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

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**Abstract**

There is much debate about how best to mitigate the effects of agricultural expansion on biodiversity, especially in the tropics. Recent studies have emphasised 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

**1. INTRODUCTION**

Conversion of lowland tropical rainforests for agricultural crops is a major driver of global biodiversity losses (Laurance, Sayer, & Cassman, 2014; Clough et al., 2016) and global demand for agricultural commodities is expected to increase by a further 70-100% by 2050 (Tilman, Balzer, & Befort, 2011; Kastner, Rivas, Koch, & Nonhebel, 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 (Green, Cornell, Scharlemann, & Balmford, 2005; Finch, Green, Massimino, Peach, & Balmford, 2020). One favours 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 favours 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 contextual environment, including the spatial scale and configuration of agricultural land and wildlife-friendly elements (Daily, Ehrlich, & Sanchez-Azofeifa, 2001; Law & Wilson, 2015; Luskin, Lee, Edwards, Gibson, & Potts, 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 enhanced provision of ecosystem services such as nutrient recycling, pollination and suppression of herbivores (Bhagwat & Willis, 2008; Milligan, Johnson, Garfinkel, Smith, & Njoroge, 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, Edwards, Medina Uribe, Haugaasen, & Edwards, 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, Chang, & Quang, 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 (Vijay, Pimm, Jenkins, & Smith, 2016; Ordway, Naylor, Nkongho, & Lambin, 2019). How to make oil palm cultivation less environmentally damaging is therefore a critical conservation question (Fitzherbert et al., 2008; Koh, 2008; 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, Njiki, & Darr, 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, Witt, & Fairhurst, 2009; Rhebergen, Fairhurst, Whitbread, Giller, & Zingore, 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, Saadun, Prideaux, & Lindenmayer, 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 (Koh, 2008; Edwards, Edwards, Hamer, & Davies, 2013; Cannon et al. 2019). Focusing first on the entire bird community then on the sub-set of forest-dwelling birds (i.e. species of greatest conservation concern; Beier, Van Drielen, & Kankam, 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, affect 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.

1. **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 log10 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 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.

**2.5. Statistical analysis**

We focused first on the whole bird community then on forest specialist bird species, using data from [www.iucn](http://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, Drake, Chan, & Bailey, 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, Potapov, Tyukavina, & Hansen, 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 (log10 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 log10 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 (Supplementary Table S1). Species accumulation curves had largely levelled 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 (Supplementary Figure S1) and for forest specialist birds (Supplementary 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 (Supplementary 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 χ21 = 6.3, *P* = 0.01 and χ21 = 5.2, *P* < 0.05, respectively) or only forest specialist birds (Figure 2; Wald χ21 = 4.6, *P* = 0.05 and χ21 = 4.8, *P* < 0.05, respectively). In addition, for forest specialist birds, species richness declined significantly faster with increasing FFB yield at farms further from forest (interaction term; χ21 = 8.3, *P* < 0.01; Figure 2c) while abundance was consistently lower at farms further from forest (additive term; χ21 = 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 (Supplementary 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 log10 FFB yield and PC2 (Wald χ21 = 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 χ21 = 7.1, *P* < 0.01; Figure 4a) and of small trees and saplings (χ21 = 7.4, *P* < 0.01; Figure 4b) but was unaffected by distance to forest (χ21 = 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 (χ21 = 4.7, *P* < 0.05; Figure 4c) but was unaffected by either the density and sizes of small trees and saplings (χ21 = 0.9, *P* = 0.3) or distance to forest (χ21 = 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; χ21 = 6.2, *P* = 0.01), while the abundance of forest specialists was significantly positively related to the density and sizes of large trees (PC2; χ21 = 4.3, *P* < 0.05) and was also consistently lower at farms further from forest (Figure 4d; χ21 = 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.

