Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes

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Smallholder-dominated agricultural mosaic landscapes are highlighted as model production systems that deliver both economic and ecological goods in tropical agricultural landscapes, but trade-offs underlying current land-use dynamics are poorly known. Here, using the most comprehensive quantification of land-use change and associated bundles of ecosystem functions, services and economic benefits to date, we show that Indonesian smallholders predominantly choose farm portfolios with high economic productivity but low ecological value. The more profitable oil palm and rubber monocultures replace forests and agroforests critical for maintaining above- and below-ground ecological functions and the diversity of most taxa. Between the monocultures, the higher economic performance of oil palm over rubber comes with the reliance on fertilizer inputs and with increased nutrient leaching losses. Strategies to achieve an ecological-economic balance and a sustainable management of tropical smallholder landscapes must be prioritized to avoid further environmental degradation.

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Large expanses of lowland tropical rainforest have been converted to large-scale commercial plantations or small-scale mosaic agricultural landscapes, in which fragments of forests are surrounded by a mixture of settlements, monocultures and mixed-species land uses. While smallholder-dominated mosaic landscapes often retain natural resources and combine land uses that support complementary ecosystem functions, services and benefits, these are subject to trade-offs and synergies. For instance, an immediate effect of the production of food and other raw materials on economic benefits could drive increases in crop production and associated returns from the land at the expense of other ecological functions. Further, land-use intensification, conversion of semi-natural habitat remnants and specialization on a few cash crops remain pervasive. Studies combining empirical evidence on land-use dynamics, economic benefits, biodiversity and ecological functions in smallholder systems are scarce but essential to better understand these dynamics.

The present study aims at quantifying land-use dynamics and their drivers, as well as economic and ecological impacts of land-use choices in smallholder-dominated tropical landscapes in Sumatra, Indonesia (Fig. 1a), using a unique multidisciplinary data set collected in a collaborative project by over 20 research groups. Originally covered by sparsely populated rainforest, large parts of the lowlands now consist of large-scale oil palm, **Acacia** plantations, and small-scale smallholder-dominated mosaics of forest remnants, jungle rubber (rubber-enriched secondary forest) and oil palm monocultures (Fig. 2a–d; see Supplementary Note 1 for historical and institutional background). While expansion of large-scale industrial plantations of oil palm in the region have raised much environmental concern, dynamics in smallholder land-use and their consequences are less well known. This is despite smallholder-managed land making up the largest share of agricultural land, even among so-called ‘estate crops’ such as rubber and oil palm. We expect the most productive and profitable agricultural land-use types to be increasing, and that underlying ecological-economic trade-offs lead to reductions not only in biodiversity, but also in key ecological functions underpinning ecosystem services such as climate regulation and water quality. We assessed land-use, profitability, agricultural inputs and outputs for 464 smallholder households from 45 villages in Jambi province, Sumatra (Supplementary Fig. 1), and attitude to risk was quantified for a subsample of farmers.

Land-use transitions over the past 20 years were assessed at household level with survey data, and at regional level using land-use classification inferred from remote sensing. For each of the studied land-use types (rainforest, jungle rubber, rubber and oil palm plantations), we empirically assessed biodiversity, ecological functions and ecosystem services in 32 core study sites (eight per land-use type, Supplementary Fig. 1). First, we evaluated biodiversity with (i) three indicators for naturalness index: forest bird species, indigenous tree species and absence of the ten common invasive weed species, (ii) local species richness across important plant, vertebrate, invertebrate, protist and prokaryote groups and (iii) plant genetic diversity. The former is a proxy for the potential to contribute to nature conservation, while the others have been shown to support ecosystem functioning. Second, we assessed stability in micro-climatic conditions on the basis that a buffering from extreme conditions is beneficial for biodiversity and ecosystem functioning. Third, we quantified leaf litter decomposition, soil microbial functioning and nutrient leaching in the soil as indicators of regulating services through sustainability of soil fertility and ground-water quality. Fourth, we measured harvested yield, net primary production (NPP) and ecosystem carbon stocks as indicators of both provisioning (yield) and regulating (carbon sequestration) services. We find that the more profitable oil palm and rubber monocultures replace forested systems that play a key role in supporting biodiversity and ecological functions. Oil palm is profitable and attractive, but degrades soil quality and causes nutrient leaching. Finding strategies to balance ecological and economic functions in these landscapes, including a more sustainable management of smallholder oil palm, is required to avert further environmental problems.

