gradient in North Sulawesi.

	Variable	Description	Source
Plot level	Canopy closure (%)	Percentage canopy cover from photographs analyzed using ‘imageseg’ R package (Niedballa <i>et al</i> 2022)	Vegetation assessments in sampling points (figure 1 and SI).
	Canopy height (m)	Average height of trees calculated within each plot	
	Large trees density (DBH > 20 cm) (m ² ha ⁻¹)	Summed basal area of intercrops or native trees within the plot divided by plot area and scaled up to a per-hectare basis	
	Small trees density (DBH between 10 and 20 cm) (m ² ha ⁻¹)		
Landscape level	Distance to roads (m)	Mean value of the Euclidean distance to roads.	Humanitarian OpenStreetMap 2024 https://data.humdata.org/dataset/hotosm_idn_roads
	Distance to villages (m)	Mean value of the Euclidean distance to villages.	Polygon feature of settlements from Rupa Bumi Indonesia (RBI) 2022 https://tanahair.indonesia.go.id/portal-web/
	Elevation (m)	Mean value of elevation derived from digital elevation model (DEM) raster layer.	DEM SRTM 30 m 2014 https://earthexplorer.usgs.gov/
	Forest proportion	The mean of a binary raster (1 = forest, 0 = non-forest)	Vancutsem <i>et al</i> 2021) https://forobs.jrc.ec.europa.eu/TMF

periods. The value of this metric (hereafter simply referred to as acoustic diversity) is also evidenced by studies across a wide range of biomes and regions, including temperate forests (Eldridge *et al* 2018, Beason *et al* 2023, Budka *et al* 2023), tropical forests (Eldridge *et al* 2018, Bradfer-Lawrence *et al* 2020, Gaspar *et al* 2023), grasslands (Shamon *et al* 2021) and urban areas (Yang *et al* 2024). This is also consistent with findings from similar landscape in Sulawesi where only the bioacoustic index was positively correlated with bird richness (Dröge *et al* 2024). Details on the enhancement of sound files and selection of the index can be found in supplementary information section 6.

The recordings were segmented into 59-second fragments, resulting in approximately 500 fragments per unit per day, and these fragments served as the temporal units for calculating the Bioacoustic index. Index values were computed using the R package ‘Soundecology’ (Pijanowski and C 2018). While index values were averaged across units and days to visualize temporal dynamics—using generalized additive models with cubic splines to smooth mean values (figure 2(a))—all subsequent modeling of environmental predictors utilized the full, non-averaged dataset. This approach ensured that fine-scale variance and transient acoustic events were preserved for the statistical modeling of environmental predictors.

2.4. Plot- and landscape-level covariates

We quantified potential predictors of acoustic activity at two spatial levels (table 1):

Four plot-level variables were measured in fixed square plots (400 m²; 20 m × 20 m), centered on each audio unit, to capture fine-scale vegetation structure that has been shown to influence bird species composition in cultivated landscapes (Azhar *et al* 2013, Lees *et al* 2015, Sam *et al* 2019). Canopy closure and canopy height were measured at the sampling point since they serve as important proxies for vegetation structural complexity and habitat quality, reflecting the availability of resources, microclimate, and niche variety for bird communities (Sam *et al* 2019). The densities of non-coconut trees (small versus large tree densities) were also measured to capture the intensity of intercropping and agroforestry practices.

Four landscape-level variables were extracted from spatial datasets for the region within a circular buffer of each point. These included anthropogenic and environmental attributes known to influence bird communities within a wider landscape context (Morante-Filho *et al* 2018, Cabral *et al* 2021). Human disturbance variables comprised distance to roads and villages, considering the direct and indirect negative impacts of traffic noise and human activity on bird populations (Mammides *et al* 2016, Scanes 2018). Elevation was also considered as a crucial factor influencing avian communities and diversity (Quintero and Jetz 2018). The proportion of land forested within the buffer was based on global forest cover data (Vancutsem *et al* 2021). We reclassified the source dataset to restrict forest cover estimates to areas

exceeding 200 hectares since visual inspection of the imagery confirmed that smaller clusters of forest pixels were typically classification errors of mature agroforestry stands. Large forest areas are known to support significantly greater avian abundance and species richness in oil palm plantations, encompassing endemic taxa, compared to smaller, spatially isolated forest patches within plantation landscapes (Edwards *et al* 2010).