1. **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 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 (Lawton et al., 1998; Clough et al., 2011). 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 Columbian Andes (Gilroy et al., 2014; Cannon et al., 2019), 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 (Şekercioğlu, Loarie, Oviedo, Ehrlich, & Daily, 2007; Gilroy & Edwards, 2017; López-Ricuarte, Edwards, Romero-Rodríguez, & Gilroy, 2017; 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 incentivise greater land conversion (Carrasco, Larrosa, Milner-Gulland, & Edwards, 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 localised 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, Verweij, Santos, & Boot, 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, Edwards, Sloan, & Hamer, 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, Báldi, Kleijn, & Tscharntke, 2011; Gilroy et al., 2014; Zhang et al., 2017; Macchi et al., 2020) 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 (Fischer et al., 2008; Carrasco et al., 2014; Finch et al., 2020), especially given constraints on smallholders’ time and other resources required to farm more intensively (Lee, Ghazoul, Obidzinski, & Koh, 2014). Nonetheless, our findings underline the importance of intact forests for tropical biodiversity, echoing previous calls (Edwards et al., 2014; Cannon et al., 2019; Macchi et al., 2020) that their protection should be a high priority.

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**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are openly available in the Supplementary Information and the Dryad Digital Repository: http://doi.org/[doi], reference number [to be provided upon upload].

**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 analysed 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.

**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.

**Ethical guidelines**

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.

**REFERENCES**

Azhar, B., Saadun, N., Prideaux, M., & Lindenmayer, D. B. (2017). The global palm oil sector must change to save biodiversity and improve food security in the tropics. *Journal of Environmental Management*,203, 457-466.

Batáry, P., Báldi, A., Kleijn, D., & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis*. Proceedings of the Royal Society London B*,278, 1894-1902.

Beier, P., Van Drielen, M., & Kankam, B. O. (2002). Avifaunal collapse in West African forest fragments. *Conservation Biology*, 16, 1097-1111.

Benedick, S., Hill, J. K., Mustaffa, N., Chey, V. K., Maryati, M., Searle, J. B., Schilthuizen, M., & Hamer, K. C. (2006). Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. *Journal of Applied Ecology*, 43, 967-977.

Bhagwat, S. A. & Willis, K. J. Agroforestry as a solution to the oil-palm debate. *Conservation Biology*, 22, 1368-1370.

Brønd, F. Territory and trade networks in the small-scale oil-palm industry in rural Ghana. *Applied Geography*, 100, 90-100.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M, Wanger, T. C, Anshary, A., …Tscharntke, T. (2011) Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United State of America*, 108, 8311-8316.

Clough, Y., Krishna, V., V., Corre, M. D., Darras, K., Denmead, L., H., Meijide, A., ...Scheu, S. (2016). Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. *Nature Communications*,7, 13137. https://doi.org/10.1038/ncomms13137.

Cannon, P. G., Gilroy, J. J., Tobias, J. A., Anderson, A., Haugaasen, T., & Edwards, D. P. (2019). Land‐sparing agriculture sustains higher levels of avian functional diversity than land sharing. *Global Change Biology*, 25, 1576-1590.

Carrasco, L. R., Larrosa, C., Milner-Gulland, E. J., & Edwards, D. P. (2014). A double-edged sword for tropical forests. *Science*, 346, 38-40.

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93, 2533-2547.

Chao, A., Kubota, Y., Zelený, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C.-L., Costello, M. J., & Colwell, R. K. (2020). Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research*, 35, 292-314.

Crawley, M. J. (2007). *The R Book*. Oxford: Wiley.

Daily, G. C., Ehrlich P. R., & Sanchez-Azofeifa, G.A. (2001). Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications*, 11, 1-13.

Donough, C. R., Witt, C., & Fairhurst, T. H. (2009). Yield intensification in oil palm plantations through best management practice. *Better Crops*, 93, 12-14.

Edwards, D. P., Gilroy, J. J., Woodcock, P., Edwards, F. A., Larson, T. H., Andrews, D. J. R., …Wilcove, D. S. (2014). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Global Change Biology*, 20,183-191.

