RESEARCH ARTICLE

No evidence for trade-offs between bird diversity, yield and water table depth on oil palm smallholdings: Implications for tropical peatland landscape restoration

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Abstract

1. Tropical peat swamp forests retain large carbon stocks and support unique biodiversity, but clearance and drainage for agriculture have resulted in fires, carbon emissions and biodiversity losses. Initiatives to re-wet cultivated peatlands may benefit biodiversity if this protects remaining forests from fire and agricultural encroachment, but there are concerns that re-wetting could reduce yields and damage livelihoods, as relationships between drainage, on-farm biodiversity, and crop yields have not been studied.

2. We examined oil palm fruit yields and bird diversity on 41 smallholder farms in Jambi (Sumatra, Indonesia), which varied in drainage intensity (12-month mean water table per plot from August 2018 to August 2019: −52 to −3 cm belowground). We also compared farm bird diversity with a neighbouring area of protected peat swamp forest (11,000 ha, 21 plots; mean water table per plot −3 to +15 cm).

3. Bird species richness (3–18 species per plot), species composition and oil palm yields (4.5–19.2 t fresh fruit bunch ha^{-1} year^{-1}) varied among farms, but were not detectably affected by water table depth, although ground-level vegetation was more complex on wetter farms. Bird richness in oil palm (mean = 10.3 species per plot) was <50% of that in forest (26 species per

plot), and only 3 of 35 conservation-priority species found in forest were recorded in oil palm.

4. *Synthesis and applications*. Tropical peatlands in Indonesia have been drained to allow farmer access and improve farm yields, but we found no trade-offs between drainage depth, yields and bird diversity on smallholder oil palm farms in our study landscape within the studied range of drainage depths. Current restoration initiatives to re-wet peat may benefit farmers by reducing fire risk, without affecting yields. Wetter farms had increased understorey vegetation complexity, but this did not affect bird diversity, so we find no evidence that re-wetting improves on-farm biodiversity. However, on-farm fire reduction efforts in cultivated peatlands, including re-wetting, will be vital for reducing the risk of fires escaping into nearby forests, which contain unique and diverse bird species assemblages. Protection of remaining peatland forests from fire and clearance is key for biodiversity conservation, and for providing a source of seed dispersers and genetic material for future forest and landscape restoration efforts. Restoration of more biodiversity-friendly land covers will improve landscape permeability and help conserve species and the ecosystem services they deliver.

1 | INTRODUCTION

Tropical peatlands in Southeast Asia contain large below-ground carbon stocks, and peat swamp forests contain unique and threatened biodiversity. However, peat forests have been cleared and peatlands drained for cultivation, resulting in carbon emissions, biodiversity losses and land subsidence (Posa et al., 2011; Wijedasa et al., 2018). Peat deposits are formed when waterlogged conditions prevent microbial decomposition of vegetation, creating accumulations of extremely carbon-rich, water-retentive and acidic soils (peatlands cover just 3% of global land area, but contain 32%–46% of all soil carbon) that accumulate over thousands of years, forming a net carbon sink (Page & Hooijer, 2016). Drainage of tropical peatlands to allow access for agriculture or development, via digging of drainage canals, draws the water table down below the soil surface, exposing peat to the air where it decomposes and releases stored carbon, leading to land subsidence, peat loss and carbon emissions. Dry peat is also very flammable, making drained tropical peatlands vulnerable to fires; in Southeast Asia peat fires cause trans-boundary haze, particularly during droughts associated with El Niño Southern Oscillation (ENSO) years, damaging human health and the regional economy, threatening local livelihoods, and putting remaining peat forests and their biodiversity at risk of loss (Page & Hooijer, 2016).

Indonesia is estimated to contain 47% of global tropical peatlands, chiefly on the islands of Borneo and Sumatra (Page et al., 2011). Forests covered 76% of Sumatra's peatland in 1990, but by 2015 66% was covered by smallholder agriculture or industrial plantations, primarily of oil palm and pulpwood (Miettinen et al., 2012, 2016). Drainage is considered necessary to maintain oil palm yields, because prolonged flooding reduces fruit production as roots cannot respire under prolonged inundation (Woittiez et al., 2017). However, peatland drainage means Sumatra is now a hotspot for peat fires (Page & Hooijer, 2016). Peatland restoration activities are now underway across Indonesia, mostly focused on re-wetting cultivated areas by blocking drainage canals to reduce the risk of fires, driven by the establishment of new legislative requirements (Dohong et al., 2018).

Legislation in Indonesia now mandates average water table depths of −40 cm (below the surface) in cultivated peatlands within active agricultural land concessions (Wijedasa et al., 2018). Regulations stipulate that water tables in the centre of plantation blocks should be maintained above −100 cm at all times, and −40 cm for half of the year, in contrast to the −70 cm drainage depth used in standard operating procedures for plantations (Evans et al., 2019). The −40 cm standard is also used as a target in other restoration activities, such as the Indonesia Peat Restoration Agency's (Badan Restorasi Gambut; BRG) work in smallholder oil palm, although resource limitations strongly constrain capacity to monitor water table depths outside of large concessions. Existing restoration projects in Central Kalimantan, Indonesia, have used -40 cm as a minimum threshold, rather than a mean, water table depth (Dohong et al., 2018), given evidence that the risk of peat ground fires is greater when water tables fall below this level (Page et al., 2009). Thus, there are compelling reasons to raise water tables, but the

consequences of re-wetting peatlands for oil palm cultivation on peat have been little studied.

In the longer term, complete withdrawal of drainage-dependent agriculture from peatlands in Sumatra may take place, and indeed is necessary if a substantial decrease in carbon emissions from peat degradation is to be achieved (Afriyanti et al., 2019), provided that alternative systems can offer comparable livelihood and economic benefits (Tan et al., 2021). Subsidence of cultivated peatland due to drainage may also mean cultivation is forced to cease, due to regular inundation (Wijedasa et al., 2018). In this case, forest restoration on degraded peatlands may become a more viable land-management option. The presence of remaining intact peat forest in the landscape will be essential for restoration success, by providing sources of seeds and seed-dispersing agents, such as frugivorous birds (Wijedasa et al., 2020).

Smallholders produce around 40% of palm oil globally, but yields vary greatly (Woittiez et al., 2017) and tend to be much lower than those of industrial plantations (Lee et al., 2014). On smallholder farms, drainage depth could affect management intensity of oil palm, shifting biodiversity-yield trade-offs (e.g. as outlined by Grass et al., 2020) towards lower intensity systems, while flooding may damage oil palm trees (Woittiez et al., 2017). Farms that are more shallowly drained (and periodically flood) may be challenging to access, increasing the difficulty of harvesting and management activities such as weeding and fertiliser application that could increase yields. Thus, shallowly drained (wetter) farms could be expected to have lower yields but greater on-farm biodiversity. However, despite evidence from Sumatra for biodiversity-yield trade-offs (Teuscher et al., 2015), the wide variation in smallholder oil palm yields is difficult to explain (Lee et al., 2014), and evidence from other smallholder production systems in the tropics indicate space for biodiversity improvements through management changes without yield declines (Clough et al., 2011). Recent work has also shown that maintenance of understorey vegetation may be beneficial for oil palm by improving soil health (Darras et al., 2019). To our knowledge, there is currently no information on responses of peatland oil palm yields to water table depth and farm management. A better understanding of possible trade-offs between oil palm yields and biodiversity is, however, key to appreciating the possible ecological and livelihood impacts of re-wetting restoration schemes and to guide farm management practices.

Birds are an important study taxon for understanding biodiversity responses to peatland oil palm management, as their habitat requirements and conservation status are well understood. For example, bird diversity in oil palm landscapes varies in relation to understorey vegetation, native tree diversity, canopy cover and distance to forest (Aratrakorn et al., 2006; Azhar et al., 2014; Hamer et al., 2021; Teuscher et al., 2015). In the context of peatland oil palm, canopy cover may be affected by drainage depth because oil palms can lean or fall in very wet ground (Woittiez et al., 2017). Additionally, vegetation structure of the herbaceous understorey on smallholder farms may be more complex in wetter areas, due to altered weeding practices, or if soil moisture conditions are more

favourable for peatland plant species. These drainage-induced changes may indirectly affect bird diversity on oil palm farms.