We tested landscape variables at four buffer radii (50, 100, 250, and 500 m), selecting the 250 m buffer based on both multicollinearity thresholds (Pearson's $|r| < 0.7$; GVIF < 3) and AIC-based model comparisons. We then calculated the mean of each landscape variable (30×30 m resolution) within this 250 m radius around each recorder. Details of variable derivation are given in the supplementary information sections 4 and 5.

2.5. Modeling the relationship between acoustic diversity and environmental factors

We modeled temporal variation in the Bioacoustic Index as a function of plot- and landscape-level predictors using linear mixed-effects models (LMM) for all habitats (forest + coconut farms) and only coconut farms separately to evaluate the isolated influence predictors have on coconut landscape when forest habitat is concealed. Because all continuous predictors were standardized prior to analysis, the reported effect sizes (β) represent the change in acoustic diversity for every one standard deviation (SD) increase in the given predictor. The effective unit of replication was the individual acoustic sampling point ($n = 56$). To account for the hierarchical structure of the data - specifically the nesting of 59 s acoustic fragments within sites - we employed LMM with recorder ID included as a random effect. This approach addressed potential pseudoreplication and the non-independence of high-frequency temporal samples while preserving the fine-scale acoustic variance necessary to describe the soundscape's ecological signature. We modeled covariates against the Bioacoustic Index as a direct empirical relationship within the soundscape. The minute interaction term was designed to capture fine-scale temporal dynamics characteristic of the soundscape, enabling us to evaluate how associations with acoustic diversity shifted across dawn and dusk.

All geospatial processing was implemented in ArcGIS pro 3.3.2 and R 4.4.2.