**Results**

**Productivity, inputs and profitability.** Farms were characterized by a low diversity (high specialization) of cultivated crops (Supplementary Fig. 2), especially in the transmigrant villages. Rubber and oil palm were most prevalent, being cultivated by 82 and 35% of smallholder farmers, respectively (Supplementary Table 1). Rubber was predominantly grown in monoculture, as only 17% of visited rubber plots could be categorized as jungle rubber. Cultivation of other crops was much less common and undertaken only in small plots (Supplementary Table 1). Distribution of land ownership was highly uneven, with 50% of...
the land area being held by about 10% of the farm households (Supplementary Fig. 3). The household survey showed that oil palm was managed much more intensively with herbicides, and soil amendments (that is, chemical fertilizers and lime) than rubber, but required less labour (see Fig. 3a,b,d; statistical results and summary statistics in Table 2 and Supplementary Table 2). Hence, oil palm cultivation resulted in a high gross margin per labour unit (high labour productivity), but lower gross margin per land unit (low land productivity), compared with rubber plantations (Fig. 3c,d). On the other hand, compared with oil palm, both jungle rubber and monoculture rubber were labour-intensive, with a low labour productivity (Fig. 3b,d), due to rubber being harvested around five times a week, compared with once in every two weeks for oil palm. This difference was crucial to explain the land-use changes in Jambi, as it helps the labour-constrained smallholders expand their farm by incorporating oil palm in the crop-portfolio. Rubber plantations had a higher land productivity than jungle rubber (Fig. 3c). In the core plots, maximum and mean rubber yield in monoculture plantation was four and two times the yield in jungle rubber, respectively (Fig. 4g). Oil palm plantations were cultivated by more risk-averse farmers than jungle rubber (Holt–Laury values; LR-test; P = 0.044; Fig. 3e), whereas farmers with monoculture rubber showed intermediate levels of risk-taking. Transmigrant villages differed from non-transmigrant villages in having higher fertilizer costs, in particular in oil palm, and in having a larger share of family labour over hired labour in jungle rubber and rubber plantations, and higher gross margins (Table 2 and Supplementary Table 2).

Regional and household-scale land-use changes. Between 1990 and 2011, unprotected forest within the study area decreased by more than 75% (Fig. 1b, Supplementary Fig. 4). For comparison, in the same period forest decrease was only 13% inside the two protected areas, Bukit Duabelas National Park and Harapan Rainforest restoration concession, where our forest core plots were located. In the same period, rubber increased by 30%, oil palm by 150%, and shrub/bushland, which were mostly fallow lands awaiting planting with rubber or oil palm, by 300% (Fig. 1b). Over 80% of farm plots belonging to the surveyed households were acquired or established after 1990 (Supplementary Fig. 5), confirming significant expansion of area under smallholder-managed plantation crops in the last two decades. Farmers reported that oil palm and rubber were developed from shrub/bushland (33% of oil palm, 27% of rubber) and direct deforestation (14% of oil palm, 32% of rubber), the latter being more commonly reported in the autochthonous villages (Supplementary Fig. 6). The remote-sensing data suggested that shrub/bushland was an intermediate state, with much of the rainforest losses being due to conversion to both oil palm and rubber (Table 1). There is still apparent potential for considerable cultivation expansion as one-fifth of the farmers possessed uncultivated fallows in 2011–2012 (mostly shrub/bushland, Supplementary Table 1).

