Received: 14 October 2020 | Revised: 26 March 2021 | Accepted: 29 May 2021

DOI: 10.1111/btp.12997

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Proximity to forest mediates trade-offs between yields and biodiversity of birds in oil palm smallholdings

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Funding information
Department for Environment, Food and Rural Affairs, Grant/Award Number: 3108

Associate Editor: Jennifer Powers
Handling Editor: Jayashree Ratnam

Abstract

There is much debate about how best to mitigate the effects of agricultural expansion on biodiversity, especially in the tropics. Recent studies have emphasized that proximity to natural habitats can enhance farmland biodiversity, yet few studies have examined whether or not such proximity mediates local trade-offs between yields and biodiversity, and hence alters conclusions about the ecological benefits of alternative farming strategies. Here we examine yield-biodiversity trade-offs, focusing on birds in oil palm smallholdings at different distances from remaining areas of forest, including a large forest reserve, in Ghana. We found significantly fewer birds on higher-yielding than lower-yielding farms, in terms of both species richness and abundance. For forest specialist birds (likely to be highly vulnerable to conversion of land to agriculture) we also found a greater trade-off (i.e., lower richness and abundance for a given yield) at farms further from forest, to the extent that increasing distance to the nearest forest from 1 to 10 km had a similar effect as a 3- to 5-fold increase in fruit yield brought about by increased intensification. Our study highlights the importance of accounting for the effects of natural forest in the landscape when considering agricultural policies for biodiversity protection, underlining the importance of a landscape-scale approach to conservation.

KEYWORDS
agroecosystems, biodiversity, land-use planning, palm oil, tropical forests

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1 | INTRODUCTION

Conversion of lowland tropical rainforests for agricultural crops is a major driver of global biodiversity losses (Clough et al., 2016; Laurance et al., 2014), and global demand for agricultural commodities is expected to increase by a further 70–100% by 2050 (Tilman, Balzer, & Befort, 2011; Kastner et al., 2012). Hence, agriculture is likely to continue to drive declines in natural ecosystems and the species they support in the coming decades. Decisions about how to manage existing agricultural land and where to create new croplands will therefore have profound effects on the conservation of tropical biodiversity as well as poverty alleviation and the growth of tropical economies (Steffan-Dewenter et al., 2007; Tscharntke et al., 2012; Zabel et al., 2019).

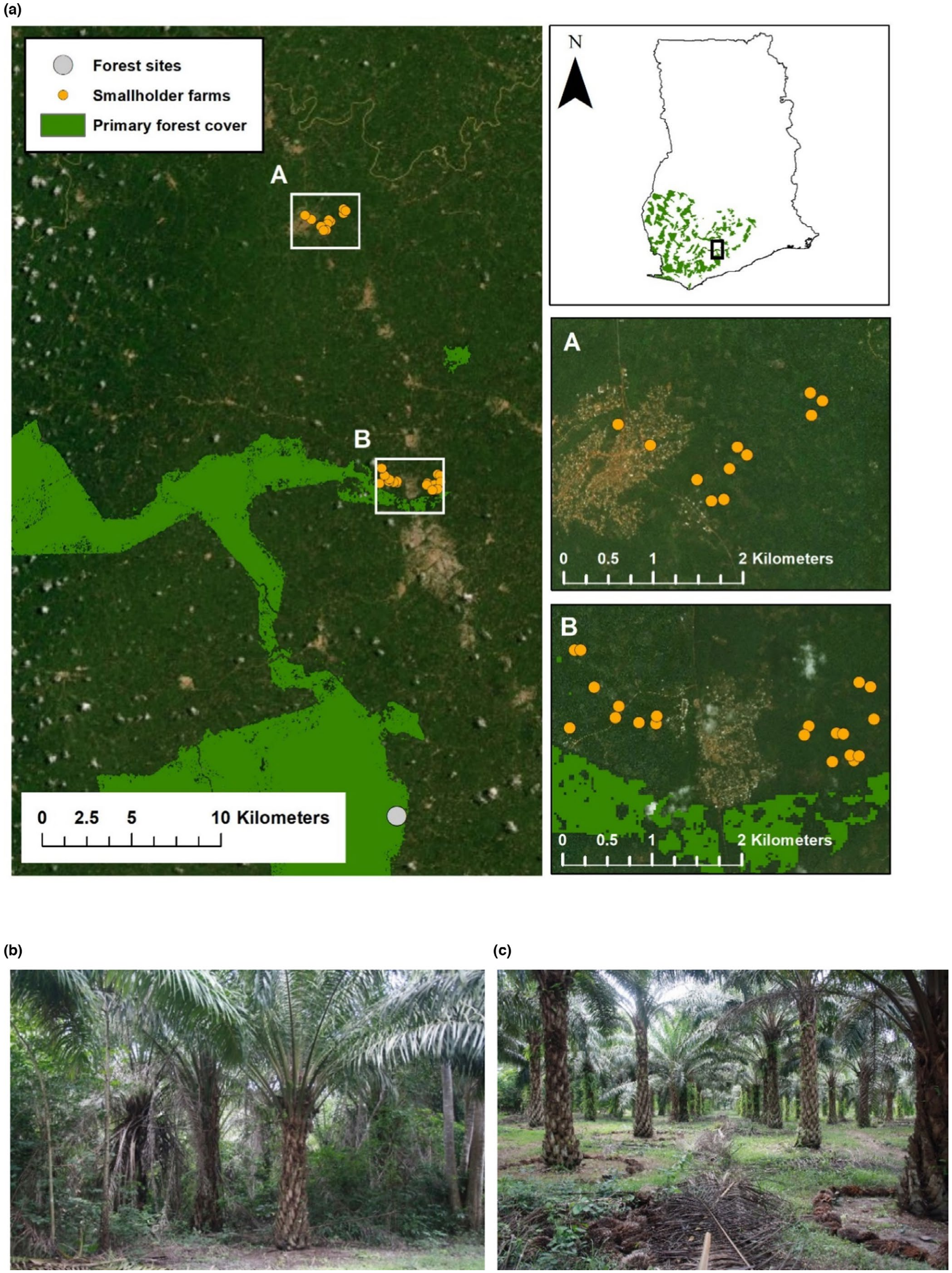
Two different approaches have been proposed to meet growing agricultural demand while mitigating impacts on biodiversity (Finch et al., 2020; Green et al., 2005). One favors increasing the intensity of farming on existing croplands to boost yields, thus reducing the need to convert additional land to agriculture (land sparing). The other favors farming at a lower intensity across larger areas (land sharing), for instance by retaining elements of "wildlife-friendly" natural vegetation throughout farmland, thus elevating biodiversity within the agricultural landscape. The relative success of these two approaches depends on the context and environment, including the spatial scale and configuration of agricultural land and wildlife-friendly elements (Daily et al., 2001; Law & Wilson, 2015; Luskin et al., 2017; Phalan, 2018). In particular, while concentrated features such as riparian strips, hedgerows, and patches of remnant forest within farmland inevitably decrease the area of land under cultivation and hence generally reduce net per hectare yields (Cannon et al., 2019), more diffuse features such as native species grown between or beneath the canopy of tree crops may have much less impact on yields and may even boost per hectare productivity through the enhanced provision of ecosystem services such as nutrient recycling, pollination, and suppression of herbivores (Bhagwat & Willis, 2008; Milligan et al., 2016). In support of this notion, Clough et al. (2011) found little relationship between yields and biodiversity in smallholder cocoa crops in Indonesia, suggesting substantial opportunities for wildlife-friendly farming in the tropics without compromising crop production benefits or adding pressure to convert natural habitat to farmland. However, the generality of this conclusion for other tropical agricultural crops is unclear.