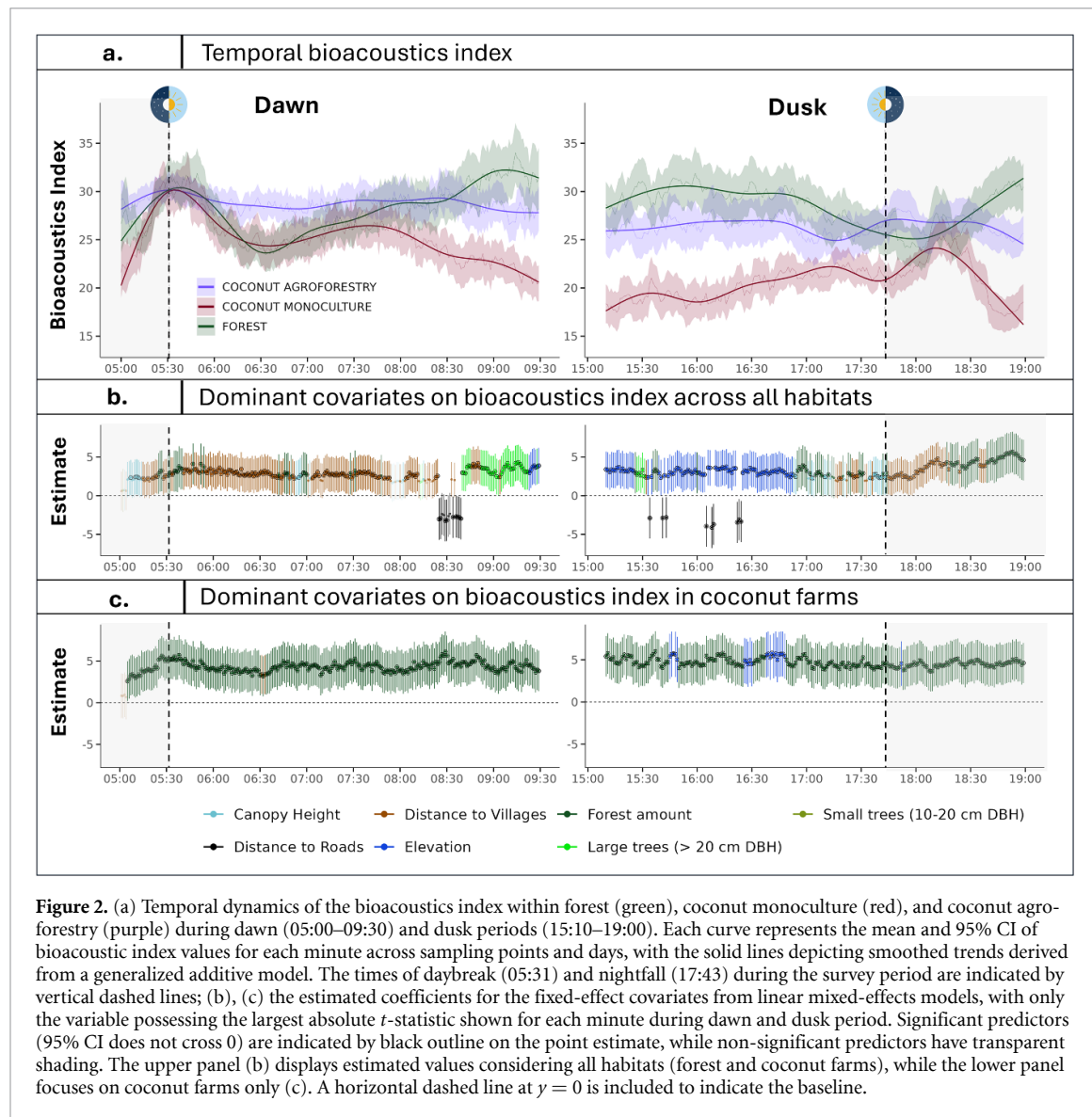
3. Results

After filtering and processing PAM yielded 2410 h of recordings across 56 sampling points, each monitored for 5–6 d. Approximately 62.5% of coconut farms surveyed were managed as agroforestry systems. The ratios of agroforestry to monoculture sampling sites in each landscape were, respectively: 12:6 (landscape A), 15:3 (landscape B), 18:0 (landscape C), and 0:18 (landscape D).

3.1. Temporal patterns of acoustic activity

Bioacoustic index values revealed distinct temporal dynamics across habitats (figure 2(a)). Forest and coconut monocultures showed similar peaks in acoustic diversity around dawn, followed by decline and divergence later in the morning, and forest maintained consistently higher activity throughout the day. By the end of dawn, mean bioacoustic index values in forest were approximately 1.5 times greater than those in monocultures, and by dusk the difference was nearly double. In contrast, coconut agroforestry systems maintained high, relatively stable acoustic diversity throughout much of the day, and were mostly intermediate between forest and monoculture.

Model outputs (figures 2(b) and (c)) revealed several dominant predictors of temporal variation in acoustic diversity. The reported estimates were averaged across all significant effects identified in figures 2(b) and (c). Tree density had negligible overall influence, although large trees showed a short-lived positive effect at the end of dawn ($\beta = 3.4$, 95% CI 1.1–5.7; figure 2(b)). Canopy height displayed sporadic positive associations across habitats ($\beta = 2.4$, 95% CI 0.2–4.7; figure 2(b)). Distance to villages showed a broadly positive effect, ($\beta = 2.9$, 95% CI 0.7–5.1; figure 2(b)), suggesting reduced bird activity near human settlements, although this was less pronounced within coconut farms (figure 2(c)). Proximity to roads was associated with brief increases in acoustic diversity in the morning and afternoon, reflected by a negative association with distance to roads ($\beta = -3.1$, 95% CI -5.8 to -0.5), but effects were inconsistent (figure 2(b)). Elevation exhibited a positive association ($\beta = 3.2$, 95% CI 0.9–5.5), particularly in the afternoon (figures 2(b) and (c)). Within coconut farms, surrounding forest cover emerged as a consistent positive predictor of acoustic diversity across the day, where a one SD increase in forest cover (equivalent to about 25.4% more forest within the 250 m buffer) was associated with an average 4.4 unit increase in the bioacoustic index ($\beta = 4.4$, 95% CI 2.0–6.8; figure 2(c)).