Edwards, D.P., Hodgson, J. A., Hamer, K. C., Mitchell, L., Ahmad, A. H., Cornell, S. J., & Wilcove, D. S. (2010). Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conservation Letters*, 3, 236-242.

Edwards, F. A., Edwards, D. P., Hamer, K. C., & Davies, R. G. (2013). Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis*, 155, 313-326.

Edwards, F. A., Edwards, D. P., Sloan, S., & Hamer, K. C. (2014). Sustainable management in crop monocultures: the impact of retaining forest on oil palm yield. *PLoS One*, 9, e91695; https://doi.org/10.1371/journal.pone.0091695.

Esri (2018). *ArcGIS Desktop: Release 10.6* (Environmental Systems Research Institute).

Esri et al. (2020). Imagery (basemap). *World Imagery 16 January 2011 to 02 February 2016* https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9.

Fairhurst, T. & Griffiths, W. (2014). *Oil Palm: Best Management Practices for Yield Intensification*. International Plant Nutrition Institute and Tropical Crop Consultants Limited.

Finch, T., Green, R. E., Massimino, D., Peach, W. J., & Balmford, A. (2020). Optimising nature conservation outcomes for a given region-wide level of food production. *Journal of Applied Ecology*, 57, 985-994.

Fischer, J. Abson, D., J., Bergsten, A., Collier, N. F., Dorresteijn, I., Hanspach, J., … Senbeta, F. (2017). Reframing the food-biodiversity challenge. *Trends in Ecology & Evolution*, 32, 335-345.

Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., … Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, 6, 380–385.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Bruehl, C. A., Donald, P. F., & Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology & Evolution*, 23, 538-545.

Folefack, A. J. J., Njiki, M. G. N., & Darr, D. (2019). Safeguarding forests from smallholder oil palm expansion by more intensive production? The case of Ngwei forest (Cameroon). *Forest Policy and Economics*, 101, 45-61.

Gilroy, J. J. & Edwards, D. P. (2017). Source-sink dynamics: a neglected problem for landscape-scale biodiversity conservation in the tropics. *Current Landscape Ecology Reports*, 2, 51-60.

Gilroy, J. J., Edwards, F. A., Medina Uribe, C. A., Haugaasen, T., & Edwards, D. P. (2014). Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of Applied Ecology*, 51, 1337-1346.

Gotelli, N. J. & Colwell, R. K. (2011). Estimating species richness. In A. E. Magurran & B. J. McGill (Eds.) *Biological Diversity: Frontiers in Measurement and Assessment* (pp. 39-54). Oxford: Oxford University Press.

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307, 550-555.

Hackman, K. O. & Gong, P. (2017). Biodiversity estimation of the western region of Ghana using arthropod mean morphospecies abundance. *Biodiversity &* Conservation, 26, 2083-2097.

Hamer, K. C., Hill, J. K., Benedick, S., Mustaffa, N., Sherratt, T. N., Maryati, M., & Chey, V.K. (2003). Ecology of butterflies in natural and selectively-logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, 40, 150-162.

Jezeer, R. E., Verweij, P. A., Santos, M. J., & Boot, R. G. A. (2017). Shaded coffee and cocoa – double dividend for biodiversity and small-scale farmers. *Ecological* Economics, 140, 136-145.

Kastner, T., Rivas, M. J. I., Koch, W., & Nonhebel, S. (2012). Global changes in diets and the consequences for land requirements for food. *Proceedings of the National Academy of Sciences of the United State of America*, 109, 6868–6872.

Koh, L. P. (2008). Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal of Applied Ecology*, 45, 1002-1009.

Koh, L. P. (2008). Birds defend oil palms from herbivorous insects. *Ecological Applications*, 18, 821-825.

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, 29, 107–116.

Law, E. A. & Wilson, K. A. (2015). Providing context for the land‐sharing and land‐sparing debate. *Conservation Letters*, 8, 404-413.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. F., … Watt, A. D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, 391, 72–76.