Another critical gap in current knowledge is the extent to which impacts of wildlife-friendly farming on yields and biodiversity in tropical landscapes are influenced by landscape-scale effects such as proximity to natural habitat. Previous studies have shown that the effectiveness of patches of remnant forest in supporting biodiversity within a landscape of cloud forest and cattle pasture in the Colombian Andes depends in part on proximity to large patches of contiguous forest (Gilroy et al., 2014; Cannon et al., 2019). Patches of natural habitat may also provide biodiversity benefits via spill-over effects into adjacent agricultural areas (Lucey et al., 2014; Zhang et al., 2017) but it is not clear how local-scale relationships between yields and biodiversity are affected by landscape-scale effects of distance from forest.

Oil crops are a leading cause of global land-use change, with oil palm *Elaeis guineensis* accounting for 2 Mha of forest cleared in the decade from 2000 to 2010 (Ordway et al., 2019; Vijay et al., 2016). How to make oil palm cultivation less environmentally damaging is therefore a critical conservation question (Fitzherbert et al., 2008; Koh, 2008a; Nájera, Simonetti, 2010; Hackman & Gong, 2017; Pardo et al., 2019). Sub-Saharan Africa holds 24% (4.5 Mha) of the world's total oil palm cultivated area but because the most rapid deforestation driven by oil palm growth in recent decades has been concentrated in SE Asia, recent expansion in sub-Saharan Africa has largely been overlooked. Oil palm is native to West and Central Africa and has a long history of cultivation in the region as both a subsistence crop and a cash crop, with smallholder farmers playing an important role in terms of both land use and the production of "artisanal" oil-palm products (Brønd, 2018). By 2050, edible oil consumption across the region is predicted to triple relative to 2013, with smallholders being the main driver of growth in this sector (Folefack et al., 2019; Ordway et al., 2019). Consequently, a number of countries in the region are proactively seeking strategies for sustainable intensification of their smallholder oil palm sectors, in particular through adoption of "Best Management Practices" (BMPs), including control of other species of native vegetation (large trees growing above the canopy, small trees and saplings potentially forming a dense understorey and herbaceous ground vegetation) that might otherwise compete with palms for light, water or nutrients and impede access for care of palms and harvesting of fruit (Fairhurst & Griffiths, 2014; Proforest, 2019). However, while adoption of BMPs can substantially increase smallholders' yields, at least under controlled experimental conditions (Donough et al., 2009; Rhebergen et al., 2018), impacts on biodiversity are less clear, particularly for smallholders, whose production is often more biodiversity-friendly than that from large-scale industrial plantations (Azhar et al., 2017; Ocampo-Ariza et al., 2019). In addition, the biodiversity value of retaining areas of natural forest in the wider landscape is unclear for smallholder farms, even though identifying and conserving such forest is an environmental criterion for sustainable management of industrial plantations via the "High Conservation Values" and "High Carbon Stocks" approaches (RSPO 2018).