Biodiversity. Naturalness was highest in forest, and successively decreased in jungle rubber, rubber plantation and oil palm plantation (Fig. 4a, summary statistics and statistical results in Table 2 and Supplementary Table 3). Overall, plot-scale species richness was higher in forest and jungle rubber than in the monocultures (Fig. 4b), but individual taxa responded differently (Table 2). Plant, bird, termite, litter invertebrate and protist richness decreased from forest and jungle rubber to monocultures (Fig. 4b), but individual taxa responded differently (Table 2). Plant, bird, termite, litter invertebrate and protist richness decreased from forest and jungle rubber to monocultures, while ant and archaenal richness did not differ among land-use systems, and bacterial richness was higher in the monocultures. Genetic diversity, assessed for ten dominant plant species in each plot, was higher in forests and jungle rubber than in the two monocultures (Fig. 4c).

Ecological functions. Stability in micro-climatic conditions (temperature and humidity in air and soil) was highest in the forest, lower in the jungle rubber and lowest in the rubber plantations, with values for oil palm intermediate between rubber and jungle rubber (Fig. 4d, summary statistics and statistical results in Table 2 and Supplementary Table 3). Soil microbial biomass, microbial decomposer activity and leaf litter were similar in forest and jungle rubber but significantly lower in monocultures (Fig. 4e). Nutrient-leaching fluxes were higher in the fertilized oil palm than in the other three land-use types (Fig. 4f). Yield, measured as harvested biomass, was highest in oil palm, intermediate in rubber and lowest in jungle rubber.

Figure 2 | Land-uses and associated ecological functions. Forest remnants (a,e), jungle rubber (b,f), rubber plantation (c,g) and oil palm plantation (d,h). Ecological functions are represented as flower diagrams. For each function, the minimum (circle centre) is the 5th quantile and the maximum (circle edge) is the 95th quantile of the standardized ecosystem function indicators, observed in a plot of any land-use types. The outer edge of the flower petals indicates the estimate for the aggregate ecosystem function in a given land use relative to these minima and maxima. Because the importance of functions may differ between stakeholders, unweighted values are presented. Photo credits: Katja Rembold (a), and Yann Clough (b-d).
Fertilization-driven soil biochemical indicators were also higher in oil palm than in the other land-use types (Supplementary Fig. 7). Values of both net primary productivity (excluding yield) and carbon stocks were highest in forest, intermediate in jungle rubber and lowest in monocultures (Fig. 4h,i). Carbon (C) stocks were equally distributed amongst the plant biomass and soil organic C in forest and jungle rubber. In the monoculture plantations, C stocks in plant biomass were much lower than in forested systems, with much less marked differences for soil organic C stocks, which were very variable even within the same land-use type (Fig. 4i).

Economic-ecological trade-offs. The trade-offs between ecological functions incurred by choosing one land-use over another are illustrated in a standardized manner in Fig. 2, and are also reflected in the ecological function correlation matrices (Supplementary Fig. 8). When considering ecological functions across a forest—agroforest—monoculture plantation sequence, production of harvested biomass increased, but most other functions decreased. Nutrient retention, calculated as the additive inverse of nutrient leaching, was the only function for which rubber monocultures, usually unfertilized in smallholder landscapes, attained similarly high relative values as forest and jungle rubber.

Figure 3 | Economic functions for three agricultural land-uses. Measures for agricultural input use (a–b), profitability functions (c–d), and farmer risk aversion (e) in three agricultural land-uses (Jambi, Indonesia): material inputs (a), labour inputs (b), gross margin per hectare (c) in units of 10³ Indonesian Rupiah (IDR) ha⁻¹ yr⁻¹ and gross margin per labour unit (d) in units of 10³ IDR h⁻¹. Farmers risk aversion (e) is measured with a Holt–Laury lottery, higher values indicate higher risk aversion. Summary statistics of all variables are in Supplementary Table 2. Boxplots indicate the lower quartile, median and upper quartile, with whiskers extending to the most extreme data point that is no more than 1.5 times the interquartile range from the edge of the box. Horizontal bars indicate the estimated mean indicator variable value; letters indicate significant differences (F/Wald-tests; \(P_o 0.05\)) in these linear model (c–e) and linear mixed model (a–b) estimates between the land-use types. Boxplots within land-use (from left to right) are labelled within the panels (from top to bottom and left to right).
Discussion