Birds are also an excellent taxon for examining the effects of habitat change on community structure and ecosystem functioning through changes in functional traits, such as feeding guild and body mass (Darras et al., 2018; Edwards et al., 2013; Prabowo et al., 2016). These avian traits are particularly important in the context of peatland restoration at the landscape scale. Therefore, examining bird species diversity, composition and functional traits in remaining peat swamp forest fragments is also important for understanding impacts of drainage in predominantly cultivated peatland landscapes.

The extent and severity of recent fires on tropical peatlands negatively impact health and livelihoods, making restoration activities vital, but the consequences of re-wetting and any trade-offs with yield or biodiversity must be understood. The ecological effects of re-wetting are poorly understood, and in many cases canal blocking activities have not yet been completed. However, variation in drainage depth across peatland landscapes provides opportunities to study yields and biodiversity in areas that vary from shallow to more deeply drained peat. In this study, we examine how variation in water table depth affects vegetation structure, avian diversity and oil palm yields on smallholder farms across a peatland landscape in Sumatra. We ask whether bird species richness, abundance and community composition are related to water table depth (drainage intensity) via changes in vegetation structural complexity on farms, and whether oil palm yields are reduced in shallowly drained (wetter) oil palm farms relative to more deeply drained farms. We also compare bird species in oil palm with a nearby protected peat forest fragment (~10,000 ha), to understand changes in diversity and ecological function following conversion of peat swamp forest to oil palm, and to assess the importance of conserving forest fragments for future restoration initiatives.

2 | MATERIALS AND METHODS

Permission to collect data was granted by Ristekdikti, The Ministry of Research, Technology and Higher Education, The Republic of Indonesia, under research permit numbers 198/SIP/FRP/E5/Dit.KI/VII/2018 and 199/SIP/FRP/E5/Dit.KI/VII/2018.

2.1 | Study location

The study was conducted in Jambi province, Sumatra, Indonesia. The study landscape lies on a single peat dome (a hydrological unit of connected peatland) that had been mostly drained for cultivation, leaving a single remaining peat forest fragment (Figure 1A). Drainage canals 2–3 m wide ran alongside the main access roads, and smaller hand-dug canals were found within the oil palm *Elaeis guineensis* smallholdings. The forest contained a patchy distribution of shallow hand-dug drainage canals, formerly used to extract timber, with wider drainage canals adjacent to the perimeter road and
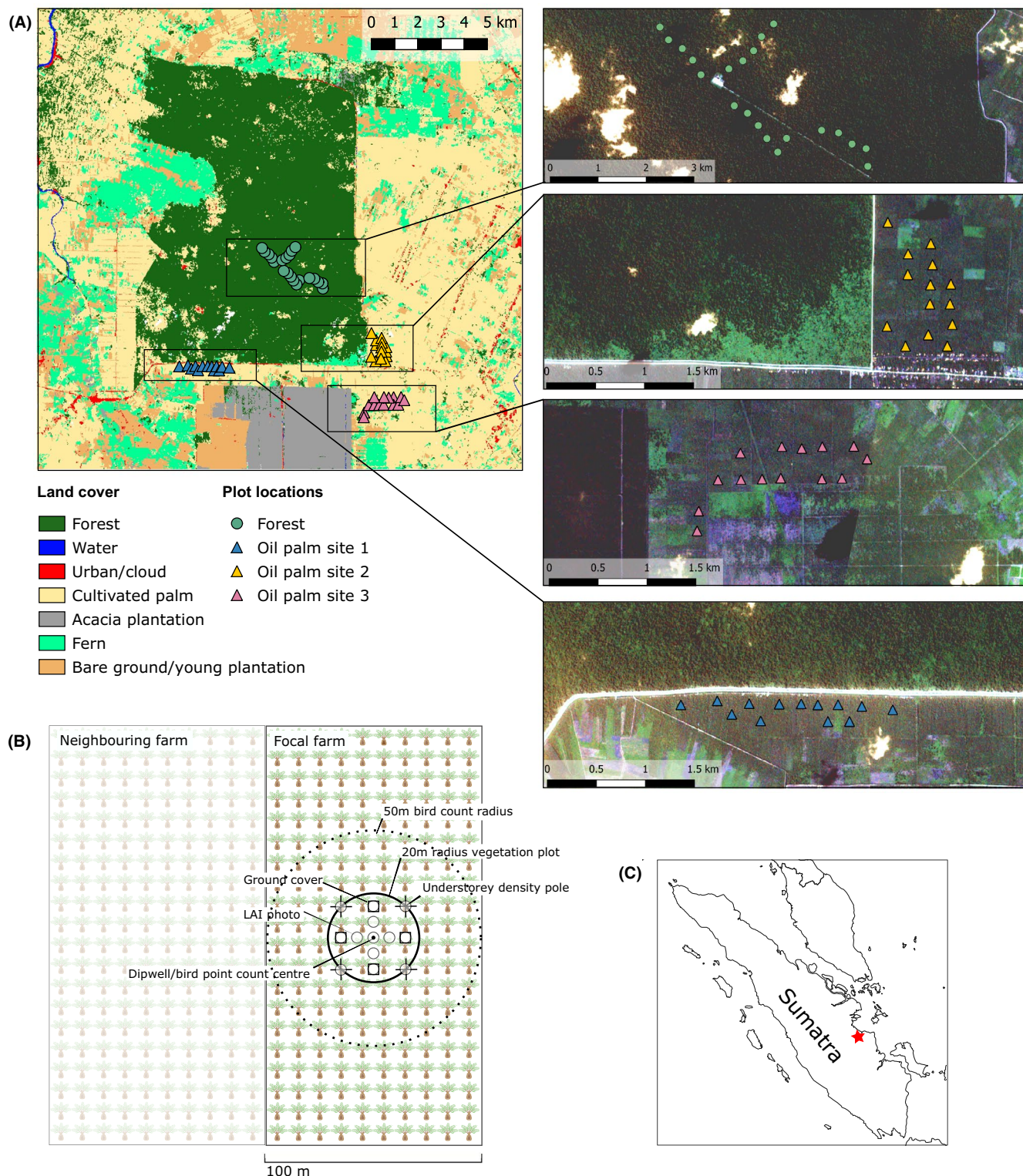
FIGURE 1 (A) Map of study area showing plots in forest and at three oil palm sites that vary in water table depth (Site 1, Site 2 and Site 3); land cover classification based on fusion of optical and radar sentinel data at 10 m resolution, with temporal information and ground-truthing conducted specifically for this study landscape; please refer to Crowson et al. (2018) and Lopes et al. (2020) for specific methods, error rates and definitions of land cover categories; inset aerial photographs of plots at each site/forest provided under licence via the Education and Research Program of Planet Labs PBC (2017). (B) sampling design for water table depth, bird diversity (50 m radius) leaf area index (LAI photo) and vegetation structure (20 m radius), shown within an oil palm smallholder farm, but an identical sampling design was used in forest; (C) location of study landscape on Sumatra

an access road that ran to the centre of the forest patch (established during surveys by a petrochemical company). Industrial *Acacia* spp. plantations lay south of the forest, while smallholdings of palm lay to the north, east and west. To the east and south, where study plots were located, the farms were all monocultural oil palm smallholdings (photographs Figure S1 in Supporting Information), while to the west some palm areas also contained betel *Areca catechu* and coconut *Cocos nucifera* which are indistinguishable using remote sensing (Lopes et al., 2020). We only studied monocultural oil palm smallholdings.

Canal blocking activities to re-wet parts of the drained smallholder oil palm areas had been planned by the BRG, but no canal blocks had yet been installed at the time of our study. We therefore used a space-for-time approach to assess the effect of water table variation, which also allowed us to assess the longer term effects of water table variation that may not manifest immediately after canal blocking activities. We established 41 sampling plots in oil palm farms in three areas (one plot per farm; farm area 2–15 ha, sites termed Site 1, Site 2 and Site 3) known from pilot fieldwork to show variation in water table depth, both within and between sites. Farmers were contacted through the head of their farmer group and were invited to voluntarily participate in the study, resulting in a clustered sampling design (Figure 1A). Those famers who agreed to participate permitted the field team to conduct surveys and install dipwells on their farms (Figure 1B), and verbally completed a questionnaire about their peatland farms (details below).