Here we evaluate biodiversity-yield relationships with data for oil palm smallholders in Ghana, and examine the importance of proximity to forest within the wider landscape. We study birds, which attain high densities and species richness in tropical forests and play important functional roles in seed dispersal, nutrient cycling, and as predators and prey (Cannon et al., 2019; Edwards et al., 2013; Koh, 2008b). Focusing first on the entire bird community then on the sub-set of forest-dwelling

FIGURE 1 The study area and variation in oil palm cultivation. (a) Map of study site showing the distribution of primary forest and locations of studied oil palm smallholdings and sampling plots in forest. Insets show location of study site in Central region of Ghana and detailed locations of studied smallholdings (A) 9.6 ± 0.5 km from forest and (B) 0.6 ± 0.2 km from forest. (b & c) Examples of smallholding with (b) low-intensity oil palm cultivation and (c) high-intensity cultivation following "Best Management Practices"


(a)
Forest sites
Smallholder farms
Primary forest cover
A
B
0 2.5 5 10 Kilometers
N
A
0 0.5 1 2 Kilometers
B
0 0.5 1 2 Kilometers
(b)
(c)

birds (i.e., species of greatest conservation concern; Beier et al., 2002), we examine oil palm smallholdings spanning a wide range of intensities of cultivation to assess how farming intensity, as measured by variation in vegetation characteristics within smallholdings arising from intensity of management practices, affects biodiversity and yields. In particular, we examine if any trade-offs between yields and the biodiversity (richness and abundance) of species on smallholdings are affected by proximity to forest within the wider landscape.

2 | METHODS

2.1 | Study area

The study focused on 31 farms in two smallholder communities situated 0.6 ± 0.2 km (mean ± SD) and 9.6 ± 0.5 km from remaining forest in the Central region of Ghana (Figure 1), where climate and soils are considered favorable for oil palm cultivation (Rhebergen et al., 2018). We also examined protected forest in the nearby Kakum National Park (Figure 1), to provide baseline biodiversity data for comparison with smallholder farms. Oil palm smallholdings were similar in size (~0.5 – 5 ha, determined by walking the perimeter of each crop with a Garmin GPS-Map 64s; Garmin Ltd, Olathe, USA), crop age (≥ 6 years post-planting and in the plateau yield phase of growth when yield is at its highest and changes little with age; Rhebergen et al., 2018), topography, soil type, and planting material (*tenera* palms).

2.2 | Yield measurements

Oil palm fruits are harvested throughout the year in Ghana, with yields typically higher during the first half of each year (Brønd, 2018), and we obtained fruit yield data for each study farm from 1st May to 30th September 2017 (~10 harvests per farm on average, including both higher- and lower-yielding periods of the year), which was considered sufficient and appropriate to characterize variation in yields across farms. A field assistant was appointed in each of the two focal communities and was responsible for liaising with the selected smallholders on a daily basis and measuring and recording the number of fresh fruit bunches (FFBs) obtained whenever harvesting took place, together with the combined weight of FFBs and loose fruit. All weight measurements were obtained using a 200 kg Silverline 251087 heavy-duty spring hanging scale (Silverline Tools Ltd, Yeovil, UK). We then used $\log_{10}$ of the sum of the combined weights over a five-month period, multiplied by 12/5 to give an annual equivalent and divided by the area (ha) of the oil palm crop on each farm, as our standardized measure of FFB yield ha^{-1} at each farm (palms were planted at a uniform density of ~150 stems ha^{-1}; see Figure 1b,c).

2.3 | Biodiversity sampling

We established 80 sampling stations (average of 2.6 per farm, depending on area of oil palm crop) to assess biodiversity in oil palm. We also sampled 12 control stations within protected forest to provide baseline data for comparison with farms. Following previous studies (Lees & Peres, 2006; Edwards et al., 2010), each station within oil palm was at least 50m from the nearest edge of the crop and from any other station, with the number of stations per farm determined by the area of crop cultivated in each case. Stations within forest were 100 m apart and ≥100 m from the nearest forest edge.

Birds were sampled at each of the 92 stations from 5:30 to 8:30 and 15:00–18:00 GMT during fine weather, with each station surveyed twice (morning and evening) on different days in July 2017. Following previous studies (e.g Edwards, Gilroy, et al., 2014; Gilroy et al., 2014), two observers walked to the middle of the station on each occasion, waited one minute for birds to return to normal activity then recorded the identity of all birds seen or heard within 30 m during a period of 15 mins, excluding African palm-swifts *Cypsiurus parvus*, which were often detected above the canopy. Unfamiliar vocalizations were recorded using a Tascam DR-05V2 handheld stereo recorder (Tascam, Montebello, USA) and subsequently compared with the Xeno-Canto online bird call database (http://xeno-canto.org/) for confirmation of identity (not to determine abundance which was always done in the field).

2.4 | Assessment of management intensity from measurement of vegetation

To quantify how variation in the intensity of farm management through adoption of BMPs affected the non-crop vegetation of potential biodiversity benefit within smallholdings (see Figure 1b,c), we measured the structure of this vegetation by recording the following data at all 80 sampling stations on farms, following Hamer et al. (2003) and Benedick et al. (2006): number of large trees (diameter at breast height [dbh] >25cm), small trees (dbh10-25cm) and saplings (dbh<10cm) within 30m in each of four quadrants centered at the station; dbh and distance to the two nearest large trees, small trees and saplings in each quadrant (up to eight large trees, eight small trees and eight saplings per station); estimated vegetation cover (%) at ground level and height of non-woody vegetation. All measurements were made to the nearest 1 cm with a tape measure. Ground cover, to the nearest 5%, was recorded as the mean of at least two independent estimates; these varied among recorders by no more than 10%. These data were used to calculate the density of large trees, small trees and saplings at each station. They were then normalized where necessary and analyzed by a principal components analysis (PCA; Benedick et al., 2006). This allowed ordination of differences among stations in vegetation characteristics, by generating a number of independent factors comprising sums of weighted variables, with each variable standardized (i.e., mean across all stations = 0, SD = 1). These factors could then be used to examine in more detail how biodiversity was related to each of the different facets of the non-crop vegetation within oil palm, and hence to management intensity.