3.2. Effects of plot- and landscape-level covariates

Across all habitats, bioacoustic index values were negatively correlated with canopy closure particularly in the evening ($\beta = -2.8$, 95% CI -5.3 to -0.3 ; figure 3), but weak and positive association emerged in the late morning and afternoon within coconut farms ($\beta = 2.5$, 95% CI 0.2 – 4.8 ; figure 3(b)). Canopy height was positively associated with the bioacoustic index ($\beta = 2.4$, 95% CI 0.2 – 4.7 ; figure 3(a)), though effects were temporally limited in the afternoon within coconut farms ($\beta = 2.8$, 95% CI 0.2 – 5.4 ; figure 3(b)). Small-tree density, dominated by cocoa trees, had modest positive effects on acoustic diversity in coconut plots ($\beta = 3.2$, 95% CI 0.5 – 6.0 ; figure 3(b)), particularly in the late morning and afternoon, whereas large-tree density had positive association with acoustic diversity across all habitats, especially in the morning ($\beta = -2.8$, 95% CI -5.3 to -0.3 ; figure 3(a)), but some negative association within coconut farms only within certain time during dawn and in the evening ($\beta = -2.4$, 95% CI -4.6 to -0.1 ; figure 3(b)).

Landscape context strongly influenced acoustic diversity. Across all habitats, bioacoustic index values increased with greater distance from villages ($\beta = 2.9$, 95% CI 0.7 – 5.1 ; figure 3) and with closer proximity to roads ($\beta = -3$, 95% CI -5.7 to -0.4 ; figure 3(a)), although the latter effect was largely absent within coconut farms (figure 3(b)). Elevation was positively and strongly associated with acoustic diversity during dusk, and this relationship remained consistently significant from the afternoon through to sunset, specifically in coconut landscapes ($\beta = 4.0$, 95% CI 1.3 – 6.7 ; figure 3(b)). Forest cover in the surrounding landscape exerted the strongest and most consistent effect, with higher proportions of forest linked to higher bioacoustic index values, particularly in coconut farms ($\beta = 4.4$, 95% CI 2.0 – 6.8 ; figure 3(b)).

