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Trade-offs between bird diversity and abundance, yields and revenue in smallholder oil palm plantations in Sumatra, Indonesia

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ABSTRACT

Global land-use change has drastic consequences for biodiversity leading to losses of ecological functioning, ecosystem services and human well-being. While species dependent on undisturbed natural habitat are most affected by conversion to agriculture, even populations of disturbance-tolerant species can be endangered in landscapes dominated by high-input mono-cultural cropping systems. This has raised the question of how, and at what cost, a diversity of species can be conserved in such habitats. Focusing on birds of smallholder oil palm-dominated landscapes, we investigated the relationship between the ecological and economic outcomes of remnant or planted trees in smallholder oil palm plantations. The study comprised a household and a field component. We gathered plot specific data on yields, revenue and inputs from 120 households owning productive oil palm plantations in the Jambi Province, Sumatra, Indonesia. Bird diversity and abundance as well as vegetation structure was assessed on the same oil palm plots. We tested the effects of a set of economic and ecological variables on measures of bird diversity, bird abundance, oil palm yield, and total revenue. Our results show that a gain in bird diversity and bird abundance conditional on increases in number of trees comes along with a loss in revenue for farmers indicating that there is a win–lose relationship between ecological and economic functions. However, since the relationship is non-linear, costs for bird species gain or gain in bird abundance change depending on the number of trees within an oil palm plantation: in a relatively extensively managed oil palm plantation (high number of trees, low oil palm yields), a further increase in the number of bird species or individuals leads to a relatively high loss in total revenue, whereas in an intensively managed oil palm plantation the same increase in number of bird species results in a smaller loss in revenue. An increase in bird abundance can be fostered at smaller costs when compared to the costs for increasing biodiversity. This suggests that there is room for tree-based enrichment of intensively managed oil palm plantations, where a relatively high increase in bird species richness or bird abundance could be achieved at relatively low cost.

1. Introduction

Land-use change is globally the most important cause for biodiversity loss (Immerzeel et al., 2014; Sala, 2000). Both the transformation of natural or semi-natural habitats into mono-cultural annual or perennial cropping as well as agricultural intensification at local and landscape-scale lead to losses in biodiversity and ecosystem functioning of species communities (Edwards et al., 2014; Sala, 2000; Sodhi et al., 2004; Steffan-Dewenter et al., 2007; Wilcove et al., 2013), with a risk of negative effects on human well-being (Cardinale et al., 2012; but see Raudsepp-Hearne et al., 2010). In the next few decades, the pressure on biodiversity will proceed or even amplify due to an increasing demand for food (Tilman et al., 2002) and biofuels (Corley, 2009; Field et al., 2008; Koh and Ghazoul, 2008; Koh and Wilcove, 2007). The mitigation of the loss of biodiversity and of land degradation is therefore one of the major challenges in the current decade (UN‘s ‘decade of biodiversity’) (Tscharntke et al., 2012a).

Almost two-third of the cropland expansion in tropical countries in the last decade can be attributed to the expansion of annual

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crops, such as soybean and maize. Oil palm (*Elaeis guineensis*), ranking the fifth of the most rapidly expanding crops in harvested area, is the most rapidly expanding perennial crop in the tropics (Phalan et al., 2013). Within 25 years, the total plantation area of oil palm has tripled, with current global estimates of over 15 million ha (Gilbert, 2012). In Indonesia, the area under oil palm cultivation almost doubled from 4.2 million ha in 2000 to around 8 million ha in 2010, which account for 46% of the world's crude oil production (Obidzinski et al., 2012). In 2009, the Indonesian government claimed that the oil palm area can be nearly doubled to 18 million ha "without disturbing [...] forest preservation efforts" (The Jakarta Post, 2009).

On the one hand, oil palm cultivation is an attractive pathway out of poverty for many rural households (The World Bank, 2011) even though smallholder productivity (in 2010, 38% of the total oil palm area was managed by smallholders (Rianto et al., 2012)) is approximately 35–40% lower than yields in the private and government sectors (Lee et al., 2013) and varies considerably conditional on institutional, agronomic and biophysical factors (Budidarsono, 2012; Koh and Ghazoul, 2010; Lee et al., 2013; McCarthy, 2010; Rist et al., 2010). On the other hand, oil palm cultivation is also a pervasive threat to biodiversity (Belcher and Schreckenberg, 2007; Fitzherbert et al., 2008). Large areas of Southeast Asia, where around 80% of palm oil are produced, belong to the most biologically diverse terrestrial ecosystems on earth, characterized by a high degree of endemicity (Fitzherbert et al., 2008). It is estimated that between 1990 and 2005 around 57% of the oil palm expansion occurred at the expense of tropical rainforest (Koh and Wilcove, 2008; Wilcove and Koh, 2010). Between 1990 and 2005, Indonesia reported an absolute decline in forested area of 280,000 km^2, ranking second among the countries which face a significant decline in forested area (World Trade Organization, 2010). Oil palm plantations are also often established on extensive complex smallholder production systems, such as "jungle rubber" (*hutan karet*), which is characterized by rubber trees mixed with other tree species forming a stand structure similar to secondary forest (Ekadinata and Vincent, 2011; Gouyon et al., 1993). Both, forest and jungle rubber, are valuable habitats for conservation. Jambi Province in Indonesia is one of the provinces with the fastest and most complete transformation of tropical lowland rainforest and extensive traditional production systems into rubber or oil palm plantations worldwide (Laumonier et al., 2010). Compared to jungle rubber as a complex agroforestry system, oil palm production is characterized by a high degree of intensification at the landscape and habitat scale, including landscape simplification (Foster et al., 2011) and rather low structural habitat complexity (uniform stand age; low canopy; low ground layer vegetation cover; low-stability micro-climate).

Oil palm landscapes are among the poorest habitats for biodiversity in tropical regions (Fitzherbert et al., 2008) and the conversion of natural or logged forest to oil palm plantations leads to dramatic losses in biodiversity in the majority of taxonomic groups (Foster et al., 2011). Fayle et al. (2010), for example, report a decline of forest ant species of 81% as forest is converted to oil palm. This loss of species is mainly caused by a loss in habitat heterogeneity. Moreover, conversion of tropical forests into oil-palm can lead to a loss in ecosystem functions that disproportionately exceeds the decline in species diversity (Barnes et al., 2014). Edwards et al. (2013) showed that functional diversity of birds experiences severe declines along a gradient from unlogged forest to logged forest to oil palm. Similar results were found by Azhar et al. (2013) who emphasized reduced bird functional diversity in oil palm compared to peat swamp forest. Species that dominantly colonized oil palm landscapes after conversion are mainly generalist disturbance-tolerant species with large geographical ranges and low conservation status (Edwards et al., 2013; Peh et al., 2006).

However, it has been highlighted that even in such impoverished landscapes, there can be significant variation in abundance and diversity of species, dependent on the management of the vegetation and the presence of nearby forests (Azhar et al., 2011; Koh, 2008), suggesting that the – from many species' perspective – inhospitable monoculture landscape can be softened up to some degree. Achieving this is valuable, not only in order to maintain populations of disturbance-tolerant species, which have been shown to keep declining elsewhere long after major changes in land use (e.g. farmland birds in Europe), but also to ensure ecosystem functions such as pest control. Birds, for instance, play an important role in an ecosystem as they maintain a wide range of ecosystem functions such as pest control, seed dispersal and pollination (Karp et al., 2013; Sekercioğlu et al., 2002; Sekercioğlu et al., 2004; Van Bael et al., 2008). Birds were shown to contribute to the control of leaf-eating oil palm pests (Koh, 2008) and have a beneficial impact on agroforestry crops as they effectively suppressed arthropod densities leading to an increase of yield by about a third (Maas et al., 2013).