TABLE 1 Species richness and abundance of birds at study plots in protected forest and on oil palm smallholdings at two different distances from protected primary forest in Ghana. n_1, number of sampling stations; n_2, number of oil palm smallholdings

	Oil palm					
			Distance from forest			
	Protected forest		0.6 ± 0.2 km		9.6 ± 0.5 km	
			$n_1 = 46$		$n_1 = 34$	
	$n_1 = 12$		$n_2 = 20$		$n_2 = 11$	
	Mean	SD	Mean	SD	Mean	SD
All birds						
Species richness	27.1	12.2	16.0	11.1	11.7	7.1
Abundance	21.2	4.6	12.3	3.4	11.7[a]	4.1
Forest-specialists						
Species richness	21.5	11.3	5.3	2.4	3.3	1.9
Abundance	14.9	2.4	5.4	2.3	3.4	2.1

[a] Excludes one sampling station with 45 colonially-nesting weavers (30 village weavers plus 15 chestnut-and-black weavers). Hence $n_1 = 33$ (n_2 was unaffected). Including this station, mean = 12.9, SD = 8.0.

2.5 | Statistical analysis

We focused first on the whole bird community then on forest specialist bird species, using data from www.iucn.org to identify those species whose major habitat was designated as forest (i.e., those for which tropical moist lowland forest was classified as being of "major importance"). In each case, we used the bias-corrected form of Chao 1 (a nonparametric species richness estimator; Gotelli & Colwell, 2011; Rajakaruna et al., 2016) to assess the complete pool of species present at each sampling station from the number of species observed and the abundance of each species, thus correcting for variation in sample coverage (the proportion of species detected at each locality; Chao & Jost, 2012; Chao et al., 2020). In addition to species richness, we also considered overall abundance (first, across all species then focusing only on forest species) by calculating the total number of individuals recorded at each station. Our yield measures were computed per farm, and so all our analyses were carried out at the level of individual farms (*N* = 31 farms), and we calculated mean values for species richness and abundance per farm (i.e., the means of values calculated at each station with equal sampling effort) to account for variation in the number of sampling stations per farm.

To determine the distance of each farm from the nearest primary forest, we downloaded primary forest cover data (30 m grid-cell resolution) for 2001 from Global Forest Watch (https://www.globalforestwatch.org/map) (see Turubanova et al., 2018 for more details). We then overlaid the GPS coordinates of every farm onto the primary forest cover map along with satellite imagery (World Imagery Basemap for 2011–2016; Esri et al., 2020) in ArcMap 10.6 (Esri, 2018). Following inspection of the base layer imagery and primary forest cover map, we estimated the distance of each farm in ArcMap 10.6 to the nearest area of remaining primary forest (i.e., excluding very small areas of primary forest, including single grid-cells, that appeared to have been cleared; Figure 1a). We subsequently verified our distance estimates using Google Earth imagery, which was predominantly for 2019. We used this primary forest map because other available tree cover maps for Ghana do not distinguish between areas of natural forest and some tree plantations. After visual inspection of recent imagery, the primary forest map appeared to be representative of the intact forest cover remaining in the landscape and hence it was used to calculate our farm distance estimates.

We used generalized linear models to examine how the richness and abundance of forest species were related to FFB yields and distance to forest. We assumed a normal probability distribution with an identity link function for species richness estimates and a Poisson distribution with a log link function for abundance data. FFB yield ($\log_{10}$ transformed) was included as a covariate, with distance to forest included as a binary fixed effect (distances were highly bimodal in practice; Figure 1a) and an additional term for the interaction between these predictor variables. To further explore how variation in farming intensity affected yields and biodiversity through its effect on the characteristics of the non-crop vegetation within smallholdings (Figure 1b,c), we also examined how each of our biodiversity measures and $\log_{10}$ FFB yield were related to vegetation characteristics (reflecting the intensity of "Best Management Practices") and distance from forest, using independent factor scores from the PCA to measure different components of the vegetation related to large trees, small trees and saplings, and ground vegetation. To find the best-fitting models and check the robustness of our results, non-significant terms were serially deleted to ensure that this did not qualitatively affect the significance of the remaining terms, producing a minimum adequate model (MAM) in each case (Crawley, 2007).

3 | RESULTS

We sampled 1,304 birds of 77 species (Table S1). Species accumulation curves had largely leveled off by the end of sampling in each habitat, with high sample coverage in each case, indicating sufficient sampling to characterize biodiversity accurately on farms and in forest for all birds (Figure S1) and for forest specialist birds (Figure S2). The mean species richness and abundance of birds at sampling stations per farm were ~40–60% of those at stations in protected primary forest, whereas the richness and abundance of forest specialist birds were ~20–30% of those in primary forest (Table 1).