We also established 21 plots in an adjacent area of protected forest (Sungai Buluh Peat Protection Forest/Hutan Lindung Gambut) to use as reference site to indicate water table variation in the landscape under minimal drainage (i.e. to understand the potential for water table recovery in this landscape), and to capture data on the biodiversity value of unprotected forest fragments in cultivated peatland landscapes for bird diversity, composition and functional traits. The forest had been commercially selectively logged sometime after 1980, but the date of cessation is unknown (see Galudra et al., 2014 for history of neighbouring district) and is the largest block of remaining forest (~10,000 ha in 2018) in the locality, because larger extents of neighbouring forest were cleared after 2000. Some illegal logging activity has taken place in the fragment since commercial logging ceased, and areas of forest were lost to fires in 1997 (the southeast corner) and 2015 (central-northwest patch; Figure 1A).

The centres of plots were at least 200 m apart and located in the centre of each farm. Peat depth was measured in each plot with a peat auger until a mineral clay layer was found, up to the maximum measurable depth of 5 m. Peat depths ranged from 1.15 m to >5.00 m across all plots, and were similar between forest and oil palm sites (mean = 3.3 m forest, 2.8 m Site 1, 4.1 m Site 2 and 3.8 m Site 3).

Bird species presence on farms can be affected by the distance to areas of forest remaining in the wider cultivated landscape (Azhar et al., 2011), which act as population sources (Hamer et al., 2021). We therefore used land cover data and aerial imagery (Figure 1A)

from existing analysis (Crowson et al., 2018; Lopes et al., 2020) to calculate the distance from plot centroids to the edge of the contiguous forest cover within the forest fragment, to use as a co-variate in analyses of bird diversity in oil palm. Understorey vegetation of oil palm farms (27 plant species recorded across all plots; Table S1) was dominated by the fern *Nephrolepis falcate* and the herb *Asystasia gangetica*. The forest included peat-specialist trees *Dyera lowii* and *Shorea uliginosa*, the critically endangered *Vatica teysmanniana* and *Gonystylus bancanus*, and the gap specialist species *Macaranga pruinosa*, reflecting its disturbance history.

2.2 | Bird surveys and functional traits

We collected data on bird species at each oil palm and forest plot to establish species richness, abundance, biomass and species composition, and to establish the representation of species of conservation concern, habitat specificity and functional traits that are important in the context of ecosystem function and future landscape restoration. Birds were surveyed at all 62 plots using 15-min point counts on four consecutive mornings (06:00–10:00) during August–October 2018 (Edwards et al., 2014). Visits were rotated so each plot was surveyed early, middle and late in the morning. All birds seen or heard within 50 m were recorded, but flyovers and fly-throughs were not included in analysis, because we could not confirm that they were using the study plot. All surveys were recorded (Olympus LS-10 digital recorder) to confirm species' identifications and check unknown sounds against verified recordings on Xeno-Canto (xeno-canto.org). All surveys were conducted by the same experienced ornithologist (PGA), who used a 2-week pilot phase to become familiar with birds in the area. Bird species richness per plot was calculated as the total of all species recorded at each plot across all four visits (including migratory species recorded within the plots, highlighted in Table S2). Total abundance per plot was calculated as the sum of the maximum number of individuals detected on any single visit per species, to avoid the risk of double-counting individuals.

Bird species habitat dependence was defined based on IUCN status (IUCN, 2019) and the Handbook of Birds of the World (del Hoyo et al., 2017), and was used to determine the capacity for oil palm plots to support species usually dependent on forests. Species were defined as 'forest dependent' if found in primary, secondary or disturbed forest, as 'high tree-cover dependent' if also reported from plantations, 'generalist' if reported from both forest and non-forest habitats, and 'open habitat species' if found only in non-forest habitats. Conservation-priority species were defined as those with IUCN status of Near Threatened, Vulnerable, Endangered or Critically Endangered.

For forest-oil palm comparisons, each bird species was assigned to one of five diet groups based on the Elton Traits database variable 'Diet-5Cat', according to their predominant diets (Wilman et al., 2014). Total bird abundance, as calculated above, was assigned to the feeding guilds, to give plot-level abundance per feeding guild. Community-weighted avian body mass was calculated per plot by

multiplying the abundance of each species by a mass value for an individual, and summing across all species (Darras et al., 2018). Body mass for each species was taken from the Handbook of Birds of the World (del Hoyo et al., 2017).

2.3 | Water table monitoring

Water table depths were manually recorded at each plot every fortnight from August 2018 to August 2019, using a 2 m dipwell installed at the centre of each plot (further methodology and schematic, Figure S2). Southern Sumatra has a marked dry season from July to September (Aldrian & Dwi Susanto, 2003), meaning our sampling period captured the end of the 2018 dry season, the 2018–2019 wet season and the start of the 2019 dry season. Rainfall in this region is reduced during ENSO events (Qian, 2019). A strong ENSO event occurred in 2015–2016, and a weaker event was underway for the duration of this study (NOAA/National Weather Service, 2019). A range of water table depth indices were calculated for each plot for the whole monitoring period (including maximum depth, number of records below 40 cm, and others) to test whether indices other than mean average water table could be informative, but these correlated strongly with each other (correlation plot, Figure S3) so we used mean water table depth in our study because this is used in legislation (Wijedasa et al., 2018), and is often reported in other peat studies. Manual measurements were supplemented by four water table depth loggers recording every 15 min (Seametrics/Van Walt LevelSCOUT 10 m), installed in one dipwell at each of the three oil palm sites and the forest site. Together with rainfall data (manually recorded daily at Sites 1 and 2) these acted as a sense-check, and showed the response of water table to precipitation, including the rapid decline in water tables with the onset of the dry season in June/July 2019 (logger vs. manual water table depths and rainfall, Figure S4).

2.4 | Vegetation structure and soil pH

We assessed the ecological impacts of farm management by quantifying the structural complexity of vegetation at each oil palm plot, and measuring soil pH. We measured six variables within a 20 m radius of the bird sampling point (Figure 1B): identity and diameter at breast height (DBH) of all non-oil palm trees ≥10 cm DBH (all trees were cultivated species); number of fallen or leaning oil palms; number of sections of a 2 m pole visible at a distance of 14 m from the plot centre (understorey density index, a measure of vertical complexity, recorded four times to the NE, NW, SE and SW (Barlow et al., 2007); herbaceous ground vegetation cover (estimated in a 1 m^2 quadrat) and height (to the nearest 10 cm, recorded four times N, S, E and W of the plot centre), and leaf area index (LAI) and canopy cover (Global LAI Project protocol, Supplementary Text S1). Maximum density of non-oil palm trees was only 0.5 stems ha^{-1} and most farms had none, so this variable was excluded from analysis (photograph of farms, Figure S1). Correlations existed among these variables (correlations

plot, Figure S5), so we analysed them using principal component analysis (PCA) to produce two principal components that together explained 70% of variance (43% by PC1 and 27% by PC2; Table S2), and enabled a reduced number of variables to be included in our statistical models, reducing the risk of over-fitting. We interpret PC1 as measuring complexity of the herbaceous ground vegetation (higher values mean greater complexity), and PC2 as measuring vertical vegetation structure and canopy openness (higher values mean greater vertical complexity, fewer fallen/leaning oil palms and a more open canopy). Soil pH (method in Table S3) was acidic, ranging from 2.83 to 3.81 in the forest, and 3.06 to 4.30 on oil palm farms.

2.5 | Oil palm yields

All farms contained mature fruiting oil palms (age 6–26 years since planting). All farmers were independent smallholders, who sold their fresh fruit bunches to oil palm mills through a local broker. Questionnaires, conducted with each farmer, collected information about annual oil palm yield estimates per plot, and other information on farm management, including frequency and amount of chemical applications, oil palm age, harvesting frequency, weeding practices and removal of dead fronds from palms (questionnaire, Supplementary Text S2 and Ward et al., 2021). Questionnaires were conducted by research assistants from the University of Jambi. The questionnaire was approved by the University of Leeds Ethics Committee before data collection started.

2.6 | Statistical analysis

Statistical analyses were conducted using plots as independent samples (excluding one of the 41 plots for which complete water table data were unavailable, $n = 40$ plots), as each farm is a unit managed independently by farmers (affecting vegetation and water tables), and bird survey points at the centre of plots were sufficiently far apart to be considered independent samples. We also used site as an explanatory variable in all models, to ask whether changes in bird occurrence, vegetation complexity or water table depths occurred at a wider spatial scale, that is, between sites. All analyses were conducted in R (R Core Team, 2018). We compared models using Akaike's information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). The best model was defined as having the lowest AICc of the model set (whether multiple alternative models, or a null model compared to a single alternative model).