One wildlife-friendly option are designer plantation landscapes in which mono-cultural plantations are enriched with trees planted in gaps within the plantation or with agroforestry buffer zones to surrounding natural vegetation. They are proposed as a means to maintain livelihood needs while increasing biodiversity and ecological functions and thus to alleviate the negative environmental impacts of intensively managed transformation systems such as oil palm (Bhagwat and Willis, 2008; Bhagwat et al., 2008; Clough et al., 2011; Koh et al., 2009). In particular, tree planting is considered an important measure. Planted trees are likely to attract seed dispersing animals by providing habitat for foraging, nesting, or roosting and thus increase seed rain and allow natural succession (Chazdon, 2008). Even within small stands, trees may alleviate stressful conditions and thus facilitate seedling establishment by creating a more favourable microclimate and amelioration of the soil (Cole et al., 2010; Fischer et al., 2010; Herrera and García, 2009; Manning et al., 2006; Zahawi and Augspurger, 2006).

The evaluation of management options that aim to conserve biodiversity, both at the landscape and habitat scale, depends on the shape of relationship between ecological and economic outcomes (Green et al., 2005; Perfecto et al., 2005; Steffan-Dewenter et al., 2007; Phalan et al., 2011a; Tscharntke et al., 2012b). The effect of mixed trees in oil palm plantations, controlling for management regimes (e.g. fertilizer and herbicides application) and habitat complexity (ground vegetation, shrubs) on yields and revenue has rarely been studied. On the one hand, oil palm yields most probably decrease with increasing number of other trees within the plantation because of competition for light and nutrients (Corley and Tinker, 2003), and depending on the method of establishment, on space forgone for planting oil palm. On the other hand, Miccolis et al. (2014) show, based on a study of oil palm grown in trial plots of ecologically diverse agroforestry systems in northern Brazil, that after five years oil palm yields in agroforestry systems were on average higher than those in mono-cultural systems. Thus, agroforests managed to be more "wildlife-friendly" do not necessarily result in a decrease in agricultural output.

Here, we investigate the relationship between the ecological and economic outcomes of remnant or planted trees in smallholder oil palm plantations, as a contribution towards the scientific basis for designing incentives for structurally complex oil palm plantations for enhanced species diversity. This study comprises a field and a household survey component. We conducted a bird and vegetation assessment and a socio-economic household survey from the same 120 smallholder oil palm plantations in four villages in the province of Jambi, Sumatra, Indonesia, along a gradient of habitat complexity and management intensity. This study aims to answer the following research questions: (1) Do remnant or planted trees within oil palm plantations affect bird diversity and bird abundance? (2) Do remnant or planted trees within oil palm plantations affect economic outcome variables, such as yield and revenue? (3) Is there a trade-off between ecological and economic functions? (4) What is the shape of the relationship between ecological and economic functions?

2. Materials and methods

2.1. Study site

The survey was conducted in four villages (Bukit Harapan 1°31′25.9746″S, 102°56′3.3864″E; Bukit Sari 1°31′59.7606″S, 103°10′16.8882″E; Karmeo 1°47′39.7242″S, 103°2′38.1402″; Pulau Betung 1°33′41.4216″S, 103°25′41.6958″E) in the Batanghari region in the Province of Jambi, Sumatra, Indonesia, between February and April 2013 (Fig. 1). Total area of all 101 plots used in the analyses (excluding missing data points) was 164 ha (70 ha in Bukit Harapan; 53 ha in Bukit Sari; 27 ha in Karmeo; 14 ha in Pulau Betung). The climate is humid tropical, with a mean temperature range from 25.9 to 26.8 °C and an annual rainfall of 2268.3 mm yr^{-1} (1960–1990 average). To establish mono-cultural oil palm and rubber cultivation area, natural lowland rainforest was cut massively in the 1970s and 1980s by concession logging. Hence, large areas of lowland rainforest do no longer exist in the Batanghari region but only small patches of jungle rubber or secondary forest. This transformation of lowland rainforest into mono-cultural rubber and oil palm plantations was fostered by the transmigration program, which was launched by the Indonesian government in the 1980s (Elmhirst, 1999; Fearnside, 1997). Within the framework of this program, households were resettled from the over-populated islands of Java or Bali to the less-populated islands of Kalimantan and Sumatra. These settlements were established in Nucleus Estates and smallholder plantations (NES), where a company-owned refinery and estate is surrounded by smallholder-owned plantations. Besides access to credit and oil palm technology, early transmigrant households obtained certified land entitlements, which include 2 ha of already established oil palm plantation within the NES plantation (McCarthy et al., 2012). Transmigrant smallholder oil palm plantations intend to be intensively used agricultural systems characterized by high input use and contribute to landscape homogenization. Oil palm plantations within one NES plantation are similar in terms of oil palm age, oil palm density, and management practices and form a large mono-cultural oil palm plantation by bordering each other.

In the last 10 years, however, the expansion of smallholder oil palm area has been mainly driven by independent smallholders, who are located in autochthonous, rather than transmigrant villages (Ekadinata and Vincent, 2011). These independent smallholders are either locals or spontaneous migrants (e.g. from other parts of the Jambi province). Autochthonous oil palm plots are considerably different compared to the transmigrant ones in terms of oil palm age, oil palm density and management practices. The landscape of autochthonous villages is characterized by oil palm plantations that incorporate a management intensity gradient and small patches with different land use types (e.g. rubber mono-culture, jungle rubber, bush fallow land, home garden, etc.).

To capture a wide range of variability in structural complexity on the habitat and landscape scale among oil palm plantations and accounting for the gradient in agricultural intensity in that region, the survey was carried out in two autochthonous villages (Pulau Betung, Karmeo) and two transmigrant villages (Bukit Sari, Bukit Harapan).

2.2. Household survey

Based on a village census, a total of 120 households that individually manage productive oil palm plots were randomly