3.1 | Biodiversity and yield

Across the 31 farms in the study, estimated oil palm fresh fruit bunch (FFB) yields ranged from 1,500 to 17,600 kg ha^{-1} year $^{-1}$ (Table S2). There were significantly fewer birds on higher-yielding than on lower-yielding farms, in terms of both species richness (Chao 1) and abundance, whether considering all birds (Figure 2; Wald $\chi^2_1 = 6.3$, $p = 0.01$ and $\chi^2_1 = 5.2$, $p < 0.05$, respectively) or only forest specialist birds (Figure 2; Wald $\chi^2_1 = 4.6$, $p = 0.05$ and $\chi^2_1 = 4.8$, $p < 0.05$, respectively). In addition, for forest specialist birds, species richness declined significantly faster with increasing FFB yield at farms

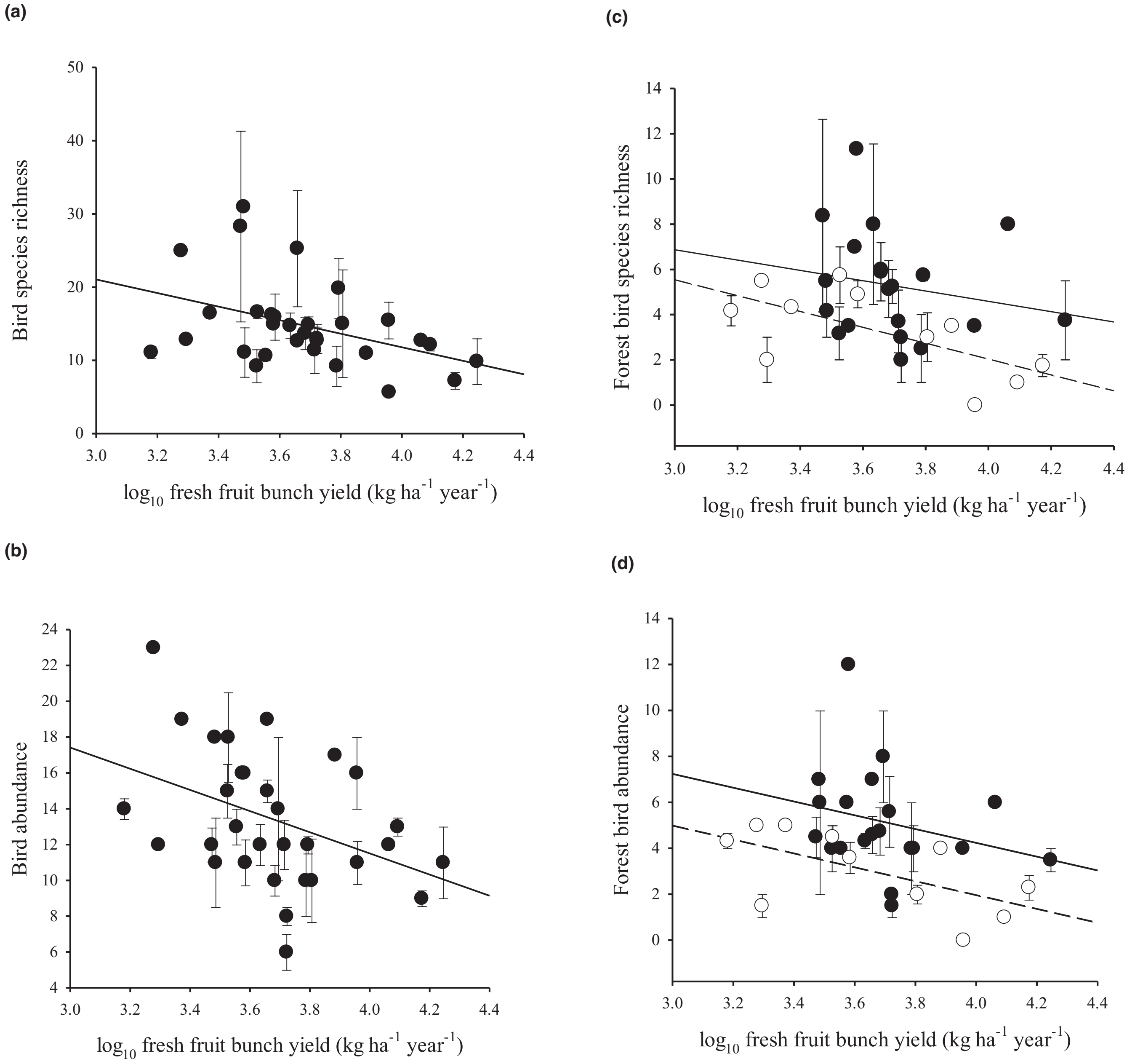


FIGURE 2 Mean species richness and abundance of (a, b) birds and (c, d) forest specialist birds at study plots in oil palm smallholdings were negatively related to log$_{10}$ fresh fruit bunch yield (kg ha^{-1} year^{-1}) of each smallholding and, for forest specialist birds, distance (km) from forest (for (c) and (d), solid symbols and solid line are farms 0.6 ± 0.2 km from forest; open symbols and dashed line are farms 9.6 ± 0.5 km from forest). Error bars for species richness and abundance are ±1 SE

further from forest (interaction term; $\chi^2_1 = 8.3$, $p < 0.01$; Figure 2c) while abundance was consistently lower at farms further from forest (additive term; $\chi^2_1 = 6.7$, $p = 0.01$; Figure 2d). Hence, overall, there were large reductions in the species richness and abundance of birds on farms compared with forest, and there were significant trade-offs between yield and biodiversity on farms, with larger trade-offs for forest specialist birds on farms further from forest.