To examine whether bird species richness, abundance and composition were related to water table depth (drainage intensity) on oil palm farms via changes in vegetation structural complexity, we first fitted a general linear model of the two vegetation complexity principal components (PC1, PC2), with mean water table depth and site as explanatory variables. These models tested whether drainage affected on-farm vegetation at the plot or site scales.

Next, we examined the response of bird species richness and total bird abundance to vegetation complexity on oil palm farms, as well as distance to forest edge, and site. We fitted models with a full set of explanatory variables, sub-models of all combinations of the variables, and a null model to identify the most informative model structure (based on comparison of AICc of standardised models). All models were Poisson log-link generalised linear models fitted using the BBMLE package (Bolker & R Development Core Team, 2017). Predictions were made from the most informative model.

Bird species composition response to the same variables was analysed using the Bray–Curtis dissimilarity index and non-metric multi-dimensional scaling (NMDS; based on abundance data with a Wisconsin double standardisation; Edwards et al., 2014). NMDS scores were correlated with environmental variables (vectors), or averages compared between factor levels, with 'significance' testing using 999 permutations of the environmental factors. Analysis was conducted using the metaMDS and envfit functions in the VEGAN package (Oksanen et al., 2017).

We examined variation in oil palm yields (fresh fruit bunch tonnes ha^{-1} year^{-1}) in relation to water table depth on farms, by fitting a general linear model and assessing AICc compared to a null model ($n = 39$ farms, omitting one farm for which yield data were not available). Nine a-priori defined alternative models of yield response to management practices were also fitted (variables Table S3, model structures Table S4) designed to investigate multiple aspects of oil palm management previously found to affect yields (Lee et al., 2014; Woittiez et al., 2017), including tree age, competition from weed growth, fertiliser application, plot management (frond removal and harvest frequency), soil pH and tree health (using leaf area index and the number of fallen or leaning trees). We were unable to use questionnaire responses on weed management in any models, as most respondents did not quantify their weeding practices. These models excluded plots for which yield data ($n = 1$), complete water table data ($n = 1$) and oil palm tree age ($n = 5$) were unknown, leaving $n = 33$ farms.

Finally, to consider the role played by the forest fragment on bird diversity in the study landscape, total bird species richness was compared between the forest plots and oil palm plots using individual-based rarefaction to account for differing sample sizes, including calculation of asymptotic species richness, using the iNEXT package in R (Chao et al., 2014). Bird abundance, species richness, abundance per feeding guild and (natural-log-transformed) community-weighted body mass (used as a measure of ecosystem function, with body size an important indicator of species function) per plot were also compared between forest and oil palm using linear models, as above, and an NMDS ordination was applied to test for differences in species composition.

2.7 | Power analysis

We conducted a power analysis to support the interpretation of the modelled relationships in our study, in order to quantify the size of

effect (R2, proportion of variance explained) we would be able to detect with our dataset, given specified Type 2 error thresholds. Di Stefano (2003) shows that the risk of making Type 2 errors (i.e. a false negative result) can be as harmful as making a Type 1 error (i.e. a false positive). In our case, erroneously concluding that there is no effect of drainage on oil palm yields, or avian biodiversity, is equally as concerning as erroneously concluding that there are trade-offs. In the case of oil palm yields, the risk of making a Type 2 error (concluding there is no effect, when there is one) is that further management to raise water tables within the ranges measured in this study could have unforeseen negative impacts on farmer yields, damaging livelihoods and reducing income. The risk of a Type 2 error in conclusions around bird diversity is less serious, but a Type 1 error (concluding there is an effect, when there is not one) could result in expected conservation gains from re-wetting not being realised.

We therefore assessed the size of effect (R2, proportion of explained variance) that would be detectable with a sample size of 40, 39 and 33 farms (reflecting the sample sizes outlined above), assuming significance levels of 0.05 (alpha, Type 1 error rates, of 5%), and power of 80% (beta, Type 2 error rates, of 20%) are acceptable, but also considering power thresholds of 90% and 95%, (Type 2 error rates of 10% and 5% respectively).

We used the PWR package in R (Champely, 2021) to estimate the sample size that would be needed to detect 10%, 20%, 30%, 40% or 50% of explained variance in a response variable to either a single predictor, or two predictor variables in a linear model (such as the response of oil palm yields to water table depth, or bird species richness response to vegetation complexity and site), using a significance level of 0.05 (5% Type 1 error rate) and a power of 80%, 90% or 95% (20%, 10% or 5% Type 2 error rates). These results are shown in Figure S6 and Table S5, and are used to assist interpretation of our model results.

3 | RESULTS

3.1 | Drainage and water table depth on farms

The entire study landscape had been drained with canals, but fortnightly water table depth measures across the 40 smallholder farms were highly variable, ranging from −169 cm to +23 cm during the study period. Hence, our farm study sites spanned a range of drainage intensities, from wet to moderately drained, representing the variation found within smallholder oil palm farms in the study landscape. Twelve-month mean (± SD) water table depths per oil palm plot ranged from −51.5 ± 29.8 cm to −6.0 ± 18.9 cm, meaning some farms were drained below the recommended -40 cm depth (as calculated on an annual average basis), and many farms had water tables below the 40 cm threshold for part of the year (Figure 2B). Site 1 farms were relatively less severely drained than those at Sites 2 or 3 (Figure 2A), but the overall mean water table depth of −27.8 ± 25.9 cm across all plots means that the surveyed landscape as a whole complied with legislative requirements for agricultural
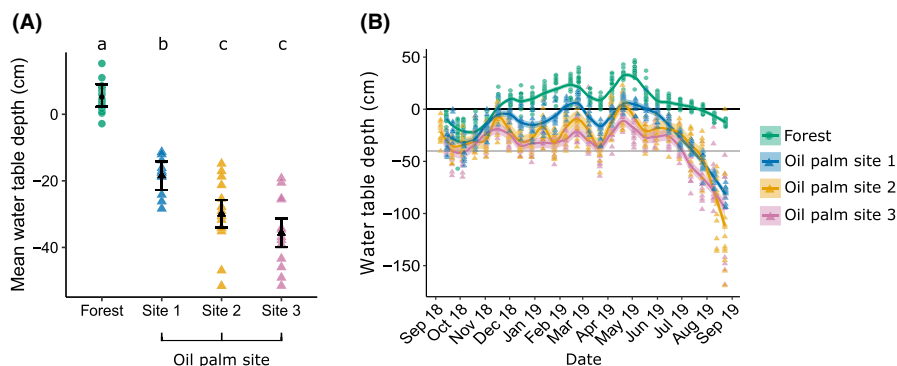
FIGURE 2 (A) Data points show mean water table depth per plot (across the 12 month monitoring period), point and range shows model predictions with 95% CI; mean water tables differed between forest and all three farm sites, and between Site 1 and Sites 2 and 3 (model of water table response to site and forest ΔAICc −104.2 relative to null model; letters are used to show differences; coefficients and CI: forest 5.6 ± 3.3 cm; relative to forest, Site 1 −24.1 ± 5.34 cm, Site 2 −35.5 ± 5.23 cm, Site 3 −41.3 ± 5.34 cm); (B) water table depths in forest and oil palm sites are shown from 7 September 2018 to 24 August 2019, with a loess smoothed curve (span = 0.2) and standard error per site. Water tables were above the soil surface (black line at 0 cm) during the rainy season in forest, but in oil palm, generally remained below the soil surface. Reduced rainfall in 2019 relative to 2018 explains the rapid drop in water tables at all three sites (Figure S4). Light grey line at −40 cm indicates legislated mean water table depth for active agricultural concessions in Indonesia (Wijedasa et al., 2018)

concessions to maintain mean water table depths −40 cm over the study period. However, due to reduced rainfall (Figure S4) water tables on farms were much lower in the dry season of September 2019, when levels mostly dropped below −40 cm from July onwards, compared with September 2018 when most farms stayed above the −40 cm threshold (Figure 2B). As expected, smallholdings were drier than forest plots, which had a mean depth of −5.6 ± 16.7 cm over the same period.