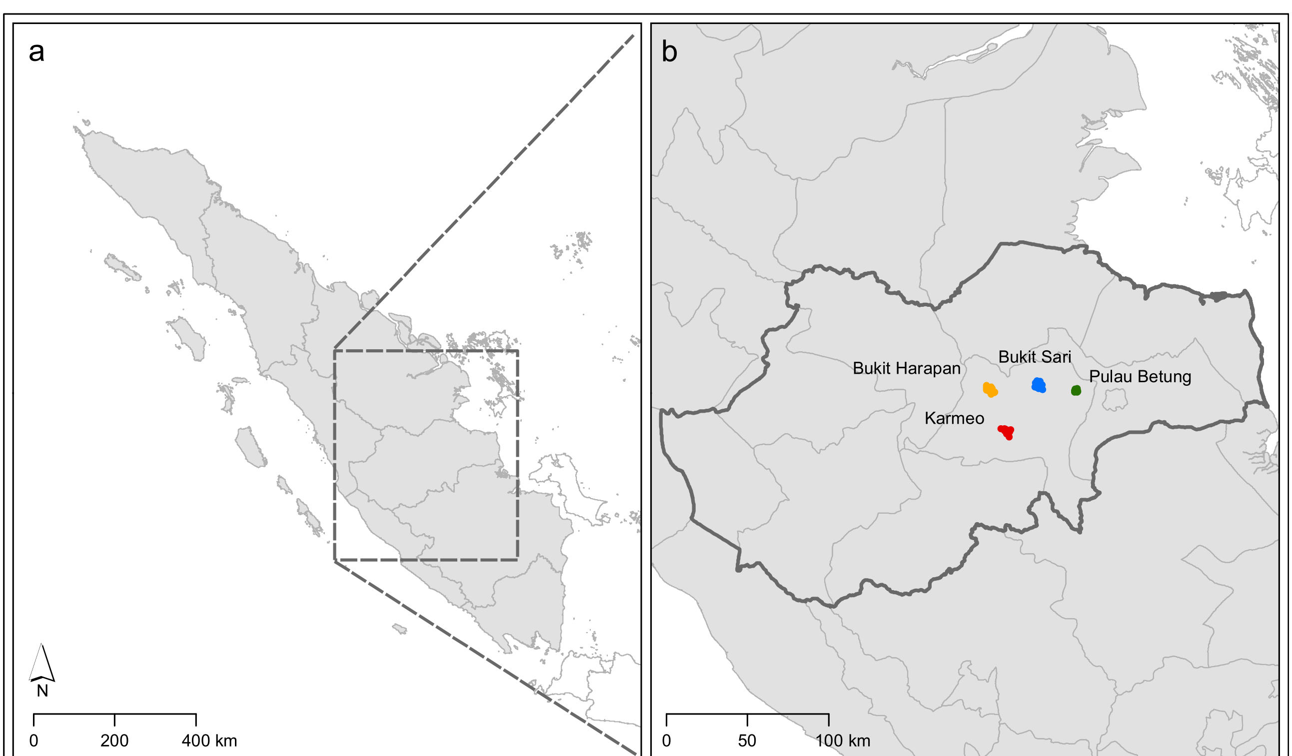

Fig. 1. Map of the study area: (a) Sumatra and (b) location of the study plots in the four study villages Bukit Harapan (yellow), Bukit Sari (blue), Pulau Betung (green) and Karmeo (red) in the Jambi province. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

selected. In the case that a household owned more than one productive oil palm plot, the largest oil palm plot was selected for further consideration. In the transmigrant villages, 70 oil palm cultivating households were interviewed. Due to the lower number of households owning productive oil palms, only 50 plots were selected in the autochthonous villages. Information on farm and household characteristics including plot specific data was obtained from the household heads. The standardized questionnaire contains information on plot characteristics (plot size, oil palm age, oil palm density, location, etc.), abundance and use of trees within or along the border of the specific plot, costs and benefits of oil palm cultivation and cultivation of trees, respectively. All plot characteristics and management related information refer to the calendar year 2012. Afterwards, we accompanied the farmer to the plot that he/she was interviewed about to take GPS coordinates and tracked the borders of each plot by surrounding it with a GPS device. Plots sizes ranged from 0.19 ha to 9.26 ha (mean plot size: 1.62 ± 0.98).

2.3. Bird sampling

Birds were recorded visually and acoustically, and by systematic tape recordings in accordance with a standardized observation method using 15 min point counts at the centre of each plot. We did only one point count per plot, independent of the plot size, as we only wanted to assess the local bird diversity and the sum of observations at the centre of each plot. Each plot was visited twice from 6 am to 10.30 am and there was a minimum of six days between the first and the second sampling period on plots within each of the villages. Point counts were only done when weather conditions were appropriate (no rain). For every species, we recorded the maximum number of individuals present simultaneously on the plot. Individuals flying only above the canopy were excluded from analyses. Migratory species were not recorded. For taxonomy we followed MacKinnon et al. (1993). To get a standardized measure for all plots for the analyses, we used bird observations within a 25 m radius only, as this was the maximum area that could fit into every plot. For vulnerability status, we used the species' IUCN (International Union for Conservation of Nature) classification (IUCN, 2014).

2.4. Vegetation assessment

Vegetation structure was assessed on 100 m × 6 m transects on each plot starting from the centre of the plot proceeding into northerly, southerly, westerly and easterly direction. We distinguished between trees and shrubs and noted the distance of each vegetation structure from the centre. The height and percentage cover of ground vegetation was assessed within circles (radius = 3 m) at the centre point and along each of the four transects at 50 m and 100 m distance from the centre. Density measures for vegetation variables were calculated only from data that was collected within each plot. Vegetation data collected outside the plot were not considered.

2.5. Data analysis

Using mixed effects models, we tested the effect of a set of economic and ecological variables on bird diversity, bird abundance (sum of bird observations in two sampling periods), yields (ton ha^{-1} yr^{-1}) and revenue (US$ ha^{-1} yr^{-1}), with village as a random effect to control for unobserved heterogeneity between the four study villages. Table 1 depicts the set of variables used, as well as their range.

For the bird models, we pooled the observations from the two sampling periods and ran a glmm with a Poisson distribution and a log-link function using the "glmer" function (R Core Team, 2014). There was no over-dispersion in the bird diversity model whereas the bird abundance model was highly over-dispersed. To deal with the over-dispersion in the abundance model, we included an observation level random effect.

For the economic models, we estimated a Cobb–Douglas production function, which was specified as a linear relationship between the log-transformed outcome variables and a range of log-transformed input variables. The "lme" function was used assuming a normal distribution and fitting the models by maximum likelihood estimation (R Core Team, 2014).

Oil palm yields were calculated as the total output of oil palm bunches divided by oil palm area. The total revenue comprises the revenue generated both from marketed oil palm bunches and from fruit and timber products of the remnant or planted trees within or at the border of the oil palm plantation. In addition, the opportunity costs of fruits and timber products generated from remnant or planted trees and consumed by the household were valued using the respective market prices. For the oil palm revenue, for each individual farmer the average fresh oil palm bunch price was calculated based on the average fresh oil palm bunch price received in the dry and in the rainy season weighted by the length of each season.

Table 1
Explanatory variables considered in the full models to explain bird abundance (number of bird individuals within a 25 m radius around the centre point), bird diversity (number of bird species within a 25 m radius around the centre point), yields (ton fresh bunches of oil palm ha^{-1} y^{-1}) and revenue (IDR ha^{-1} y^{-1}); transformed values in parentheses. Offsets used for log transformation of variables including zeros in parentheses.

Variable name	Description	Min	Mean	Max
Village	Factor with four levels, Bukit Harapan, Bukit Sari, Karmeo and Pulau Betung, entered the model as random effect	–	–	–
Number of trees (ecology models)	Number of all trees >2 m per ha, log transformed (offset: 2.51)	0	27.93	314.72
Number of trees (economic models, negative input)	Number of trees per ha, log transformed (offset: 0.22)	0	12.26	125.67
Number of oil palms	Number of oil palms per ha, log transformed	86.98	159.26	349.99
Forest border	Factor with two levels, forest patch bordering the oil palm plot (1) and no forest patch at the border of the plot (0)	0	–	1
Shrubs	Number of shrubs >1.5 m per ha, untransformed	0	30.63	193.72
Height ground vegetation	Factor with five levels: (1) 0–15 cm, (2) 16–30 cm, (3) 31–50 cm, (4) 51–100 cm, (5) 101–150 cm	0	–	5
Age of productive plantation	Age of oil palms	1	12.39	21
Age of productive plantation, squared	Age of oil palms, squared transformed	1	189.41	441
Quantity of fertilizer	Total amount of applied fertilizer (kg) per ha and year, log transformed (offset: 1.14)	0	771.10	2493.22
Value of herbicides	Total value of applied herbicides (IDR) per ha and year, log transformed (offset: 14127.2)	0	184094.6	3461947
Labour hours	Total working hours of family and non-family labourers per ha and year, log transformed	32.43	286.31	2190.72
Marehat	Factor with two levels, marehat clones plantes (1) and no marehat clones planted (0)	0	–	1