3.2 | Relationships with management intensity

To understand the proximate drivers of trade-offs between yield and biodiversity, we examined the characteristics of the vegetation within smallholdings, reflecting differences among smallholders in the adoption of BMPs (Table S3). Our PCA (see Methods: Assessment of management intensity from measurement of vegetation) extracted three components of variation in the non-crop vegetation characteristics within oil palm (PC1, PC2, and PC3), which accounted for 73% of the variability in the vegetation data (Table 2). The first component (PC1) increased mainly with increasing density and sizes of small trees and saplings, the second component (PC2) increased mainly with increasing density and sizes of large trees, and the third component (PC3) increased mainly with increasing ground cover of vegetation and herb height. There was a significant negative relationship between $\log_{10}$ FFB yield and PC2 (Wald $\chi^2_1 = 5.9$, $p = 0.01$) indicating higher yields on farms with lower densities and sizes of large trees (Figure 3) but there was no significant relationship with the other principal components or with distance from forest.

The estimated species richness (Chao 1) of birds in oil palm was significantly greater on farms with a higher density and sizes of large trees (PC2; Wald $\chi^2_1 = 7.1$, $p < 0.01$; Figure 4a) and of small trees and saplings ($\chi^2_1 = 7.4$, $p < 0.01$; Figure 4b) but was unaffected by distance to forest ($\chi^2_1 = 0.4$, $p = 0.8$). Conversely, the abundance of birds in oil palm was significantly greater on farms with a higher density and sizes of large trees ($\chi^2_1 = 4.7$, $p < 0.05$; Figure 4c) but was unaffected by either the density and sizes of small trees and saplings ($\chi^2_1 = 0.9$, $p = 0.3$) or distance to forest ($\chi^2_1 = 1.8$, $p = 0.2$).

In contrast to the pattern for all birds, the species richness (Chao 1) of forest specialist birds in oil palm was not related to any vegetation factor scores but was significantly lower on farms further from forest (Table 1; $\chi^2_1 = 6.2$, $p = 0.01$), while the abundance of forest specialists was significantly positively related to the density and sizes of large trees (PC2; $\chi^2_1 = 4.3$, $p < 0.05$) and was also consistently lower at farms further from forest (Figure 4d; $\chi^2_1 = 4.7$, $p < 0.05$). Hence, while there was variation in responses to vegetation factors, both the species richness and abundance of forest specialist birds were significantly lower at sites further from forest.

TABLE 2 Contributions of different variables to three principal components of variation in vegetation structure. Variables making main contributions to each principal component (factor loading >0.65) are in bold. dbh is diameter at breast height

Variables	PC1	PC2	PC3
Small tree density	**0.871**	−0.073	0.088
Small tree dbh (cm)	**0.717**	0.181	0.260
Sapling density	**0.691**	0.309	−0.144
Sapling dbh (cm)	**0.659**	0.360	0.056
Large tree density	0.145	**0.934**	−0.003
Large tree dbh (cm)	0.173	**0.814**	0.138
Ground Cover (arcsine %)	−0.034	−0.029	**0.826**
Herb height (m)	0.162	0.110	**0.751**

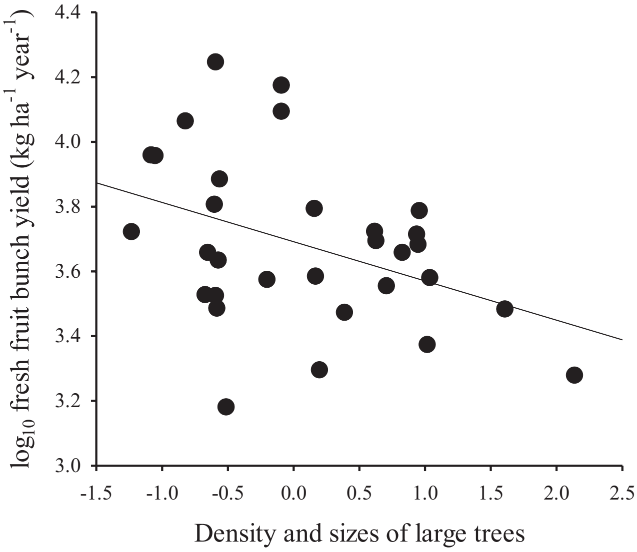


FIGURE 3 Log_{10} fresh fruit bunch yield (kg ha^{-1} year^{-1}) was negatively related to the sizes and densities of large trees excluding palms (see Table 2) within oil palm smallholdings in Ghana

4 | DISCUSSION

We found that on average, the species richness and abundance of birds in oil palm smallholdings were ~40–60% of those in primary forest for all birds and ~20–30% of those in primary forest for forest specialist birds. In contrast, industrial oil palm plantations in Malaysia supported only ~10–15% of forest species (calculated from Figure 1 in Edwards et al., 2010) whereas overall species richness at point-count stations in protected forest were similar in Malaysia (mean ± SE = 28 ± 1; Table 1 in Edwards et al., 2013) and Ghana (27 ± 3; this study). While not directly comparable, these findings suggest that smallholdings in Ghana could support about twice the proportion of forest-specialist birds as industrial plantations in Malaysia, despite similar species richness within forest in each case. This difference could reflect the fact that oil palm is a native species in Ghana but not in SE Asia. However, the species richness of forest specialist birds in the highest-yielding (i.e., most agriculturally intensive) smallholdings in our study was only ~15% of that in primary forest (see Figure 2), suggesting that the main difference between studies was due to more intensive management of industrial plantations compared to smallholdings.