The persistence of biodiversity and ecosystem-service delivery in human-dominated tropical mosaic landscapes depends on land-use dynamics and the contribution of the dominant land uses to bundles of ecosystem services and local benefits, where significant trade-offs may be expected between economic and ecological functions. In smallholder-dominated landscapes of lowland Sumatra, forest cover has diminished drastically over the past 20 years and current land-use choices favour the adoption of the most profitable monocultures. These changes led to higher
crop production and incomes among smallholders, but were accompanied with declines in multiple ecological functions directly related to biodiversity conservation, climate regulation and water quality.

The province of Jambi is a model of crucial dependency on its agricultural sector. In 2013, approximately half of the workforce was employed in the agricultural sector, a share which has not changed much over the past four years, while the total population in the province is increasing\(^7\). Rural poverty is low in Jambi (7\%) in comparison with national urban-poverty value (14\%). This is true in both absolute terms and in relation to urban poverty\(^10\), making the Jambi agricultural sector attractive for migrants. Between 1990 and 2010, the population of Jambi increased from 2 to 3 million, and that of the five regencies constituting our study area from 0.8 to 1.4 million\(^10\). Increased numbers of smallholders as well as increased area of large-scale plantations has gradually reduced the area of accessible farmland for smallholders. The increase in land scarcity has several effects: extensification to secure land, forced agricultural intensification as farmers’ subsistence strategies shift from extensive ‘slash-and-burn’ cultivation to cash-crop production, and increased agricultural transition\(^11\).

In agreement with previous studies\(^11,12\), we found that the total area under cultivation had increased, mainly due to the conversion of forest to oil palm and rubber. Deforestation, especially of near-primary forest, causes biodiversity losses that are impossible to compensate with other land uses, which is clearly visible from all three measures of biodiversity used in the present study. Besides the local loss in naturalness and biodiversity, the regional persistence of species even in larger, protected forest fragments (such as the Harapan Rainforest where there was a more stable forest cover, Supplementary Fig. 4) may be jeopardized in the long-term by increasing isolation from other forested habitats and by reducing connectivity of the landscape matrix following monoculture establishment\(^2\). With low values of naturalness and biodiversity of conservation-relevant groups, rubber and oil palm monocultures cannot contribute to the maintenance of the characteristic fauna and flora of the studied landscapes in general\(^13\), unless effective regional planning achieves the combination of high yields under monocultures with land set aside for forest regrowth\(^14,15\). Jungle rubber is associated with intermediate levels of biodiversity, but its usefulness for conservation is impeded by low yields and poor economic performance, which may potentially lead to increased deforestation elsewhere.

Jungle rubber was formerly the main rubber production system\(^9\), but low land and labour productivity (Fig. 3c,d) explain why jungle rubber decreased in area, while both monocultures increased (Table 1). Rubber and oil palm plantations were complementary\(^16\), in that rubber plantations had high labour productivity and oil palm high return-to-labour. Although the per hectare land productivity was comparable between monoculture rubber and oil palm plantations, households facing labour constraints could increase and diversify their farm income by adopting oil palm, which required relatively less involvement of labour. In interviews of smallholders, respondents stated that they viewed oil palm as an easier crop to cultivate. The risk-averseness of farmers cultivating oil palm over farmers owning jungle rubber may seem surprising given the flexibility of the agroforestry systems\(^17\), but suggests other causes of oil palm expansion besides the attractiveness of higher and quicker returns. Substantial economic benefits of the expansion of monoculture cultivation were apparent from our data and are visibly linked to increased human welfare in the region, as is the case elsewhere\(^14,18\). Focusing mainly on contribution to average farmer income may mask that human welfare is not limited to economic variables, and that the impact of land-use change may affect different persons differently, depending on gender, ethnicity, social and economic status\(^19\). For instance, our results support differences in agricultural inputs and profitability between systems for transmigrant and non-transmigrant villages. The data analysed in this study do not allow for a full assessment of impacts of land-use changes on human wellbeing. However, welfare impacts are found strongly linked to the farmer heterogeneity and differential factor (especially human labour) endowment of the farm-household\(^20\), indicating potentially negative implication of plantation expansion on economic equality. The degree to which these developments benefit the whole population thus is uncertain and the inequality in holding size—with 10% of the farmers holding over 50% of the land area—suggests significant disparities\(^21\). Besides these potential socio-economic caveats, our study highlights pervasive negative side effects on ecological functions and the natural capital and ecosystem services they support.