The choice of explanatory variables considered in the economic models was guided by the production technologies and practices hypothesized to influence oil palm output and output generated from remnant or planted tree stands. Oil palm smallholders use three main discretionary inputs: herbicides, fertilizer and labour. Since herbicides are partly used as concentrates, we considered the total value of the applied herbicides in the analyses, assuming a positive correlation between the concentration of active substances and price. For fertilizers, it was feasible to use the total amount of applied fertilizer. Labour reflects the total working hours of family and hired labourers spent on weeding of ground layer vegetation and epiphytes, herbicide, fertilizer and soil amendment applications and harvesting. All management-related explanatory variables are given per hectare and year. Previous studies have shown that the yield potential is determined by the quality of the seedlings (Phalan et al., 2009) and that transmigrant smallholders tended to receive better quality seedlings (McCarthy et al., 2012). While most of the transmigrant oil palm plantations in our sample were planted with *Marehat* clones, the variety can be found on a significantly lower share of the autochthonous plots. To control for differences in yields and revenues conditional on the seedling quality, we considered a dummy for *Marehat* clones.

As for the ecological predictors, besides height and percentage cover of ground vegetation as well as number of trees, a forest factor describing whether or not a forest patch (>1 ha) was bordering the plot was included because we assumed that forest patches at the border should function as source habitats and influence bird diversity and abundance on the plot (Anand et al., 2008; Clough et al., 2009). Nearest fragment distance or nearest forest fragment size could not be adequately assessed as there were neither suitable maps with a detailed enough land-use classification, nor recent enough aerial pictures available from which size and distance of forest fragments could have been derived. Collecting this information in the field was not possible due to time and labour constraints.

We used two different tree variables – one for the economic models and one for the bird models – because in the economic survey all the information (e.g. number of oil palms, amount of fertilizer) relates to an entire plot, whereas the ecological variables were derived from only part of a plot (100 $\times$ 6 m transects for vegetation, 25 m radius for birds). As the tree variable is our determining factor and links the economic and ecological parts of the study, we decided to maintain the same scales for the tree variable as for the corresponding response variables (data on bird diversity and abundance for only part of the plot; data on yield and revenue for the whole plot). Hence, for the bird models we used the tree densities that were derived from data collected on transects. In the economic models we included a tree variable, which was based on household survey data and related to the area of the whole plot; it is the number of trees which the farmer recalled having within his plot. The field and household based data on number of trees is significantly correlated ($p = 0.008$). In the economic models we included the tree variable as a negative input given that this better described the data (lower AIC). Additionally, we multiplied the tree variable with a constant term (1.05), as this better approximated the correct shape of the function. In the case of the bird models, the tree variable was entered as a positive input.

Due to incomplete data we only considered 101 of the originally 120 observations in the analysis (37 plots in autochthonous villages, 64 plots in transmigrant villages).

We checked for correlations between the explanatory variables. Not surprisingly, correlation between percentage cover and height of ground vegetation was relatively high (Pearson's $r = 0.59$). Both variables are known to be important structural parameters for birds (Atkinson et al., 2005; Azhar et al., 2013; Clough et al., 2006), but due to the correlation we only included height of ground vegetation. All of the other variable pairs were not strongly correlated (Pearson's $r < 0.5$).

Number of oil palms, number of trees (both variables), labour hours, amount of fertilizer, and value of herbicides were log-transformed. As those variables – except for number of oil palms – contained zeros, we added the smallest value of each variable divided by two to each value of the variable in order to be able to do the log-transformation. Age of oil palms entered the model untransformed and with an additional squared term, as we expected optimal yields at intermediate palm age. All other terms entered the models without transformation. To avoid a leverage effect of some explanatory variables as compared to others, we normalized all predictors by subtracting the mean and dividing by the standard deviation (Schielzeth, 2010).

We checked for spatial autocorrelation by calculating Moran's I values for each of the model's residuals. Using the Moran's I standard deviate in the 'spdep' package in R (R Core Team, 2014), we tested for spatial autocorrelation but found no support for spatial autocorrelation of variation in any of the response variables (Moran's I test results yielded $p > 0.1$).

Model adequacy of full and best models, including normality, homoscedasticity of the residuals, and whether a linear relationship was likely to be appropriate, was checked graphically using diagnostic plots. A forward and backward selection was done with each full model. The best models were chosen on the basis of the Akaike Information Criterion (AIC). All analyses were conducted in R (R Core Team, 2014), with additional functions provided by the packages lme4 and nlme.

3. Results

3.1. Household survey: trees

For almost half of the sampled oil palm plantations (47.9%) trees were reported by the respondents. 1843 trees were recorded on all plots in total. The five most common tree species in the oil palm plantations were rubber *Hevea brasiliensis* ($N = 1495$), banana *Musa spec.* ($N = 120$), durian *Durio zibethinus* ($N = 46$), langsat *Lansium domesticum* ($N = 42$) and alstonia *Alstonia scholaris* ($N = 30$), which account for 94% of the total number of trees. Some other species occurred infrequently; overall 35 species of trees were found. Of those, 19 tree species could be classified as fruit trees and 15 tree species as timber trees (and rubber). When considering only the plantations with trees, on average 1.9286 (SD = 0.1817) different tree species were cultivated, indicating a rather low level of tree species diversity. Even though the number of trees and the number of tree species are significantly correlated, the strength of the relationship is relatively weak (Pearson's $r = 0.31$). Respondents indicated that 85.8% of the trees were planted, while the remaining 14.2% are remnants from former cultivation systems. Unfortunately, the data does not contain information on the age of the trees to assess whether the trees were planted before or after the establishment of the oil palm plantation. With respect to the management of the trees, results revealed that 40% of the trees were pruned, herbicides were applied to 27.9% of the trees and only 2.7% of the trees received fertilizer application. Manure and pesticides were not used.

3.2. Bird species composition and abundance

727 birds of 33 species were detected across all plots within a 25 m radius around the centre point of each plot. The Yellow-Vented Bulbul *Pycnonotus goiavier* was the most common species ($N = 197$), followed by the Olive-Winged Bulbul *Pycnonotus plumosus* ($N = 156$) and the Bar-Winged Prinia *Prinia familiaris* ($N = 127$).

There was one observation of the Green Iora *Aegitina viridissima*, which was the only recorded species listed as "nearly threatened" according to the IUCN. All other recorded species are listed as "least concern" (IUCN, 2014).

The three most important parameters for explaining variation in bird diversity were number of trees, height of ground vegetation and whether or not high quality oil palm seedlings (*Marehat*) were planted on the plot, as shown in Table 2. The number of trees and height of ground vegetation had a positive effect on species richness, whereas the presence of high quality seedlings had a negative effect on species diversity. Similar results were found for bird abundance, which was also positively affected by number of trees and height of ground vegetation. However, the *Marehat* variable did not enter the model. Instead, the number of oil palms was included and had a negative effect on the number of bird observations.