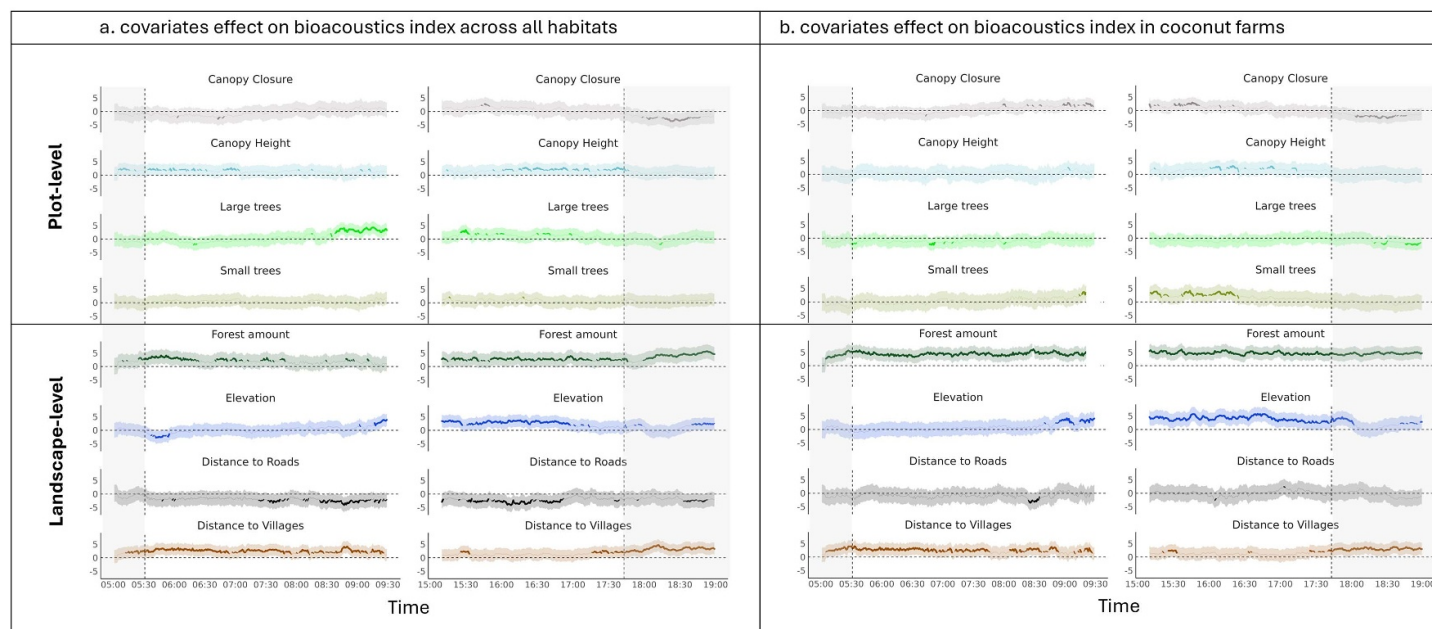


Figure 3. Interaction effects on temporal index variation during dawn and dusk, derived from linear mixed-effects models. The left panel displays estimated values for all habitats, while the right panel isolates the effects within coconut farms where the influence of forest habitat indices is suppressed. Thick line represents significant effect (95% CI does not cross 0), and shaded areas represent 95% CI. The baseline is indicated by a horizontal dashed line at $y = 0$.

4. Discussion

Our study provides new insights into the temporal dynamics of animal communities across forests, coconut monocultures, and coconut agroforestry systems. Using PAM, we identified consistent differences in bird vocal activity between habitats, with forests typically supporting the highest acoustic diversity and coconut monocultures the lowest. By contrast, coconut agroforestry systems exhibited relatively stable acoustic diversity across the day, often intermediate between forest and monoculture, and in some morning periods exceeding levels in forest. These patterns highlight the ecological importance of forested habitats, while also showing that coconut agroforestry can serve as a more biodiversity-supportive alternative to monoculture production.

4.1. Interpreting temporal dynamics of bird activity

The contrasting acoustic diversity between forest and coconut monocultures across the dawn and dusk periods reflects the well-established role of multi-layered vegetation and dense canopy cover in sustaining bird diversity. Forests provide abundant food resources, microclimatic buffering, and structurally diverse habitats, all of which support richer bird communities (Nájera and Simonetti 2010, Gibson *et al* 2011, Yahya *et al* 2022). By contrast, coconut monocultures lack vertical structure and resource diversity, similar to patterns in oil palm and rubber, supporting primarily generalist species and fewer specialists (Prabowo *et al* 2016, Winarni *et al* 2023). In monoculture systems, older oil palm plantations (>11 years) are structurally similar to coconut plantations, and continue to exhibit lower species richness even compared to younger plantations, likely due to reduced habitat complexity as the palms mature and the understory becomes sparser (Lees *et al* 2015). The observed morning divergence, where forest acoustic diversity remained high while in monoculture it declined, likely reflects the tendency of birds to seek shaded and cooler habitats for thermal regulation and foraging efficiency (Ferber *et al* 2014, Ceresa *et al* 2021). In contrast, the partial reversal of this divergence in the afternoon may indicate increased socializing or opportunistic foraging in relatively open monoculture areas as temperatures became less extreme (Rozen-Rechels *et al* 2025). Evening patterns reinforce these differences: sharp increases of acoustic diversity in forests after dusk, accompanied by declines in monoculture, are consistent with forest birds engaging in roosting and social calls, including vocalizations by nocturnal species (Moraes *et al* 2018, Mitchell and Clarke 2019).