While oil palm plantations have attracted more attention than rubber for their negative environmental impacts, we show that both monocultures perform similarly in terms of most ecological functions and services, despite the crop plants and the resulting vegetation structure being very different. The lower taxonomic and genetic plant diversity (Fig. 4a–c), simpler vegetation structure and more variable microclimate of monocultures (Fig. 2a–d) in comparison with forested systems were concordantly associated with low species richness of birds, invertebrates and protists, as expected. However, similar plot-scale diversity of ant and archaea diversity across systems, and higher bacterial diversity in monocultures than forested systems showed that communities were not always simpler in monocultures. The detailed linkages between biodiversity and ecosystem functions assessed in our study are still being investigated, yet first results show that the observed changes in biodiversity are accompanied by strongly altered soil food webs\(^22\), leading to equally strong alteration of ecosystem functioning and soil processes (Fig. 4e).

### Table 1 | Land-use/land cover change (%) from 1990 to 2011 in the study landscapes in Jambi Province (Indonesia) based on land-use classification inferred from remote sensing.

<table>
<thead>
<tr>
<th>Land-use/Land Cover</th>
<th>2011</th>
<th>Total 1990</th>
<th>Loss</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>36.60</td>
<td>10.59</td>
<td></td>
</tr>
<tr>
<td>Oil palm</td>
<td>7.46</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>0.66</td>
<td>1.10</td>
<td></td>
</tr>
<tr>
<td>Rubber</td>
<td>0.03</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Shrub/bush</td>
<td>0.04</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>36.60</td>
<td>18.77</td>
<td>13.04</td>
</tr>
<tr>
<td>Gain</td>
<td>0.00</td>
<td>11.31</td>
<td></td>
</tr>
</tbody>
</table>
As examples, decomposition and specific respiration, a key process controlling carbon and nutrient cycling, shifted from being large in forest and jungle rubber with high biodiversity and stable abiotic factors to being reduced in oil palm and rubber monocultures. In contrast to findings of previous study, our results show where a dominant termite species maintained similarly high decomposition rates in oil palm as in forest. In a recent pan-tropic study, including Jambi Province, lowland forest conversion to smallholder oil palm and rubber plantations was associated by the loss of up to 50% of stored soil organic carbon (SOC) in the original forest soils\textsuperscript{24}. These SOC losses were contributed by an increase in soil erosion\textsuperscript{25}, a decrease in NPP and thus in organic matter input (Fig. 4e) and changes in abiotic conditions (Fig. 4d) that altered leaf litter decomposition (Fig. 4e) in rubber and oil palm monoculture.

The fertilized oil palm plantations stand out as having very high nutrient-leaching fluxes. Amongst the environmental aspects which autochthonous residents most frequently associated with oil palm expansion were periodic decreases in water quality and quantity\textsuperscript{26}, resulting in scarcity of water for drinking, bathing and washing clothes (see Carlson et al.\textsuperscript{27} for freshwater data from Kalimantan). In oil palm, fertilization is an important management practice, without which decline in soil fertility with years of cultivation after deforestation would be inevitable\textsuperscript{28}. Nitrogen fertilization in oil palm plantations was associated with high nutrient leaching (Fig. 4f) which may have negative impacts on ground-water quality. In addition, N-oxide emission from the soil may have increased as can be inferred from the increased soil