3.2 | Vegetation structure and drainage of farms

The model of PC1 score (complexity of herbaceous ground vegetation) response to water table depth and site (ΔAICc −7.4 relative to null model, adjusted R^2 0.25) showed that there was no overall detectable relationship with water table depth across the measured gradient (coefficient and 95% CI: 0.02 ± 0.04 change in PC1 score per 1 cm of water table depth reduction). However, plots at Site 1 tended to have higher PC1 scores, and thus greater herbaceous ground vegetation complexity than Sites 2 or 3 (compared to Site 1, Site 2 PC1 score −1.44 ± 1.08, and Site 3 PC1 score −2.59 ± 1.23; Figure 3A,B).

The PC2 score, representing vertical vegetation complexity and canopy openness, also varied among sites, but not with water table depth (ΔAICc −4.9 relative to null model, adjusted R^2 0.20). PC2 score differed by 1.62 ± 0.88 at Site 2 and 1.15 ± 0.99 at Site 3, relative to Site 1 (Figure 3C,D). Plots in Site 1, which was the wetter site, therefore tended to have reduced vertical complexity, a greater number of fallen/leaning palms and a less open canopy.

Taking these results together with the relationship between site and water tables (see above) shows that water tables and vegetation complexity co-varied at the site scale, but not farm scale. Therefore, we conclude that vegetation complexity could be influenced by other site-level effects that covary with water table effects.

3.3 | Variation in avian diversity in response to farm vegetation, distance to forest and among sites

In total, we observed 1093 individual birds in oil palm (maximum observed abundance of each species per plot on any single sampling day, summed across all plots), comprising 48 species (Table S2). Bird species richness varied among farms (3–18 species per farm), and the majority of species in oil palm were defined as generalist or open-habitat species (NMDS plot with habitat dependence, Figure S7).

We found no relationships between species richness of birds per plot on oil palm farms and any of the measured variables, with no models performing better than the null model (Table 1). There was also no difference in cumulative species richness among sites (rarefaction shown in Figure S8). Power analysis suggests that with our sample size (n = 40) we should have been able to detect effects where the R2 of a model containing one or two predictors was approximately 0.20 or below. Effect sizes smaller than this (i.e. resulting in a lower R2, or explaining less than 20% of variance in bird species richness) would likely be undetectable with our study design, so there is a possibility that smaller changes in bird species richness were present but not detected in this analysis. We conclude that vegetation complexity, moderated by water table depth, is not a strong driver of local bird species richness on oil palm farms.

However, the best model explaining variation in species abundance on farms revealed that abundance was lower on farms with lower vegetation complexity (PC1 score), greater distance to forest and at the driest Site 3 (ΔAICc −15.49 relative to null, r^2 = 0.30; Table 1, Figure 4), although all effect sizes were small.

Fitting environmental variables to an NMDS, based on Bray–Curtis dissimilarity, of bird species composition on farms showed that site had a small but significant influence on species composition, but there was considerable overlap in species composition of plots across all three sites (Table S6; Figure S9).
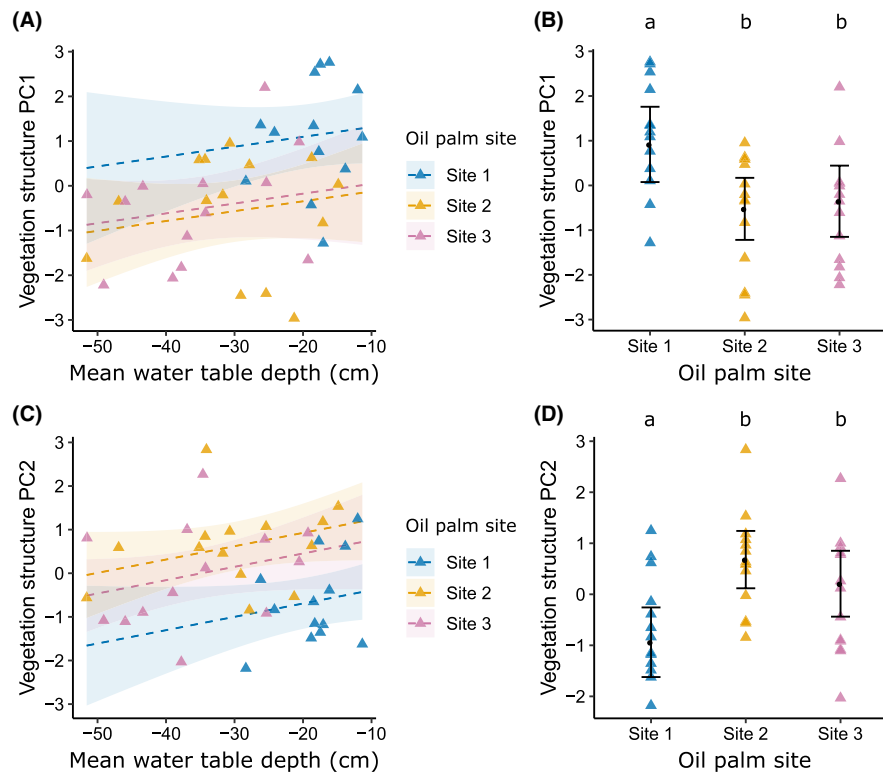
FIGURE 3 (A) Predicted values of vegetation principal component 1 (ground vegetation complexity) response to mean water table depth and site; dotted lines show predicted relationship between PC1 and water table depth per site, points are original data; coefficient for overall relationship: 0.02 ± 0.02 95% CI, that is, no relationship; (B) predicted values of PC1 per site relative to Site 1, Site 2 PC1 score −1.44 ± 0.55, and Site 3 PC1 score −2.59 ± 0.01, that is, greater understorey vegetation complexity at wetter Site 1 as indicated by letters; (C) predicted values of vegetation principal component 2 (vertical vegetation structure and canopy openness) response to water table depth and site; dotted lines show predicted relationship between PC2 and water table depth per site, points are original data; coefficient for overall relationship: 0.03 ± 0.04, that is, no relationship; (D) predicted values of PC2 per site relative to Site 1, Site 2 PC2 score 1.62 ± 0.88, and Site 3 PC2 score 1.15 ± 0.99, that is, reduced representing vertical vegetation complexity and canopy openness at wetter Site 1 as indicated by letters

3.4 | Oil palm yields responses to water table depth and management

Oil palm yields varied considerably among farms from 4.5 to 19.2 t ha^{-1} year^{-1} (mean 11.7 ± 4.2 SD t ha^{-1} year^{-1}). However, yields were not detectably related to drainage within the measured range of drainage depths (Figure 5), nor to any other measured variables representing management strategies, oil palm age, tree health chemical applications or by site (Table S4; Figure S10). Our power analysis indicated that smaller changes in yields would not have been detectable (i.e. we would not be able to detect effects that explained less than 20% of variance in oil palm yields; Figure S6). Thus, we conclude that variation in yields was driven by factors not examined in our study.

3.5 | Forest bird diversity and composition

Bird species richness on oil palm farms (total observed richness = 48 species, predicted asymptote 56 ± 6 SE) was about half of that in forest (observed = 90 species from 1,013 individuals, predicted

asymptote = 113 ± 12 SE; Figure 6A). Richness and abundance of birds per plot in oil palm (mean 10.3 ± 2.9 SD species; 26.9 ± 8.1 SD individuals) were also about half those of forest (mean 26 ± 3.9 SD species; 48.2 ± 15.3 SD individuals (Figure 6B,C, ΔAICc −195.6 relative to null richness model, ΔAICc −164.3 relative to null abundance model)).