The predicted bird diversity conditional on the number of trees ranged from 2.58 species (*N* tree $ha^{-1} = 0$) to 5.15 species (*N* tree $ha^{-1} = 125$) (Fig. 2a). Predicted sums of bird observations ranged from 3.66 individuals (*N* tree $ha^{-1} = 0$) to 8.05 individuals (*N* tree $ha^{-1} = 125$) (Fig. 2c). Bird diversity and the sum of bird observations showed a positive nonlinear response to an increase in the number of trees (Fig. 2a and c), with a decrease in the marginal effect of trees on bird diversity and abundance with increasing number of trees (Fig. 2b and d). This implies that a further increase in the number of trees in a plantation with low numbers of remnant or planted trees has a larger effect on bird diversity and abundance than the same increase in the number of trees on an oil palm plot with high numbers of remnant or planted trees.

3.3. Determinants of yields

As expected, yields were highest at intermediate oil palm age, as both the age of the oil palm plantation and its squared value entered the best model. Oil palm yields were positively affected by the amount of labour hours (family and hired labour hours) spent on weeding of ground layer vegetation and epiphytes, herbicide, fertilizer and soil amendment applications and harvesting. The cultivation of *Mareha*t clones (improved oil palm seedlings) positively affected oil palm yields. Further management parameters such as the amount of applied fertilizers and the value of applied herbicides did not enter the best model. Yields were not affected by landscape variables, such as the dummy for neighbouring forest patches, which was not considered in the best model. In contrast, both variables capturing the habitat complexity determined the yield of the oil palm plantation; the height of the ground vegetation layer and the number of shrubs >1.5 m negatively affected the yields. We found the number of trees within or at the border of the oil palm plantation to negatively affect yields, too. The predicted oil palm yields conditional on the number of trees ranged from 11.15 ton $ha^{-1} yr^{-1}$ (*N* tree $ha^{-1} = 0$) to 1.80 ton $ha^{-1} yr^{-1}$ (*N* tree $ha^{-1} = 125$) (Fig. 2e). Testing for the functional form of the relation between yields and number of trees, results indicated that the predicted yields conditional on the number of trees follow a non-linear pattern, with an increase of the marginal effect of trees on yields with increasing numbers of trees.

3.4. Trees and revenue

To test whether or not the benefits generated from trees compensated for the loss in oil palm yield, we tested the effect of the set of predictors on total revenue (US$ $ha^{-1} yr^{-1}$) (Phalan et al., 2011b). Again, the total revenue was highest at intermediate age of the oil palm as both, the age and the squared term of age, entered the model. Similar to yield, revenue was not affected by neighbouring forest patches, the amount of applied fertilizer or the value of applied herbicides. Revenue was positively affected by the amount of labour hours (considering family and hired labour hours) and negatively by height of ground vegetation, being one of the proxies for habitat complexity. As opposed to the yield model, the cultivation of *Marehat* clones and shrubs were not important parameters to explain variation in revenue. Again, we found that the number of trees within or at the border of the oil palm plantation negatively affected the total revenue. The predicted revenue conditional on the number of trees ranged from 1010.83 US$ $ha^{-1} yr^{-1}$ (*N* tree $ha^{-1} = 0$) to 222.87 US$ $ha^{-1} yr^{-1}$ (*N* tree $ha^{-1} = 125$). Similar to the functional form of the production function for yield, the relation between predicted revenue and number of trees is non-linear, with an increase in the marginal effect of trees on predicted revenue with increasing tree stands (Fig. 2f).

3.5. Bird diversity and abundance – revenue relationship

The predicted bird diversity and the predicted revenue can be defined as a "yield set", since both outcome variables can be parameterized with respect to trees (Perfecto et al., 2005). The functional form of the "yield set" revealed a "win–lose" relationship between the revenue and the bird diversity (Fig. 3a). Thus, the bird diversity loss can only be mitigated at the cost of revenue. It implies that external incentives have to be provided to encourage profit-maximizing farmers to conserve (Kragt and Robertson, 2014). The slope, also called marginal rate of transformation (MRT), measures how much of revenue is given up for one more unit of bird diversity or vice versa. It also reflects the (marginal) shadow prices of bird diversity (the shadow prices of bird diversity in terms of revenue at the margin). The "yield set" curve is convex, indicating that the MRT increases with increasing revenue

Table 2
Coefficients of variables (±SE) included in the bird and economic models.

	Bird species	Bird abundance	Yield	Revenue
Village	Random effect	Random effect	Random effect	Random effect
Number of trees (ecology models, positive input)	0.243 ± 0.059	0.277 ± 0.093	–	–
Number of trees (economic models, negative input)	–	–	0.404 ± 0.053	0.256 ± 0.143
Number of oil palms	–	−0.205 ± 0.099	–	–
Forest border	–	–	–	–
Shrubs	–	–	−0.068 ± 0.049	–
Height ground vegetation	0.144 ± 0.056	0.194 ± 0.097	−0.123 ± 0.051	−0.131 ± 0.052
Age of oil palm			1.247 ± 0.272	1.655 ± 0.299
(Age of oil palm)^2	–	–	−1.016 ± 0.271	−1.226 ± 0.297
Quantity of fertilizer	–	–	–	–
Value of herbicides	–	–	–	–
Labour hours	–	–	0.309 ± 0.053	0.344 ± 0.056
Marehat	−0.227 ± 0.141	–	0.212 ± 0.127	–