Our findings support the notion that native vegetation integrated among crops can enhance species richness and abundance within

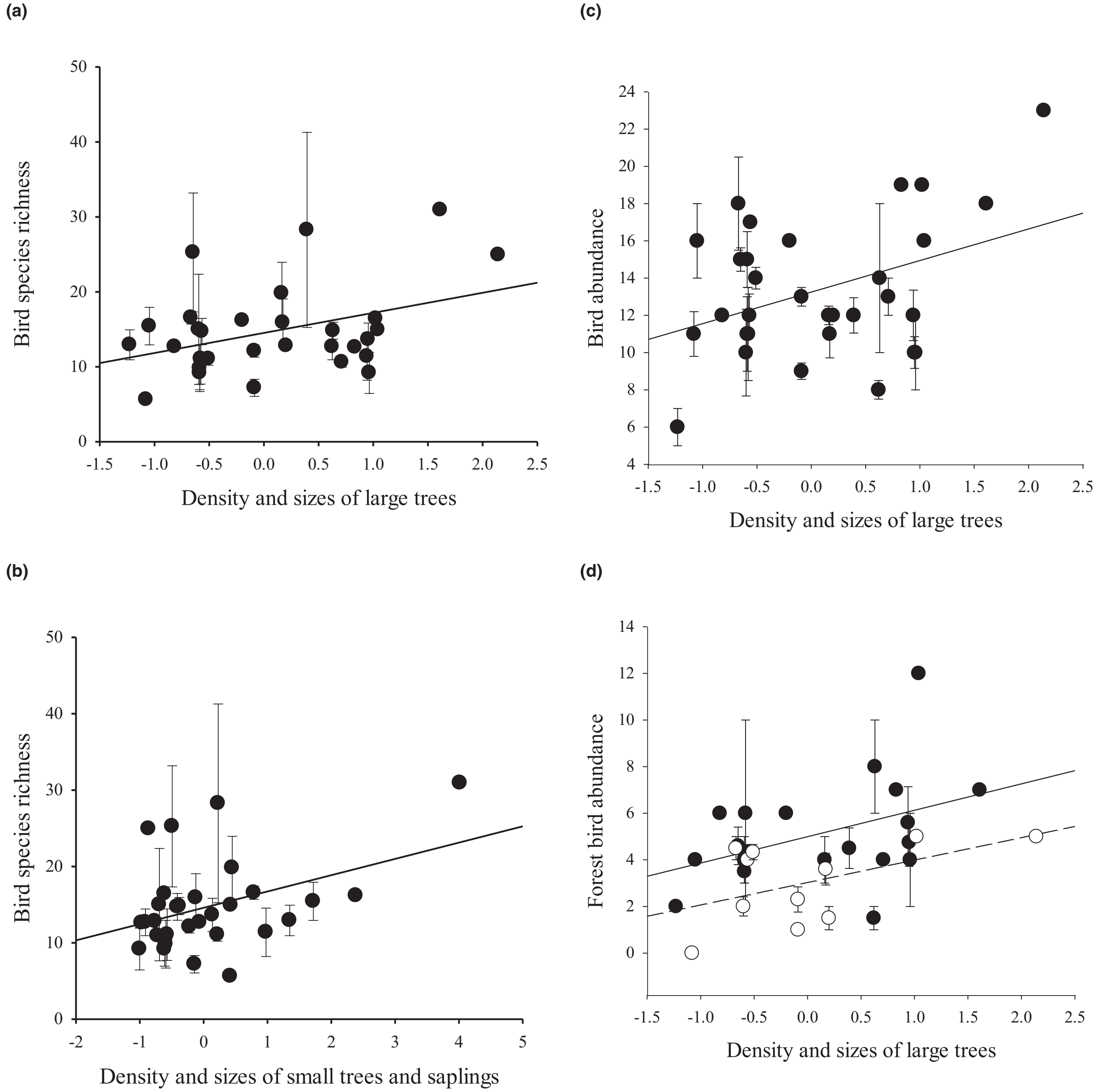


FIGURE 4 (a, b) Mean species richness of birds at study plots within oil palm smallholdings was positively related to the sizes and densities of (a) large trees and (b) small trees and saplings. (c) Mean abundance of birds was positively related to the density of sizes of large trees. (d) Mean abundance of forest specialist birds was positively related to the density and sizes of large tees and negatively related to distance (km) from forest (solid symbols and solid line, farms 0.6 ± 0.2 km from forest; open symbols and dashed line, farms 9.6 ± 0.5 km from forest). Error bars for species richness and abundance are ±1 SE

tropical farmland (Bhagwat & Willis, 2008; Clough et al., 2011). However, for forest-specialist species, there was a marked difference in the size of these benefits over a relatively short range of distances to forest (1 – 10 km), and even the least intensively grown oil palm supported only a fraction of the avian species richness and abundance recorded in forest. Birds are considered good indicators of wider responses of biodiversity to environmental change (Clough et al., 2011; Lawton et al., 1998). Hence the effect of isolation from forest in this study suggests that a similar pattern may also occur in other mobile taxa. Moreover, the effect we recorded was similar to that observed for birds and dung beetles in the Colombian Andes (Cannon et al., 2019; Gilroy et al., 2014), providing further support to the suggestion that natural forests play an important role as population sources, providing conditions and resources necessary for species persistence in both forest and farmland (Gilroy & Edwards, 2017; López-Ricuarte et al., 2017; Şekercioğlu et al., 2007; Scriven et al., in press).