Coconut agroforestry likely buffered these extremes by integrating crops such as cocoa, nutmeg, or clove. Agroforestry systems provide additional canopy layers and food sources, sustaining animal activity more evenly throughout the day (Yahya *et al* 2022). The coconut farms in our study area were senescent, suggesting that the recorded acoustic diversity reflects relatively assembled and stable bird communities rather than transient spillover from recent deforestation (Stouffer *et al* 2011, Zhao *et al* 2013). This extended timescale, combined with relatively low-intensity management practices, has allowed coconut agroforestry systems to mature over decades, providing the structural complexity—though not equivalent to forest—to support higher ecological function than monocultures and enable both specialist and generalist species to co-occur (figure S1).

4.2. Methodological reflections on PAM

Our use of PAM allowed for near-continuous sampling across dawn and dusk choruses, capturing fine-scale temporal variation that traditional point counts would likely miss. We found that the Bioacoustic Index provided an effective proxy for vocal activity, as also demonstrated in a comparable agroforestry study elsewhere in Sulawesi (Dröge *et al* 2024). The Bioacoustic Index performs best when recordings are filtered to isolate target biophony (i.e. biological sounds), thereby reducing interference from non-avian sources and improving the robustness and generalizability of its predictive power (Eldridge *et al* 2018, Metcalf *et al* 2021), as confirmed through our manual verification.

However, PAM is not without limitations. Our validation demonstrated that bioacoustic index values were associated with bird species richness, but it should be noted that such indices are fundamentally proxies based on sound energy or signal patterns rather than direct measures of taxonomic diversity. As such, variation in the acoustic index data across contrasting habitats could be driven in part by how sound travels through different vegetation structures, such as dense forest understories versus open monocultures. Acoustic indices cannot fully disentangle abundance from diversity, and they are biased towards vocally active species and guilds, while quieter or infrequently vocalizing taxa are under-represented (Zhao *et al* 2019, Bradfer-Lawrence *et al* 2020).

Anthropogenic and biotic noise (e.g. insects, rain) can also mask acoustic signals despite filtering efforts. For example, insect sounds may be more prominent in forest, potentially inflating or deflating acoustic index values. Our application of a band-pass filter (187–6437 Hz) captured the vast majority

of bird vocalizations with minimal overlap from non-target sounds (figure S6). While some non-target sounds persisted after the filtering, the signal-to-noise ratio (SNR) remained relatively similar across both forest and coconut sites (figure S8). This uniform SNR suggests that any residual noise was distributed consistently across habitats, implying that any habitat-related bias was minimal. Similarly, a small proportion of target sounds exceeded the upper frequency threshold of the filter (6437 Hz) and were thus excluded from analyses, as they overlapped with invertebrate signals. While the exclusion of these signals could introduce a secondary habitat-dependent bias, the effect is likely negligible in the context of our study because the vast majority of avian vocalizations (~90%) fall within the target frequency range according to our validation (figure S6). Furthermore, because our recording schedule focused on dawn and dusk, we targeted the peak of avian activity while avoiding periods when high-frequency nocturnal vertebrates (e.g. bats, tarsiers, and some amphibians) are most vocal.

Complementary methods such as species-level call identification or standardized point counts remain essential for validating ecological patterns, while adequate spatial replication and careful control of non-target sounds are required for acoustic indices to effectively monitor biodiversity across varied habitats (Mitchell *et al* 2020). Extending sampling to other times of the year may also strengthen the representation of migratory species in the bird community. Nevertheless, the fine-grained temporal insights from PAM strengthen our understanding of habitat-specific activity trends; rather than simply ranking habitats, they reveal the diurnal dynamics of bird vocalizations and their relationship to bird behavior in coconut-dominated landscapes.