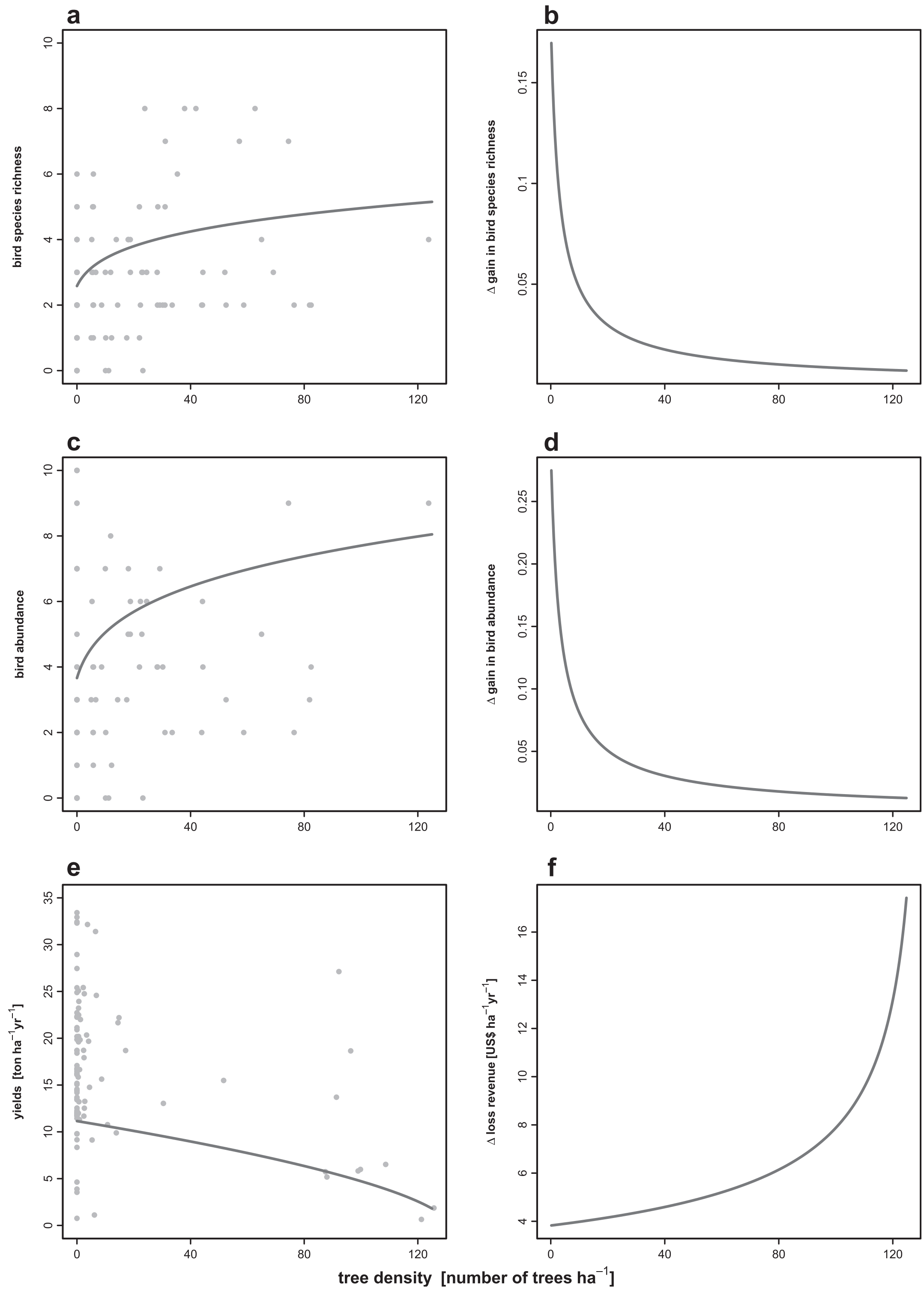

Fig. 2. Effects of trees within oil palm plantations on bird species richness (a), bird abundance (c) and oil palm yields (e). The marginal gain in bird species (b) and bird abundance (d) as well as the marginal loss in revenue (f) conditional on the number of trees are given. Grey dots indicate original observations.

(agricultural intensification). Given a relatively extensively managed oil palm plantation (high number of trees, low revenue), a further increase in number of bird species leads to a distinct loss in revenue. In contrast, given a relatively intensively managed oil palm plantation (relatively low number of tree stands and high revenue), the same increase in number of bird species results in a smaller revenue loss. Thus, up to a certain level of intensification, bird diversity shows a relatively low sensitivity to an increase in intensification.

Similar results were found for the bird abundance – revenue relationship. There was also a "win–lose" relationship between bird abundance and revenue (Fig. 3c) with distinct losses in revenue when bird abundance is increased on relatively extensively managed oil palm plantations and only small losses in revenue

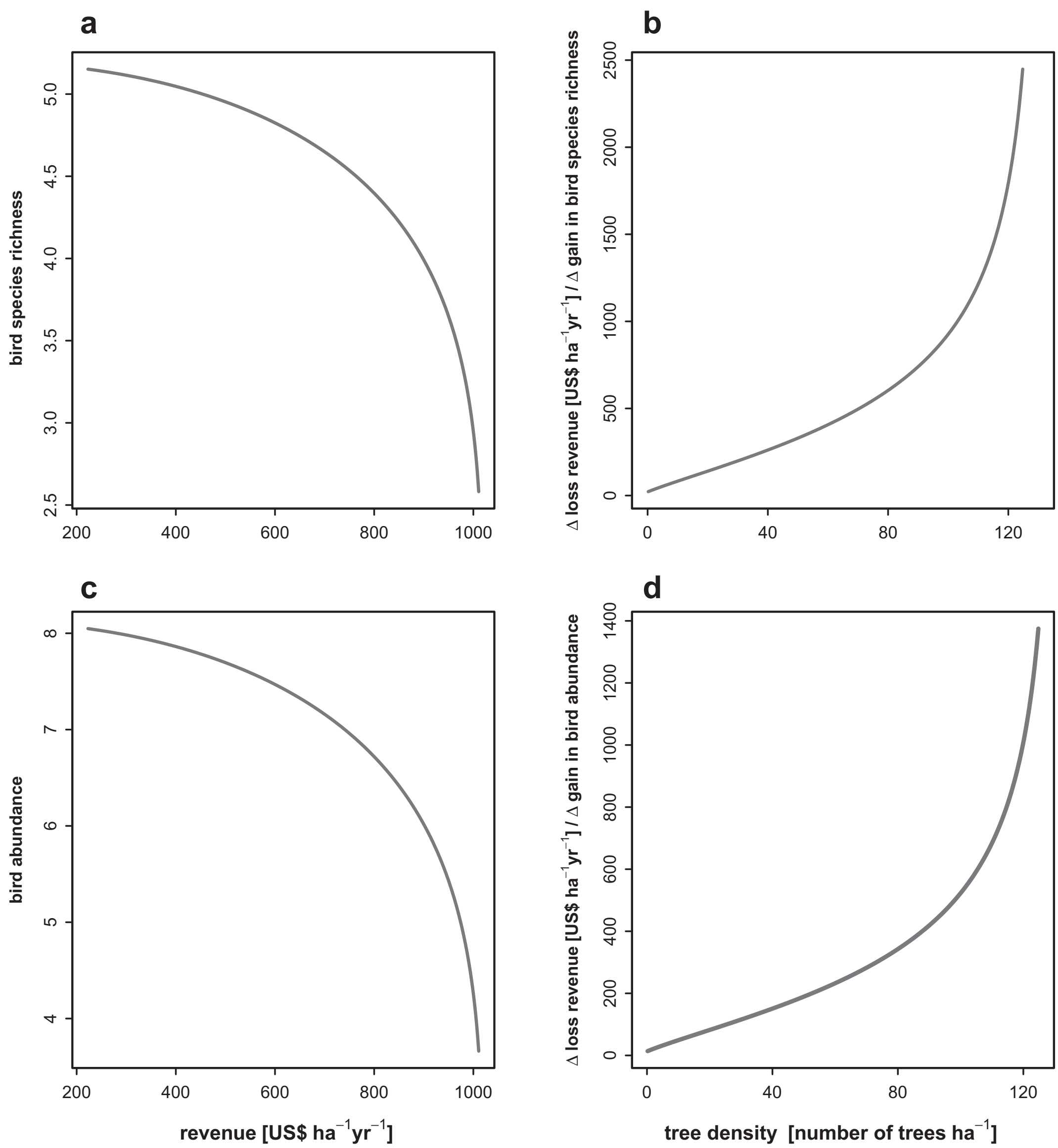

Fig. 3. Relationship between predicted revenue and predicted bird diversity (a) and predicted bird abundance, respectively (c). The functional form of the "yield set" revealed a trade-off between the revenue and the competitive bird diversity/abundance. Marginal loss in revenue with every one-unit change in bird diversity conditional on the tree stands within or at the border of the oil palm plantation (b). The marginal loss in revenue per additional bird species increases with increasing tree abundance. The marginal loss in revenue per additional bird also increases with increasing tree abundance (d). However, the loss in revenue per additional bird observation is lower compared to the loss in revenue per additional bird species.

with increases in bird abundances on intensively managed plantations. However, in general, the revenue loss for additional bird individuals is smaller than for additional bird species, meaning that for the same amount of funds more individuals could be locally conserved compared to species.