Lee, J. S. H., Ghazoul, J., Obidzinski, K., & Koh, L. P. Oil palm smallholder yields and incomes constrained by harvesting practices and type of smallholder management in Indonesia. *Agronomy for Sustainable Development*, 34, 501-513.

Lees, A. C. & Peres, C. A. Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biological Conservation*,133, 198-211.

López-Ricuarte, L., Edwards, D. P., Romero-Rodríguez, N., & Gilroy, J. J. (2017). Impacts of oil palm expansion on avian biodiversity in a neotropical natural savanna. *Biological Conservation*, 213, 225-233.

Lucey, J. M., Tawatao, N. B., Senior, M. J., Chey, V. K., Benedick, S., Hamer, K. C., … Hill, J. K. (2014). Tropical forest fragments contribute to species richness in adjacent oil palm plantations. *Biological Conservation*, 169, 268-276.

Lucey, J. M., Palmer, G., Yeong, K. L., Edwards, D. P., Senior, M. J. M., Scriven, S. A., … Hill, J. K. (2017). Reframing the evidence base for policy-relevance to increase impact: a case study on forest fragmentation in the oil palm sector. *Journal of Applied Ecology*, 54, 731-736.

Luskin, S. M., Lee, J. S. H., Edwards, D. P., Gibson, L., & Potts, M. D. (2017). Study context shapes recommendations of land‐sparing and sharing; a quantitative review. *Global Food Security*,16, 29–35.

Macchi L., Decarre, J., Goijman, A. P., Mastrangelo, M., Blendinger, P. G., Gavier-Pizzaro, G. I., … Kuemmerle, T. (2020). Trade-offs between biodiversity and agriculture are moving targets in dynamic landscapes. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.13699.

Matson, P. A. & Vitousek, P. M. (2006). Agricultural intensification: will land spared from farming be land spared for nature? *Conservation Biology*, 20, 709–710.

Milligan, M. C., Johnson, M. D., Garfinkel, M., Smith, C. J., & Njoroge, P. (2016). Quantifying pest control services by birds and ants in Kenyan coffee farms. *Biological Conservation*, 194, 58–65.

Nájera, A. & Simonetti, A. J. (2010). Can oil palm plantations become bird friendly? *Agroforestry Systems*, 80, 203-209.

Ocampo-Ariza, C., Kupsch, D., Motombi, F., N., Bobo, K. S., Kreft, H., & Waltert, M. (2019). Extinction thresholds and negative responses of Afrotropical ant-following birds to forest cover loss in oil palm and agroforestry landscapes. *Basic and Applied Ecology*, 39, 26-37.

Ordway, E. M., Naylor, R. L., Nkongho, R. M., & Lambin, E. F. (2019). Oil palm expansion and deforestation in Southwest Cameroon associated with proliferation of informal mills. *Nature Communications*,10, 114. http://doi.org/10.1038/s41467-018-07915-2.

Pardo, L. E., Campbell, M. J., Cove, M. V., Edwards, W., Clements, G. R., & Laurance, W. F. (2019). Land management strategies can increase oil palm plantation use by some terrestrial mammals in Colombia. *Science Reports*, 9, 7812. http://doi.org/10.1038/s41598-019-44288-y.

Phalan, B. (2018). What have we learned from the land sparing-sharing model? *Sustainability*, 10, 1760. http://doi.org/10.3390/su10061760.

Proforest (2019). *Shifting towards sustainability. How the APOI is changing palm oil production in West and Central Africa.* <https://proforest.net/en/publications/shifting-towards-sustainability-how-the-apoi-is-changing-palm-oil-production-in-west-and-central-africa>.

Rajakaruna, H., Drake, D. A. R., Chan, F. T., & Bailey, S. A. (2016). Optimizing performance of nonparametric species richness estimators under constrained sampling. *Ecology & Evolution*, 6, 7311-7322.