4.3. Local vegetation and the role of small trees

At the plot level, vegetation variables were not consistently strong predictors of temporal acoustic variation. Canopy closure, canopy height, and large tree density had sporadic or no effect on acoustic activity within coconut farms. However, the density of small trees, primarily representing cocoa intercrops, had a moderate positive effect among coconut farms in the afternoon. This suggests that vertical complexity and understory resources play a role in maintaining animal foraging and activity during hotter parts of the day, by moderating microclimate and providing food such as fruits and insects (Nájera and Simonetti 2010, Yahya *et al* 2022). These results align with broader evidence that shaded cocoa systems with tall trees have substantially higher bird diversity than open, full-sun cocoa monocultures (Clough *et al* 2009, Rocha *et al* 2019). In our context, cocoa-coconut agroforestry appears to foster complementary relationships that benefit both production and biodiversity. Such systems may therefore represent ‘win-win’ configurations, as also supported by life-cycle assessments showing lower environmental impacts for cocoa-coconut compared to other intercrop combinations (Utomo *et al* 2016).

4.4. The importance of landscape context

While local vegetation complexity influenced acoustic diversity to some degree, our models showed that landscape-scale factors, particularly forest extent and elevation, were more decisive drivers of acoustic dynamics. The road effect appears to exert a positive influence across all habitats, although this is likely an artefact of (i) very low traffic volumes on the rural roads, and (ii) spatial confounding: road locations are moderately correlated with higher surrounding forest cover ($r = 0.6$). Thus, elevated bioacoustic index values near roads probably reflect edge-related structural and resource heterogeneity associated with adjacent forest, rather than any direct ecological benefit of roads themselves. Coconut farms with higher proportion of forest in the surrounding landscape tended to have higher bird vocal activity. Agroforestry systems embedded in forested landscapes tend to harbor greater species diversity and abundance than deforested or fragmented landscapes, especially of forest-dependent and frugivorous birds (Morante-Filho *et al* 2018, Rocha *et al* 2019, Cabral *et al* 2021). Elevation also positively correlated with acoustic diversity, particularly in the afternoon. While this may partly reflect ecological preferences for cooler, more structurally complex upland environments, the effect is likely confounded by the distribution of forest, as remaining tracts of forest in Sulawesi are disproportionately concentrated at higher elevations (Voigt *et al* 2021).

These findings reinforce the value of maintaining continuous forest cover within agricultural landscapes. Large tracts of forest have limited spillover to surrounding areas when permeability is low (Cardoso *et al* 2025); therefore, agroforestry systems are important for increasing landscape heterogeneity, facilitating greater dispersal of species from forest habitats and thereby enhancing local diversity (Morante-Filho *et al* 2018, Cabral *et al* 2021). Coconut agroforests embedded in forest-rich landscapes are therefore more likely to harbor forest specialists, while those in deforested landscapes risk being dominated by generalists, leading to biotic homogenization - a pattern already apparent across insular Southeast Asia (Mitchell *et al* 2022, Winarni *et al* 2023). We observed a similar trend from our point count observation where endemic forest specialists, while most abundant in forests, were more common

in coconut agroforestry than in monocultures (figure S1). These results imply that agroforestry systems provide a viable intermediate habitat for forest bird species that is otherwise lost in simplified agricultural matrices. This underscores the forest–coconut interface as a critical conservation frontier.

Taken together, our findings mirror trends from other tropical perennial tree crops (Struebig *et al* 2025). In oil palm, bird diversity consistently declines in monocultures relative to large contiguous forest, with some mitigation possible in polyculture or structurally complex stands (Edwards *et al* 2010, Azhar *et al* 2013, Lees *et al* 2015). Cocoa agroforestry has long been recognized as a biodiversity-supportive alternative to cocoa monocultures (Clough *et al* 2009, Utomo *et al* 2016, Niether *et al* 2020, Dröge *et al* 2024). Coconut, a globally traded but understudied commodity, appears to sit between these extremes: ecologically impoverished in monoculture, but capable of supporting diverse communities when intercropped and embedded in forested landscapes.