### Table 2: Statistical results including interactions between indicator variable and land-use system.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Explanatory variable</th>
<th>numDF</th>
<th>denDF</th>
<th>Wald/F-value</th>
<th>P value</th>
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<tr>
<td>Material inputs</td>
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<td>1</td>
<td>955</td>
<td>45.41</td>
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</tr>
<tr>
<td></td>
<td>Variable</td>
<td>2</td>
<td>955</td>
<td>0.00</td>
<td>1.0000</td>
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<td></td>
<td>Village type</td>
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<td>3.40</td>
<td>0.0655</td>
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<td></td>
<td>Interaction LUS × Var</td>
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<td>955</td>
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<td>1.77</td>
<td>0.1713</td>
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<tr>
<td></td>
<td>Interaction Var × VT</td>
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<td>955</td>
<td>11.42</td>
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<tr>
<td></td>
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<td>0.9676</td>
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<tr>
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<td>3</td>
<td>199</td>
<td>10.29</td>
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<tr>
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<td>Variable</td>
<td>8</td>
<td>199</td>
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<tr>
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<td>Interaction LUS × Var</td>
<td>24</td>
<td>199</td>
<td>6.58</td>
<td>&lt;0.0001</td>
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<tr>
<td>Genetic plant diversity</td>
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<tr>
<td>Stability in climatic conditions</td>
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<td>112</td>
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<td>&lt;0.0001</td>
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<td>28</td>
<td>6.81</td>
<td>0.0014</td>
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<td>Variable</td>
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</table>

The multiple indicator variables used for each response variable are shown in Figure 4; because indicator variables may systematically differ in responses to land use, we test the interaction between indicator variable identity (listed in the table as Variable) and land-use. Linear models and F-tests were used with models with a single indicator variable, linear mixed models and Wald-tests for models with multiple indicator variables. denDF, denominator d.f. for F-tests; LUS, land-use system; NPP, net primary production; numDF, numerator d.f. for F-tests; Var, variable; VT, village type.
losses and decrease in soil phosphorus availability, Fig. 4f and will lead to more deleterious effects (for example, further increases in aluminium solubility and base cation leaching losses and decrease in soil phosphorus availability, Fig. 4f and Supplementary Table 3), which cover 50% of the land area in Sumatra, continued N fertilization buffer capacity of Acrisol soils, which, especially if agriculture is not to be segregated from capital and ecosystem services in smallholder-dominated landscapes, smallholder jungle rubber produced less and generated less income than monocultural rubber (Fig. 3c,d). A combination of monocultures and reforestation may therefore, at least theoretically, be more efficient in combining agriculture and conservation. Unless land-use policy options provide economic incentives for their preservation, primary forests, secondary forest and jungle rubber have little future in smallholder-dominated landscapes despite their contribution to biodiversity and ecosystem services. In principle, however, opportunities for combining agriculture and conservation already exist. A priority region called the RIMBA (Riau, Jambi and Sumatra BArat) Integrated Ecosystem to the north of our study area, which straddles Jambi as well as Riau and West Sumatra, has been designated by the Indonesian Ministry of Public Works as a demonstration area for implementing ecosystem-based spatial planning, which could facilitate the allocation of land to forested land-uses. Proper implementation of the REDDþ (reducing emissions from deforestation and forest degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries) program may open up economic incentives for communities to reforest. The positive correlations of C stocks and non-harvested NPP with other ecological functions (Supplementary Fig. 8) suggest that this would benefit multiple ecosystem services. However, at present, concrete incentives to conserve natural capital and ecosystem services in smallholder-dominated landscapes are absent, and REDDþ may not be economically attractive on mineral soils as an alternative to oil palm development. A cornerstone of the economic development plan for Sumatra is the intensification of smallholder rubber and oil palm, which could be seen on the one hand as an opportunity to achieve higher production levels on less land. On the other hand, it could simply reinforce negative environmental impacts of monocultures, without gains in productivity being translated to increases in land spared for forests. The question is whether increasing wealth, locally, regionally and nationally, could in the long-term place improvement of environmental performance higher up on the agenda, which could then lead to the development and enforcement of agri-environmental regulations and incentives. Recent findings suggest that this will depend on the strengthening of environmental governance, and, especially if agriculture is not to be segregated from ecosystem-service generation, on rewarding land managers for increased ecosystem services delivery.