Rhebergen, T., Fairhurst, T., Whitbread, A., Giller, K. E., & Zingore, S. (2018). Yield gap analysis and entry points for improving productivity on large oil palm plantations and smallholder farms in Ghana. *Agricultural Systems*, 165, 14-25.

RSPO (2018). *RSPO Principles and criteria for the production of sustainable palm oil*. https://rspo.org/principles-and-criteria-review.

Scriven, S. A., Williams, S. H., Ghani, M. A., Agama, A. L., Benedick, S., Brodie, J. F. … Hill, J. K. (2020). Assessing the effectiveness of protected areas for conserving endemic rainforest butterflies on Borneo. *Biotropica*, 52, 380-391.

Scriven, S. A., Suggitt, A. J., Madrid, R. S., Lucey, J. M., Fleiss, S., Waddell, E., … Hill, J. K. (in press). The conservation value of forest set-asides in oil palm landscapes. *Frontiers in Forests and Global Change*.

Şekercioğlu, C. H., Loarie, S. R., Oviedo, B. F., Ehrlich, P. R., & Daily, G. C. (2007). Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology*,21, 482-494.

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., … Tscharntke, T. (207). Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences of the United State of America*,104, 4973-4978.

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United State of America*,108, 20260–20264.

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I.,

… Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151, 53–59.

Turubanova, S., Potapov, P. V., Tyukavina, A., & Hansen, M. C. (2018). Ongoing primary forest loss in Brazil, Democratic Republic of the Congo, and Indonesia. *Environmental Research Letters*, 13, 074028. https://doi.org/10.1088/1748-9326/aacd1c.

Vijay, V., Pimm, S. L., Jenkins, C. N., & Smith, S. J. (2016). The impacts of oil palm on recent deforestation and biodiversity loss. *PLoS One*, 11, e0159668. https://doi.org/10.1371/journal.pone.0159668.

Zabel, F., Delzeit, R., Schneider, J. M., Seppelt, R., Mauser, W., & Václavík, T. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*, 10, 2844. https://doi.org/10.1038/s41467-019-10775-z.

Zhang, M. X., Chang, C., & Quang, R. C. (2017). Natural forest at landscape scale is most important for bird conservation in rubber plantation. *Biological Conservation*, 210, 243-252.

**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. n1, number of sampling stations; n2, number of oil palm smallholdings.

Oil palm

Protected Distance from forest

forest 0.6 ± 0.2 km 9.6 ± 0.5 km

n1 = 12 n1 = 46 n1 = 34

n2 = 20 n2 = 11

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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\* 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

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\*Excludes one sampling station with 45 colonially-nesting weavers (30 village weavers plus 15 chestnut-and-black weavers). Hence n1 = 33 (n2 was unaffected). Including this station, mean = 12.9, SD = 8.0.

**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 | **.871** | -.073 | .088 |
| Small tree dbh (cm) | **.717** | .181 | .260 |
| Sapling density | **.691** | .309 | -.144 |
| Sapling dbh (cm) | **.659** | .360 | .056 |
| Large tree density | .145 | **.934** | -.003 |
| Large tree dbh (cm) | .173 | **.814** | .138 |
| Ground Cover (arcsine %) | -.034 | -.029 | **.826** |
| Herb height (m) | .162 | .110 | **.751** |