The average fresh fruit yield obtained by smallholders in our study (equivalent to 5.7 t ha^{-1} yr^{-1}) was very similar to the overall average for smallholders in Ghana (5.8 t ha^{-1} yr^{-1}; Rhebergen et al., 2018) but the highest yields obtained under BMP in our study (up to 17.6 t ha^{-1} yr^{-1}) approached those attainable with intensive industrial methods, suggesting substantial scope to increase incomes through BMP, as also found by Rhebergen et al. (2018). Hence promotion of BMPs among smallholders could reduce pressures to increase the area of land under oil palm cultivation to meet national production targets, although increasing profitability might also incentivize greater land conversion (Carrasco et al., 2014). However, the species richness and abundance of birds and the populations of forest specialist species were boosted mainly by retaining large trees above the oil palm canopy, which reduced yields, indicating that making oil palm more wildlife-friendly by encouraging greater coverage of large trees would come at a cost of reducing per ha crop production. There was also variation in species richness and abundance among study plots on some farms, probably reflecting localized variation in crop management and yields at sub-farm level.

Large trees may have some economic value as a source of non-timber forest products and potentially of timber, providing a form of financial insurance for farmer livelihoods in times of acute financial need, and leading to smaller trade-offs with income than with yield, at least in the long term. This supports the notion that yield alone is an incomplete measure of financial performance in diversified farming systems, especially if intensifying management to increase yields entails opportunity costs such as less time available to manage other crops (Fischer et al., 2017; Jezeer et al., 2017). Nonetheless, our data show that trade-offs can occur in tropical tree crops, especially where boosting biodiversity entails shading of the crop. Moreover, while proximity to forest had no discernible effect on yields, as also found to be the case in industrial oil palm plantations in Borneo (Edwards et al., 2014), trade-offs with both the richness and abundance of forest birds were significantly increased by greater isolation from forest, to the extent that increasing the distance to the nearest forest from ~1 to 10 km had a similar effect as a 3–5 fold increase in fruit yield brought about by increased intensification (Figure 2). These data support previous studies highlighting a need to account for the effects of isolation from natural habitat when considering agricultural policies for biodiversity protection (Batáry et al., 2011; Gilroy et al., 2014; Macchi et al., 2020; Zhang et al., 2017) and underline that in tropical regions, failing to account for the importance of large tracts of natural habitat within the landscape may lead to incorrect conclusions about the biodiversity benefits of land-sharing agriculture and hence to inappropriate land management strategies.

Our results highlight the importance of retaining large blocks of intact forest within tropical landscapes, even if low-intensity agriculture provides significant wildlife-friendly habitat through land-sharing practices. Hence, in those regions where large tracts of natural forest persist, biodiversity may be best supported by land-sparing policies, provided that forest "spared" in this way is afforded genuine protection (Matson & Vitousek, 2006; Phalan, 2018). Land-sharing practices can in turn provide important biodiversity benefits, including facilitating dispersal between tracts of forest (Tscharntke et al., 2012; Lucey et al., 2017), which may become increasingly important to allow tropical species to track changing climates (Scriven et al., 2020). Hence both strategies can play important roles in future agricultural development, and a mixture of strategies may also be more pragmatic (Carrasco et al., 2014; Finch et al., 2020; Fischer et al., 2008), especially given constraints on smallholders' time and other resources required to farm more intensively (Lee et al., 2014). Nonetheless, our findings underline the importance of intact forests for tropical biodiversity, echoing previous calls (Cannon et al., 2019; Edwards, Gilroy, et al., 2014; Macchi et al., 2020) that their protection should be a high priority.

ACKNOWLEDGMENTS

This work was funded by the UK Darwin Initiative (Project 3108). We thank the smallholder farmer communities of Assin Breku and Assin Juaso and the Wildlife Division of the Ghanaian Forestry Commission for their cooperation and support in facilitating data collection, and John Mason (NCRC Ghana) for logistic support and advice.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTIONS

KCH, JKH, RA, WA and RA conceived and designed the research; BO, MAS and LO collected field data, assisted by KCH and JKH; KCH analyzed the data, assisted by JKH, SAS, MAS and LO; RA, WA and RA facilitated the work in Ghana and provided logistic support and advice; KCH drafted the manuscript and all authors provided manuscript modifications and gave approval for publication.

ETHICAL APPROVAL

Ethical approval was obtained from the University of Leeds Research Ethics Committee to work with smallholder farmers and carry out observational work on birds, including prior informed consent and confidentiality and privacy compliance.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh710r (Hamer et al., 2021).

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SUPPORTING INFORMATION

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How to cite this article: Hamer, K. C., Sasu, M. A., Ofosuhene, L., Asare, R., Ossom, B., Parr, C. L., Scriven, S. A., Asante, W., Addico, R., & Hill, J. K. (2021). Proximity to forest mediates trade-offs between yields and biodiversity of birds in oil palm smallholdings. *Biotropica*, 00, 1–12. https://doi.org/10.1111/btp.12997