3.6. Marginal shadow price of bird species richness and abundance – tree relationship

To evaluate potential target groups of conservation programs that aim to foster bird diversity and abundance by giving external incentives to establish or expand the number of trees within oil palm plantations, we illustrate the marginal loss in revenue with every unit increase in bird diversity (Fig. 3b) and bird abundance (Fig. 3d) conditional on the trees within or at the border of the oil palm plantation. Results revealed that the marginal loss in revenue induced by a one unit increase in bird diversity, and hence the shadow price of bird diversity expansion, increases with increasing numbers of trees (extensification of oil palm cultivation). We calculated the percentage of revenue that has to be given up for an additional bird species exemplified for a plantation with 10 and 50 trees per ha, respectively. A farmer that has ten trees within his/her plantation experiences a 20% loss of total revenue for an additional bird species, whereas on a plantation with 50 remnant or planted trees the same increase in bird species results in a 67% loss of total revenue.

Similarly, for every unit increase in bird abundance, the marginal loss in revenue increased with increasing number of trees. However, a farmer that has ten trees within his/her plantation experiences a 12% loss of total revenue for an additional bird individual, whereas on a plantation with 50 remnant or planted trees the same increase in bird individuals results in a 39% loss of total revenue. This shows, that an increase in bird abundance can be enhanced at smaller costs when compared to the costs for increasing bird diversity.

4. Discussion

Forests and traditional cultivation systems with a high degree of habitat complexity in Southeast Asia are being converted to oil palm plantations at high rate and there is growing interest in oil palm agriculture in other tropical regions, such as South America and Western Africa. Besides the obvious need to conserve large expanses of natural habitats, this raises the question on how to maintain a baseline level of biodiversity in oil palm-dominated landscapes. Focusing thus on a "wildlife-friendly" strategy of having remnant or planted trees within or at the border of oil palm plantations, we investigated the relationship of bird diversity and bird abundance with oil palm yield and total revenue along a gradient from low-intensity oil palm plantations enriched with trees to intensively managed mono-cultural oil palm plantations. Consistent with our expectations, we found a trade-off between these ecological and economic functions indicating that a gain in bird diversity and bird abundance conditional on an increase in the number of trees comes along with a loss in revenue for farmers. It implies that profit-maximizing farmers do not have a private incentive to conserve. However, incremental increases in bird diversity and bird abundance come at different costs depending on the initial number of trees (and therefore the initial level of bird species diversity or bird abundance).

Overall, our study confirmed that bird communities supported by oil palm plantations are extremely impoverished in comparison to natural forests (Peh et al., 2006). Only a few common and widespread species are found in this type of habitat and there is a loss of species with high conservation status and restricted ranges. We observed one forest species and five edge-tolerant species besides mostly edge-tolerant, open habitat and generalist species (for definitions see Rotenberg and Stouffer, 2007) (Supplementary Table 1). With one exception, all sampled bird species had low conservation status. Oil palm sites, however, differed significantly in their bird diversity and abundance depending on the vegetation in the plantation.

Even though oil palm plantations are often pure monocultures, especially in large estates, (Foster et al., 2011), almost half of the sampled smallholder oil palm plantations had remnant or planted trees on them, and varying levels of ground vegetation. We found that the number of trees and the height of ground vegetation were important parameters in explaining variation in bird abundance and species richness. Structural complexity is in general known to positively affect avian community structure (Gordon et al., 2007; Stein et al., 2014; Tews et al., 2004; Van Bael et al., 2007). Azhar et al. (2011) showed that oil palm plantation estates and smallholdings supported similar bird assemblages, but the latter supported slightly more species due to higher complexity of vegetation structure compared to a typical mono-cultural plantation estate. However, our findings suggest that large-scale plantations could also create similar situations like in smallholdings by planting trees for conservation outcomes. A positive effect of trees on bird diversity was also found in the studies by Abrahamczyk et al. (2008) and Clough et al. (2009), where cacao plantations in Sulawesi, Indonesia, with interspersed trees harboured more bird species than plantations without trees. On oil palm plantations in Thailand, Peninsular Malaysia, and Guatemala bird species richness was enhanced by a well-developed understory vegetation (Aratrakorn et al., 2006; Azhar et al., 2011; Nájera and Simonetti, 2010). While we observed a considerable range in density of different fruit and timber trees (0–314.7 trees ha^{-1} (trees >2 m)), the average number of tree species per hectare was low compared to traditional agroforestry crop plantations, such as coffee and cacao, where tree abundance and diversity can be much higher (8–128 trees ha^{-1} (trees >10 m); 12–104 tree species ha^{-1}) (e.g. Clough et al., 2009). In our study, bird diversity and abundance showed a positive non-linear response to increasing numbers of remnant or planted trees. With increasing numbers of trees, however, there was a decreasing marginal effect of trees on predicted bird diversity and abundance.

In line with findings by Azhar et al. (2011), landscape-level attributes such as small secondary forest patches bordering the oil palm plantation, which we included as a landscape parameter, did not explain any variation in bird diversity and abundance in our study. This may be attributed to the low dependency of the majority of bird species (non-forest species) in oil palm plantations on forest habitats and resources as they find food within the plantations (Azhar et al., 2013), and the limited value of neighbouring small secondary forest patches as a source habitat for birds. The study region is characterized by highly isolated forest fragments in wide areas of homogenous oil palm monocultures. Harapan rainforest and the National Park Bukit Duabelas are the only two significant forest areas left in the study area and are not bordering the study sites.

While the number of trees benefited bird diversity and bird abundance, they negatively affected oil palm yields. Assuming that trees within or at the border of the oil palm plantation compete with oil palm for nutrients and light, we included the tree variable in the economic models as a negative input. Indeed, controlling for management practices, landscape, and habitat complexity, the results of the analyses showed that the oil palm yield (ton ha^{-1} yr^{-1}) decreased with increasing number of remnant or planted trees within or at the border of the oil palm plantation. Results indicated that the predicted yield conditional on the number of trees follow a non-linear pattern, with an increase of the marginal effect of trees on predicted yields with increasing numbers of trees. This is in accordance with findings by Corley and Tinker (2003) who stated that oil palm productivity is low when they are shaded by trees (also see Phalan et al., 2009). Oil palm, as a water-demanding plant with high light requirements would likely face intensive competition with intercropped trees for water, nutrients and light (Koh et al., 2009).

The use of a proxy measure for yields such as management intensity indices (e.g. number of trees) would not give the quantitative information on yields necessary to assess the trade-off between economic outcome and bird diversity (Phalan et al., 2011a; Steffan-Dewenter et al., 2007).

Since the economic outcome generated from the remnant or planted trees may compensate for the oil palm yield penalties, we considered the total revenue including the opportunity costs of fruit and timber products consumed by the household, even though this measure is affected by market fluctuations (Phalan et al., 2011a). The predicted total revenue also decreases with increasing number of trees within or at the border of the oil palm plantation (with increasing marginal loss in revenue).