The conservation value of the forest fragment for birds was confirmed by the occurrence of 35 conservation-priority bird species in forest, and only three in oil palm. Forest supported a very different avian community to farms (Figure 6D); none of the 18 forest-dependent bird species were found on farms, and only 26/123 bird species (21%) were recorded in both oil palm and forest (Table S2). Birds on farms were typically generalist and open-habitat species (Figure 6D), with smaller body mass (Figure S11). Oil palm supported fewer invertebrate-feeding birds, but a higher abundance of frugivores, nectarivores and granivores (Figure S12). These body mass patterns were primarily due to the absence of large-bodied frugivorous families (Bucerotidae and Trogonidae) on farms, which are important seed dispersers, as well as the absence or rarity of predominantly insectivorous bird families

TABLE 1 Models of bird species richness response to vegetation complexity, distance to forest and site on oil palm farms. No model of bird species richness was more informative than the null model, but the best model of bird abundance included site, forest distance and vegetation PC1 score

Response	Model	Intercept	Site	Distance to forest	Veg PC1	Veg PC2	df	logLik	AICc	Delta AICc	Weight
Species richness	Best	2.34				0.15	2	−97.34	199.01	0.00	0.23
	Null	2.34					1	−98.46	199.02	0.01	0.23
		2.34		0.06			2	−98.30	200.92	1.91	0.09
		2.34			0.05		2	−98.36	201.04	2.02	0.08
		2.34		0.05		0.14	3	−97.23	201.13	2.12	0.08
		2.34			0.05	0.15	3	−97.24	201.14	2.13	0.08
		2.26	+				3	−97.83	202.32	3.31	0.04
		2.34		0.09	0.08		3	−98.03	202.73	3.72	0.04
		2.34		0.07	0.07	0.14	4	−96.99	203.13	4.12	0.03
		2.20	+		0.15		4	−97.05	203.23	4.22	0.03
		2.30	+			0.13	4	−97.18	203.49	4.48	0.02
		2.27	+	0.01			4	−97.83	204.80	5.78	0.01
		2.24	+		0.12	0.10	5	−96.71	205.18	6.17	0.01
		2.28	+	0.18	0.16		5	−96.98	205.71	6.70	0.01
		2.32	+	0.06		0.13	5	−97.17	206.10	7.09	0.01
		2.32	+	0.18	0.13	0.10	6	−96.63	207.81	8.80	0.00
Abundance	Best	2.98	+	0.41	0.07		5.00	−132.70	277.17	0.00	0.54
		2.95	+	0.40	0.08	−0.04	6.00	−132.08	278.71	1.54	0.25
		3.07	+		0.06		4.00	−135.88	280.90	3.74	0.08
		3.04	+	0.29	0.06		5.00	−135.20	282.17	5.00	0.04
		3.09	+			−0.04	4.00	−136.71	282.57	5.40	0.04
		3.14	+				3.00	−138.37	283.41	6.24	0.02
		3.08	+	0.28		−0.01	5.00	−136.67	285.10	7.93	0.01
		3.13	+			−0.01	4.00	−138.26	285.66	8.49	0.01
		3.24		0.07			2.00	−143.23	290.78	13.61	0.00
		3.24		0.07		0.03	3.00	−142.66	291.98	14.81	0.00
		3.23		0.08	0.02		3.00	−142.93	292.52	15.35	0.00
	Null	3.31					1.00	−145.27	292.65	15.49	0.00
		3.31				0.03	2.00	−144.57	293.47	16.30	0.00
		3.23		0.08	0.02	0.03	4.00	−142.39	293.92	16.75	0.00
		3.31			0.00		2.00	−145.27	294.87	17.70	0.00
		3.31			0.00	0.03	3.00	−144.57	295.81	18.64	0.00
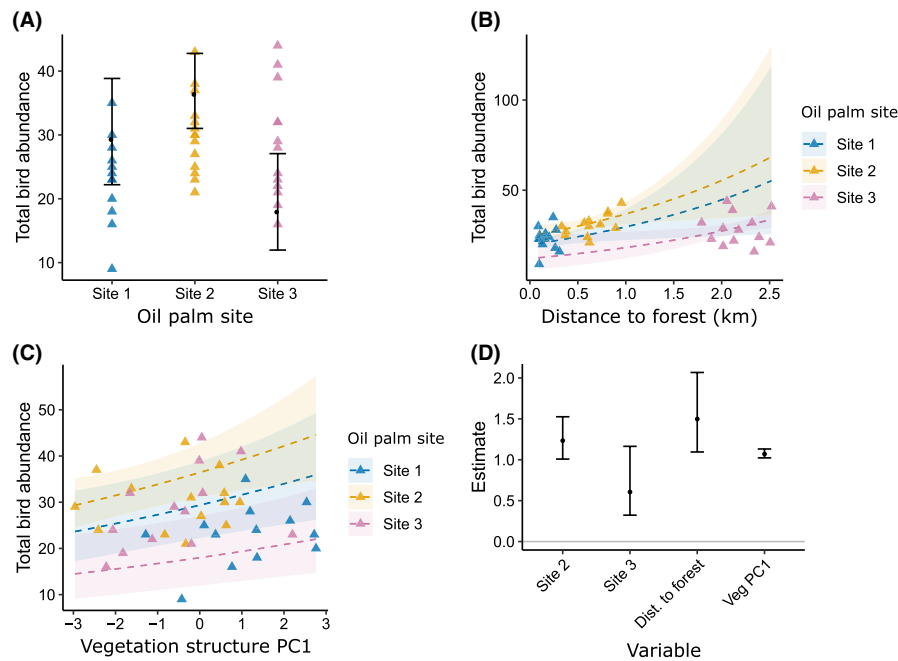
FIGURE 4 Results of model of total bird abundance per plot in response to site, distance to forest and vegetation structure; predictions made from whole model for each variable, holding other variables at mean/mid values: (A) predicted bird abundance per plot in Site 1 was 19.7 ± 2.7 individuals (95% CI), increased relative to Site 1 by 1.2 ± 0.2 in Site 2, and decreased by 0.6 ± 0.2 in Site 3; (B) predicted change in bird abundance with increasing distance to forest was 1.5 ± 0.4 individuals per km, with no detectable relationship within each site (dotted lines); (C) predicted change in bird abundance with increasing values of vegetation structure measure PC1 was 1.1 ± 0.1 individuals per unit of PC1, with no detectable relationship within each site (dotted lines); (D) all effect sizes were therefore small, and in many cases close to zero (effect sizes relative to intercept = Site 1)
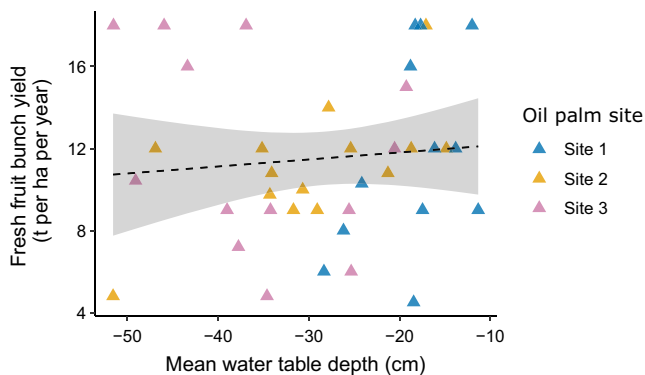

FIGURE 5 Oil palm yield response to water table depth, with prediction and SE from general linear model (n = 39) showing no relationship between reported yields and water table depth (model performed no better than null model, ΔAICc = 2.00, coefficient = 0.03 ± 0.12 t ha^{-1} year^{-1})

(Aegithinidae, Campephagidae, Chloropseidae, Dicruridae and Timaliidae) (Figure S13).