4.5. Implications for management, policy, and research

Our results highlight three major implications for the sustainable management of coconut landscapes. First, promoting agroforestry practices in coconut plantations, particularly by integrating cocoa or other understory crops that enrich structural complexity, can significantly enhance habitat quality relative to monoculture. Farmer-level practices such as retaining small trees, promoting vertical complexity, and reducing understory clearance should all contribute to improved bird habitat based on observations from other agroforestry systems (De Beenhouwer *et al* 2013, Arroyo-Rodríguez *et al* 2020, Yahya *et al* 2022).

Second, conserving large tracts of contiguous forest within and around coconut-producing landscapes is paramount. Large tracts of forest not only sustain higher biodiversity but also amplify the ecological value of surrounding agroforests by enabling species spillover (Morante-Filho *et al* 2018, Cabral *et al* 2021). Landscape planning that integrates forest conservation with diverse planted trees in the form of agroforestry offers the greatest potential for biodiversity-friendly coconut production, with higher bird diversity within plantations providing ecosystem services, particularly natural pest suppression, that can reduce pesticide reliance and potentially increase yields (Maas *et al* 2016, Arroyo-Rodríguez *et al* 2020, Messier *et al* 2022).

Third, country-led sustainability initiatives and voluntary certification schemes should incorporate biodiversity safeguards that explicitly recognize the value of forest–coconut interfaces and agroforestry practices. Schemes such as the Sustainable Coconut Partnership (www.coconutpartnership.org/) or cross-commodity collaborations with Rainforest Alliance (www.rainforest-alliance.org/) could embed ecological criteria (such as proximity to forest, retention of intercropped, and vertical vegetation structure) into certification standards. Even the more established certification standard, the Roundtable on Sustainable Palm Oil (RSPO), in its latest 2024 principles and criteria (<https://rspo.org/>), still provides limited guidance explicitly referring to agroforestry practices. Nevertheless, diversified plantings and intercropped are clearly compatible with, and can help demonstrate RSPO compliance with pest management, soil, water, carbon stock, and conservation indicators. Our study promotes the concept of agroforestry as a crucial prescription within sustainability standards and would align coconut with broader conservation efforts already in place for cocoa, coffee, and palm oil.

Finally, future research should integrate ecological monitoring with socio-economic and governance dimensions of these systems. Coconut production in North Sulawesi is dominated by smallholder farmers managing plots of only 2–4 ha. Their management choices, shaped by economic incentives and market access, directly influence biodiversity outcomes. Research linking ecological monitoring with farmer livelihoods, value chains, and certification uptake will be critical for identifying scalable interventions that balance production and conservation goals. Such research has strong potential to guide the formulation of certification schemes for managers to put biodiversity friendly agroforestry practices in place.

Acknowledgments

This work was supported by the ARIES-SeNSS Doctoral Training programme (Project Ref. 2872410) as part of a PhD studentship awarded to R B by the UK Natural Environment Research Council (NERC) and Chester Zoo (Award No. NE/S007334/1), and a Leverhulme Research Leader Award (RL-2019-054) granted to M J S's research team. We thank Indonesia's National Research and Innovation Agency (BRIN) and Ministry for Environment and Forestry for providing permissions and ethical clearance to conduct our research in Sulawesi, and the numerous coconut farmers who allowed us access to their land.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.5281/zenodo.19552445>.

Supplementary information available at <https://doi.org/10.1088/2752-664X/ae7605/data1>.

Conflict of interest

The authors have no conflicts of interest to report.

Ethics statement

Ethical approval was provided by Indonesia's National Research and Innovation Agency (BRIN), and the University of Kent Research Ethics Board.

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