4.1. Implications for conservation

The win–lose relationship between the bird diversity and total revenue conditional on the number of remnant or planted trees within or at the border of the oil palm plantation implies that profit-maximizing farmers do not have, at least in economic terms, a private incentive to mitigate bird diversity loss by extensifying the oil palm cultivation. As in Europe, where land-sharing is encouraged by agri-environment payments for farmers (Kleijn et al., 2006), one could imagine that economic incentives could be implemented to foster the extensification of oil palm cultivation in terms of increasing the number of trees. The marginal loss in revenue with every unit increase in bird diversity conditional on the number of trees within or at the border of the oil palm plantation follows a positive non-linear pattern (see Fig. 3b). Thus, with increasing extensification of the oil palm plantation in terms of the number of trees, the loss in revenue per additional bird species increases suggesting that conservation measures are relatively cheap at low abundances of trees within a plantation. While farmers of a rather intensively managed oil palm plantation (e.g. 10 trees per ha) lose 20% of their total revenue per additional bird species, farmers, who already harbour many trees (e.g. 50 trees per ha) on their oil palm plantation lose 67% of the total revenue per additional bird species. Similar results were found for bird abundance, but the loss in revenue per additional bird individual is in general lower than for an additional bird species (Fig. 3d): on an intensively managed oil palm plantation with 10 trees per ha the farmer experiences a loss in revenue of 12%; farmers of extensively managed oil palm plantations with 50 trees per ha lose 39% of their revenue. Given a fixed conservation payment, farmers of highly intensified oil palm plantations with no or few trees therefore have a relatively strong incentive to expand the number of trees within the oil palm plot compared to farmers of already extensively managed oil palm plantations with many trees on the plot. In fact, the absolute number of bird individuals and bird species would still be lower in relatively intensive plantations with only a few trees compared to a more extensive plantation with more trees to start with. But even a slight increase in bird abundance on intensively managed plantations might already contribute to the system being more stable and resilient towards disturbance or pests due to increased ecosystem functioning and provision of ecosystem services such as pest control and soil fertility. Interestingly, such a gain in ecosystem functioning may exceed the associated increase in diversity (Barnes et al., 2014). Future studies need to address whether or not an increase in bird diversity also results in higher ecosystem functioning.

To compensate for a revenue loss associated with the increased abundance of trees within the oil palm plantation, both, the implementation of a premium price for eco-friendly certified palm oil products and relevant extension services financed through national or international environmental funds, are potential solutions. The rising public debate about the social and environmental impacts of oil palm cultivation prompted the establishment of the Round Table on Sustainable Palm Oil Production (RSPO, 2014). The RSPO certification requirements cover a range of sustainability criteria, such as controlling of soil erosion, groundwater and chemical pollution. However, specific certification schemes requiring foliage cover, tree height and diversity, like in the Smithsonian Migratory Bird Centre (SMBC) bird friendly coffee certification scheme, do not exist for palm oil. In Europe, palm oil, as the "secret in the shopping basket" has often been hidden as generic vegetable oil in processed food (Paddison, 2014). In 2014, the EU launched the law on food information to consumers (FIC), determining that hiding ingredients under generic titles is no longer permitted. Whether the labelling of palm oil translates into a change in consumer preferences towards more eco-friendly produced palm oil products still remains to be seen (Smedley, 2014).

Critics of wildlife-friendly interventions argue that they tend to reduce actual or potential farmland yields compared to conventional farming and thereby increase encroachment on natural habitat (Clough et al., 2011; Donald, 2004; Green et al., 2005; Phalan et al., 2011b; Tscharntke et al., 2012b). Indeed, in the majority of management intensity gradients ranging from no or minor management to high management intensity, biodiversity declines steeply in response to a slight increase in intensification (with a decreasing marginal rate of substitution), indicated by a concave function. It implies that the target species would benefit more from land-sparing associated with maximum attainable yield agriculture than from land-sharing (Baudron and Giller, 2014; Phalan et al., 2011a, 2011b). This shape holds for multiple taxa in Europe and the tropics (Gabriel et al., 2013; Hulme et al., 2013; Phalan et al., 2011b). Of course, also in our study region, large differences in bird diversity and abundance between forests and oil palm plantations suggest that when having to choose between diversification of oil palm and forest conservation (and assuming both are effective), the latter would be a more efficient way to maximise crop production and species conservation. The degree to which both the causal linkages (lower yields → encroachment on natural habitat) implicit in the models as well as the model assumptions hold, and whether the focus on two desired outcomes rather than a breadth of ecosystem services is relevant for resource management and policy, are issues severely debated elsewhere (Baudron and Giller, 2014; Tscharntke et al., 2012b; Phalan et al., 2011a; Koh et al., 2009). The debate suggests that oil palm diversification, such as the maintenance of trees in oil palm plantations, while not an alternative to conserving forests, should not be rejected a priori.

Interestingly, our results show that farmer choices are not governed purely by economic considerations: although yield and revenue were negatively affected by density of trees on the plantation, a significant part of the smallholders have either implicitly or explicitly chosen to keep and/or plant trees on their plantation, despite the likely perceived standard of oil palm management as a pure monoculture, which can be easily observed on nearby estate plantations. In this study, long-term resilience, as opposed to short-term yield maximization, was not considered as an economic objective, even though it might be pursued by risk-averse decision-makers. In our rather simplistic approach, other factors, such as cultural services (spiritual enrichment, recreation and aesthetic experiences), are also neglected (Kragt and Robertson, 2014). Further progress on understanding farmer choices and value systems is critical to inform possible conservation actions.

Further research is needed to provide more specific recommendations on how to design potential oil palm plantations with high habitat complexity provided through the presence of trees and a well-developed ground layer vegetation. While this study investigated the effect of the presence of remnant or planted trees on bird diversity and abundance as well as on yields and revenue, we did not distinguish between remnant and planted trees, fruit trees and other trees nor was the size structure of trees considered. Other studies suggest that factors such as tree age, tree diversity, presence of specific functional groups of trees or tall trees, are decisive when it comes to associated animal diversity (Clough et al., 2011; Erskine et al., 2005; Kanowski et al., 2003). To test the effect of tree species diversity, size structure and composition on biodiversity and oil palm yields, a long term biodiversity enrichment experiment which systematically alters tree species richness and composition and the size of tree islands was established in the same region (Jambi Province, Sumatra, Indonesia). Monitoring the growth of trees, oil palm yield, bird and invertebrate diversity and abundance, this will allow us in the near future to address questions regarding the planting strategy under which biodiversity and ecosystem functions can be restored – which includes choosing the appropriate tree species for habitat enrichment – and how the economic functions of an oil palm plantation are affected by different types of enrichment plantings.

5. Conclusion

Our study confirmed that bird communities supported by oil palm plantations are extremely impoverished in comparison to natural forests. Nevertheless, the restoration of wildlife-friendly oil palm plantations associated with higher structural complexity can mitigate the loss of bird diversity with respect to edge-tolerant, open habitat and generalist species. Furthermore, we found a positive relationship between bird abundance and tree density. Thus, a slight increase in bird abundance on intensively managed plantations might already increase ecosystem functioning and provision of ecosystem services such as pest control and soil fertility. Studies, which investigate the ecological role of birds in oil palm plantations by identifying and analysing functional groups separately, are hence needed. The negative revenue – bird diversity and revenue – bird abundance relationship, respectively, suggests that profit-maximizing farmers do not have an incentive to establish or restore wildlife-friendly oil palm systems. However, since the relationship is non-linear, in a relatively extensively managed oil palm plantation (high number of trees, low oil palm yields), a further increase in the number of bird species and bird individuals leads to a relatively high loss in revenue, whereas in an intensively managed oil palm plantation the same increase in number of bird species and individuals results in a smaller loss in revenue. This indicates that there is room for tree-based enrichment of intensively managed oil palm plantations, where a relatively high increase in bird species richness and bird abundance could be achieved at relatively low cost.

Author contributions

All authors designed the study. Field work was carried out by M.T. and M.V. M.T., M.V., M.W., U.B. and Y.C. analysed the data; M.T. and M.V. wrote the first draft of the manuscript and all authors contributed to revisions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.03.022.

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