4 | DISCUSSION

We found variation among farms in water table depths, oil palm yields and avian biodiversity, but no evidence for any trade-offs between them within the range of drainage intensities we studied. Less heavily drained (i.e. wetter) farms had more complex ground vegetation, but there was no detectable relationship between the increased vegetation complexity on wetter farms and on-farm avian diversity, and no relationship between water table depth and oil palm yields. Power analysis indicated that our sample size was sufficient to detect effects resulting in a model R2 (proportion of explained variance) of 0.20 or above, but that we would have been unable to detect small effects that explained less than 20% of overall variation. Hence, we conclude that even with larger sample sizes, while we may have had better statistical power to explain small amounts of variation in response, the effect size would still be very small, and our overall conclusion would qualitatively be the same: that water tables had minimal influence on oil palm yields or bird diversity on oil palm farms in our study system. Avian richness and abundance were ~50% lower on farms than in neighbouring forest, and farm bird community composition was characterised by more generalist species, fewer invertebrate-feeding birds, higher abundance of frugivores, nectarivores and granivores, and species with smaller body masses. The forest fragment retained large-bodied frugivorous bird species that are important for future peatland restoration potential, and for retaining genetic diversity and gene flow among isolated forest fragments. However, the forest fragment is vulnerable to drainage and fires in surrounding cultivated land.
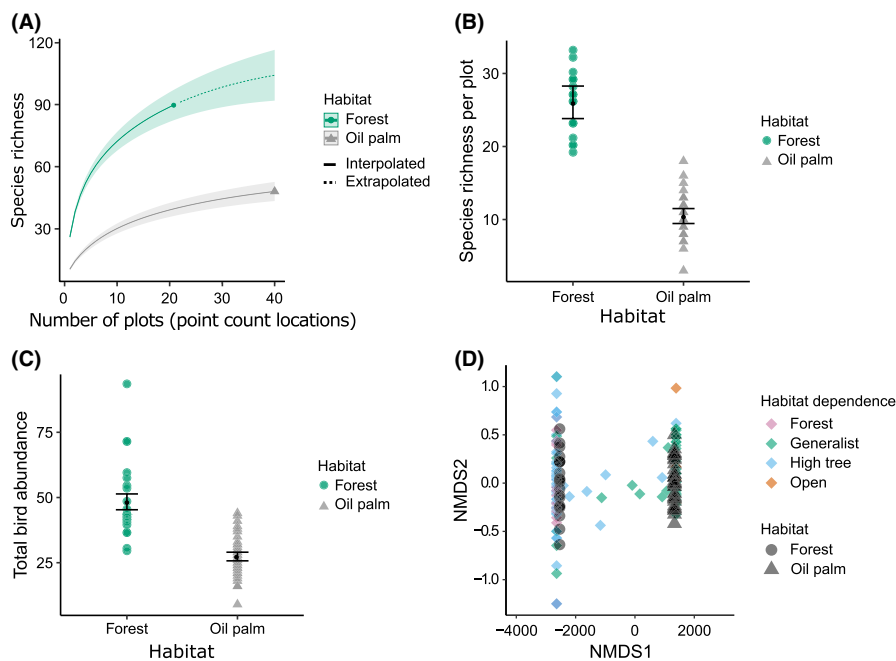
FIGURE 6 Bird species: (A) sample-based rarefaction in forest versus oil palm extrapolated to the largest sample size (oil palm, $n = 40$ farms/plots; FO = forest, OP = oil palm), (B) points show observed bird species richness per plot, error bar shows model prediction of 25.9 ± 2.0 species per plot in forest, reduced by a factor of 0.4 ± 2.1 in oil palm; (C) points show observed bird abundance per plot, error bar shows model prediction of 48.2 ± 1.1 individuals per plot in forest, reduced by a factor of 0.6 ± 2.0 in oil palm; (D) NMDS ordination of bird species composition across all plots, based on Bray–Curtis dissimilarity index and Wisconsin double standardisation (stress <0.01); plot points (grey triangles or circles) are positioned in space such that the distances between points match the dissimilarity ranking of the plots in multi-dimensional space according to Bray–Curtis dissimilarity (i.e. points further apart are less similar in species composition); species points are positioned in relation to plot scores, and represent the optimum position of each species in the NMDS space, and show that few species used both habitats. Species habitat dependence categories are defined in the methods

4.1 | Oil palm water tables, vegetation, yields and bird diversity

Our finding that understorey vegetation complexity was greater on farms with shallower water tables could be driven by at least two processes: increased soil moisture could favour peat-dependent herbaceous plants that might otherwise be suppressed by unfavourable dry soil conditions, or farmers could be reducing weed management due to access difficulties on wetter peatland. Given the similarity of plant species found across the 10 plots that had botanical surveys (Table S1), an effect of farm management seems more likely. However, farms with both higher water tables and greater vegetation complexity occurred at the same site (Site 1), that is, were spatially autocorrelated. Therefore, there may be differences in farm management practices among sites that are not linked to water tables. For example, farmer access to inputs, capital or differences in land tenure may affect management, and so our conclusions about the response of on-farm vegetation to variation in water table depths remain tentative.

The lack of detectable bird species richness and composition responses to vegetation complexity contrasts with other research emphasising the importance of understorey vegetation for enhanced bird richness in oil palm (e.g. Aratrakorn et al., 2006; Azhar et al., 2011). This lack of consensus may be due to differences in

heterogeneity of oil palm management across farms in different studies. For example, in Peninsular Malaysia, a positive effect of understorey vegetation on bird richness was seen only in polyculture oil palm farms, not in monocultures (Azhar et al., 2014). In our study landscape, the predominance of monocultural oil palm may result in fewer bird species capable of responding to local variation in understorey vegetation. While we sampled across the full range of understorey vegetation complexity in the study landscape (Figure S1) it is also possible that this range is limited relative to other landscapes. An alternative explanation is that the heterogeneity of farm management practices in a fine-grained mosaic (most plots were 100 m × 200 m in size) meant that birds were easily able to find relatively complex understorey vegetation within the wider landscape, and so local plot-level effects were not detectable.

While we have focussed on birds, variation in local vegetation complexity may influence other taxa, such as ants, termites, moths, beetles, butterflies, mammals or reptiles that respond to environmental change at different spatial or temporal scales (Neoh et al., 2017; Yong et al., 2016). For example, understorey vegetation affects mammal occurrence in oil palm in Colombia (Pardo et al., 2019). Peat swamp forests are also home to numerous fish species, including local endemics (Posa et al., 2011), and we know little about their responses to peat management. Therefore, the impact of peatland

re-wetting on other taxa will differ from the responses of birds, and our results cannot be generalised to all biodiversity.

We found highly variable oil palm yields among farms, but there was no evidence that drainage depth or vegetation complexity accounted for this, and variation was not explained by oil palm age, farm management or chemical and fertiliser applications. At 11 t ha^{-1} year^{-1}, average reported yields in this landscape were below regional averages (Indonesian smallholders 13 t ha^{-1} year^{-1}, national average 17 t ha^{-1} year^{-1}, while best performing Malaysian industrial estates yield up to 40 t ha^{-1} year^{-1}; Hoffmann et al., 2014; Woittiez et al., 2017). A wider study of smallholder oil palm farmers in Sumatra also found that agronomy practices explained little variation in self-reported yields, although lack of fertiliser reduced yields (although effects of fertiliser can take 2 years to appear; Darras et al., 2019), and that independent smallholders (as in this study) tend to have the lowest yields (Lee et al., 2014). Retaining some 'weed' vegetation cover on non-peat soils may reduce the risk of soil compaction and erosion, enhance porosity and water infiltration, providing benefits for oil palm production relative to weeding practices that clear all vegetation (Darras et al., 2019). Similar benefits might be expected for peat soils. However, these previous studies support our finding that the presence of understorey vegetation has little relationship with oil palm yields.

All sites surveyed were relatively shallowly drained in the year of study, although there was an indication of a relatively dry period leading to deeper drainage towards the end of the study. So, we cannot draw conclusions about the effect of deeper drainage on yields or biodiversity. We analysed self-reported yields and data from questionnaires rather than taking measurements over time, due to logistical constraints, and were unable to account for the potential time-lag between management or weather effects on palms and changes in yield. A time-lag of 20–30 months has been reported between stress factors impacting palms, and resulting variation in yields (Woittiez et al., 2017), while fertiliser applications increase oil palm root biomass but can take 2 years to impact fruit yields (Darras et al., 2019). However, discussions with farmers indicated that water table and farm management had not been substantially altered in the months prior to data collection.

The water table data collected in this study, and made publicly available by this project, offers a good opportunity to monitor yield outcomes in coming months, as part of wider restoration planning. This information will be vital for helping to close yield gaps, produce oil palm to meet growing demands and improve smallholder livelihoods, without increasing plantation area (Afriyanti et al., 2016). However, increased yields on farms may not result in avoided deforestation unless there is accompanying forest governance and enforcement of protection, but higher yields are required if production is to match increasing demand without further deforestation (Woittiez et al., 2017). Our results highlight the huge variability in smallholder yields, and the low productivity in the area. There is also an urgent need for studies of industrial plantations, where management, oil palm age, water tables and yields are likely to be more closely controlled, allowing potential trade-offs to be examined.

Comparisons of yield-drainage relationships between smallholders and industrial scale oil palm would be very informative, especially in the context of sustainability initiatives such as guidance from the Roundtable on Sustainable Oil Palm.

4.2 | Peat swamp forest supports a distinct and more diverse bird community than oil palm

We found that bird species richness in the peat swamp forest fragment was double that of surrounding smallholder oil palm farms, with an almost completely distinct species composition, and at least 35 conservation-priority species. This finding highlights the conservation value of large patches of forest in agricultural landscapes. Drainage of cultivated land affects neighbouring forests (e.g. up to 300 m away in the nearby Kampar Peninsula; Evans et al., 2019), and in dry years (such as during ENSO events) fires in cultivated lands have escaped into unusually dry, drainage-affected neighbouring forest, as occurred in the western portion of our study forest fragment in 2015. Raising water tables in surrounding oil palm farms may therefore provide protective co-benefits for biodiversity by reducing the risk of future forest loss or degradation from fires.