**Figure legends**

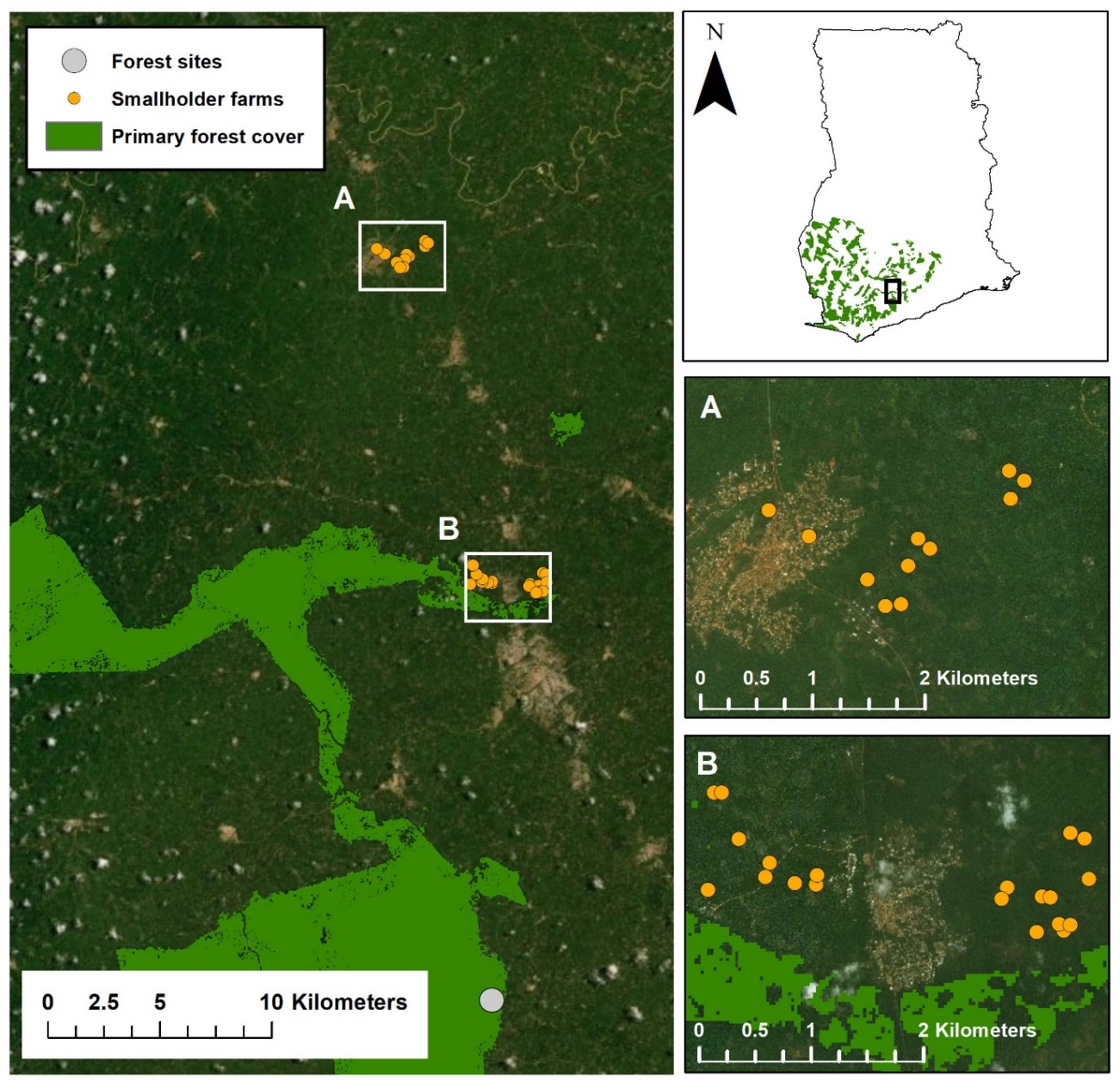
**Figure 1.** The study area and variation in oil palm cultivation. (a) Map of study site showing the distribution of primary forest and locations of studied oil palm smallholdings and sampling plots in forest. Insets show location of study site in Central region of Ghana and detailed locations of studied 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’.

**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 log10 fresh fruit bunch yield (kg ha-1 year-1) of each smallholding and, for forest specialist birds, 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.

**Figure 3.** Log10 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.

**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.

(a)



(b) (c)

Figure 2

(a)



(b)



Figure 2

(c)



(d)



Figure 3



Figure 4

(a)



(b)



(c)



(d)