Our finding that peat swamp forests contained about twice the avian biodiversity of oil palm smallholdings adds support to other studies emphasising their importance for bird conservation (e.g. Azhar et al., 2011; Posa et al., 2011). Total bird species richness of the Sungai Buluh forest fragment in our study (90 species) is similar to the total species richness recorded in nearby Berbak National Park (88 species across primary, secondary and swamp forest habitats; Darras et al., 2018). Another study of logged peat swamp forest in Peninsular Malaysia recorded 194 bird species over a 9-month sampling period (Azhar et al., 2011), suggesting Sungai Buluh may harbour greater bird diversity than we were able to record in our relatively short survey. Our findings of greater avian body mass, and reduced abundance of invertebrate-feeding birds, in forest plots compared to oil palm reflects findings of other studies (Edwards et al., 2013), although responses to land use can vary among landscapes (Prabowo et al., 2016). The increased abundance of frugivorous and/or nectarivorous birds in oil palm may be explained by the presence of relatively complex understorey vegetation on some farms and small patches of uncultivated land between oil palm farms, that could support flowering and fruiting understorey plants. This information could be used to boost bird diversity on farms without reducing yields.

Together, our findings emphasise the biodiversity value of remaining large peat swamp forest fragments for bird conservation in Sumatra, and the importance of efforts to reconnect them with other fragments, especially those recently isolated that are early in the 'relaxation' stage of the extinction debt process (Wearn et al., 2012). Conservation of bird species diversity and composition is also essential from the perspective of future peatland landscape restoration efforts. Cultivated peatlands are subsiding, and in coastal areas will become inundated, forcing a withdrawal

of agriculture (Wijedasa et al., 2018), while targets to reduce carbon emissions from Sumatra's peatlands may also incentivise withdrawal of oil palm in the longer term (Afriyanti et al., 2019). This withdrawal of agriculture could result in opportunities for low-cost forest restoration. However, successful restoration is on the assumption that peat subsidence ceases, because regular inundation of sites would make forest recovery impossible (Giesen, 2018). If preserved, remaining forest fragments, such as Sungai Buluh in this study, could act as reservoirs of peat swamp forest animals, plants and their seed dispersers, including large-bodied frugivores with long dispersal abilities such as hornbills, thus facilitating forest recovery (Wijedasa et al., 2020), and potentially providing gene flow between peat-specialist plant and animal populations in isolated forest fragments.

The loss of ~50% of bird species richness following conversion of logged peat swamp forest to smallholder oil palm in this study is similar to other studies reporting conversion of logged peat swamp forest to smallholder or industrial oil palm in Peninsula Malaysia (48%–60%; Azhar et al., 2011), non-peat rainforest to smallholder oil palm in Jambi, Sumatra (43%–45%, Prabowo et al., 2016) and smallholder oil palm in Thailand (60%; Aratrakorn et al., 2006). This suggests that smallholder oil palm landscapes are not necessarily any better than industrial oil palm estates for conserving bird diversity.

Our finding that distance to the nearest continuous forest block (0.13–3 km) had no effect on bird diversity in oil palm farms could be explained by the presence of a paved road and wide canal surrounding the forest, which could act as an impermeable barrier to the movement of many forest birds into surrounding plantations (Johnson et al., 2017). This fits with our finding that very few species were shared between forest and oil palm. This concurs with existing evidence that distance to large blocks of continuous forest had no effect on bird diversity on oil palm smallholdings in Malaysia at distances of 8–50 km (Azhar et al., 2011), but contrasts with findings from Ghana, where bird diversity on oil palm smallholdings increased at proximities of 0.6 km compared to 9.6 km from contiguous forest (Hamer et al., 2021), and evidence that smaller forest patches near oil palm smallholdings increased bird diversity at distances of 0.01–5 km (Azhar et al., 2011). This suggests that some bird dispersal from forest into oil palm may occur for several km, if landscapes are relatively permeable. Landscape permeability for bird movement was not addressed directly in our study, and we did not survey other land covers including *Acacia*, homegardens or patches of scrub vegetation that could facilitate bird movement. However, our findings that dispersal of forest birds into oil palm smallholdings appears very limited in this landscape has important implications for forest recovery or restoration at the landscape scale in the longer term. We conclude that without interventions to improve landscape permeability for birds, processes such as seed dispersal and gene flow across the landscape may remain limited. For example, findings from the same province as our study indicate potential for the use of 'framework' species, such as abandoned or unmanaged *Acacia* plantations, to encourage forest recovery processes including seed dispersal (Wijedasa et al., 2020).

5 | CONCLUSIONS

Declining oil palm yields could drive livelihood losses and further deforestation, but we find that re-wetting peatlands to the levels assessed in this study is unlikely to negatively impact yields. Hence, we conclude from our study that re-wetting will conserve both forest biodiversity and livelihoods if fires are reduced. We found no evidence for trade-offs between yields, water table depth and on-farm bird diversity, and our power analysis indicates that missed effects are likely to be small. There are challenges in understanding drivers of yield variation on heterogeneous smallholder farms, and more studies are needed, but we conclude that re-wetting should have net positive effects for smallholders by reducing the risk of fires that can damage property, plantations and human health. It is important that any prolonged flooding following re-wetting does not negatively impact farm access or yield, given that oil palms can only tolerate temporary flooding (palms can develop root pneumatodes, but submerged roots cannot respire normally; Woittiez et al., 2017). The long-term success of canal blocking varies, and requires long-term local support (Dohong et al., 2018), to mitigate any impacts on farmer livelihoods (Ward et al., 2021). However, even the wettest farms still had water tables below the ground most of the time, meaning carbon emissions and land subsidence continue. Full hydrological restoration would involve sustained flooding (as observed in the nearby forest) which is incompatible with oil palm production.

Nearly all farms in our study met the legislative requirement for maintaining a mean water table depth of −40 cm. However, −40 cm is considered a threshold below which surface peat can become dry enough to combust (Page et al., 2009), meaning this threshold should be considered a minimum, rather than mean, value above which the risk of fires is minimised. We note that in the 2019 ENSO event most farms dropped below −40 cm from July onwards, a pattern not found in 2018. This inter-annual variation highlights the need for monitoring and adaptive management of water tables during any re-wetting scheme, to enable responses to long-term rainfall variation, especially that associated with ENSO events when severe droughts are common. Further data on oil palm yield–water table relationships are urgently needed, including from industrial plantations, to enable quantification of trade-offs between production, water tables, carbon emissions and land subsidence, in order to develop more sustainable agricultural practices. In the long term, withdrawal of drainage-dependent agriculture from peatland is necessary to avoid carbon emissions and land loss to subsidence (Wijedasa et al., 2017), with forest restoration or flood-tolerant agriculture the sustainable alternatives (Tan et al., 2021).

Our findings highlight that peat forest protection in these landscapes is vital for conserving biodiversity, because we find no evidence that re-wetting of peatland oil palm improves on-farm bird diversity, and only 3/35 conservation-priority bird species occurred on farms. Recent research indicates that drainage impacts extend 300 m into forest from a plantation boundary (Evans et al., 2019), highlighting the fundamental connections between management of drained cultivated peatlands and forest conservation. Thus,

management practices to reduce on-farm fires in peatland oil palm, including re-wetting, are crucial to protect forests from escaped fires. Given the halving of bird diversity in smallholder oil palms relative to forest, restoration of more biodiversity-friendly land covers that could improve landscape permeability, and improve connectivity between forest areas, will benefit landscape biodiversity, assuming such efforts do not drive further deforestation by reducing yields.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare. Nathalie Pettorelli is a Senior Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

Study conceived and planned by E.W.-T., J.K.H., K.C.H.; Field data collected by E.W.-T. (vegetation, water tables, sampling locations), P.G.A. (birds), B.H. (plants), W.D.K. (plants), D.M. (birds), W.S. (vegetation, water tables), G.S. (vegetation, water tables) and C.W. (farmer questionnaires); Land cover data generated by M.C., M.L. and N.P.; F.A., J.A.H., J.M.L. and L.C.S. contributed substantively to the manuscript ideas; E.W.-T. conducted all analyses; E.W.-T. and J.K.H. led paper writing; J.K.H. and F.A. were principal investigators of the wider project. All authors reviewed drafts and approved manuscript for submission.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.rr4xgxd9v (Warren-Thomas et al., 2022).

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