**Methods**

**Study region, households and study sites.** The province of Jambi, on the island of Sumatra, covers a total land area of 5 Mha (million hectares). We focused on the five regencies that comprise most of the lowland, non-peat smallholder systems: Sarolangun, Bungo, Tebo, Batanghari and Muaro Jambi. From a questionnaire-based farm household survey, covering 701 smallholder farmers randomly selected from 45 villages (covering both autochthonous/transmigration villages), we used the data of four smallholder respondents whose main parcel of cropland was the village and categorized as either jungle rubber (n = 33), monoculture rubber plantation (n = 162) or monoculture oil palm plantation (n = 269). These respondents were independent smallholders, with the exception of 50 oil palm farmers which were associated with an oil palm company during establishment. The interviews were conducted in the second half of 2012. For the ecological studies, we selected withing the study-region two landscapes, ‘Harapan’ and ‘Bukit Duabelas’, with loam and clay Acrisol soils, respectively (see details below). In each landscape, we selected four 50 × 50 m replicate plots for each land-use systems: primary degraded forest, jungle rubber, monoculture rubber plantation (10–17 years old) and monoculture oil palm plantation (12–16 years old). More details on the cloud cover and categorized mosaics for the years 2009–2011 were used to produce less cloud cover mosaics of images for the years 1990, 2000 and 2011, respectively. Due to the high cloud coverage in the study area, satellite images acquired in a period of ±2 years was considered for each

**Household survey.** The aim was to assess the micro-level determinants of recent changes in land-use in the lowlands of Jambi Province, as well as their impacts on smallholder welfare. We examined the adoption patterns, compared the economic performance of the different land-use systems in the different districts of the study region, which was followed, fixing the number of districts per regency and the number of villages per district a priori. A total of forty villages—two rural villages per district, four districts per regency in each of five regencies—were selected randomly. In addition, five villages were selected near to the Bukit Duabelas National Park and the Harapan Rainforest Restoration concession (PT REKI). A total of 464 smallholder respondents whose main parcel of cropland was the village and categorized as either jungle rubber or monoculture oil palm plantation were surveyed. The positive correlations of C stocks and non-harvested NPP with other ecological functions (Supplementary Fig. 8) suggest that this would benefit multiple ecosystem services. However, at present, concrete incentives to conserve natural capital and ecosystem services in smallholder-dominated landscapes are absent, and REDDþ may not be economically attractive on mineral soils as an alternative to oil palm development. A cornerstone of the economic development plan for Sumatra is the intensification of smallholder rubber and oil palm, which could be seen on the one hand as an opportunity to achieve higher production levels on less land. On the other hand, it could simply reinforce negative environmental impacts of monocultures, without gains in productivity being translated to increases in land spared for forests. The question is whether increasing wealth, locally, regionally and nationally, could in the long-term place improvement of environmental performance higher up on the agenda, which could then lead to the development and enforcement of agri-environmental regulations and incentives. Recent findings suggest that this will depend on the strengthening of environmental governance, and, especially if agriculture is not to be segregated from ecosystem-service generation, on rewarding land managers for increased ecosystem services delivery.

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acquisition. The less cloud mosaic for each acquisition was produced after
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on-screen digitation was conducted with a band composite of 5,
4, 3 for the red, green and blue combination, respectively. The classification was
enhanced by assisting the visual interpretation with higher resolution RapidEye
imagery from 2013 for the 2011 acquisition, and with the use of the guidelines for
land-cover mapping published by the Indonesian Ministry of Forestry (MoF) and
with the expert knowledge for all the acquisitions. The initial maps was produced
based on 23 classes considered by the MoF, and the additional target land-use
systems such as jungle rubber, rubber and oil palm plantations. For the purpose of
this study, the following land-uses were aggregated into: forest, rubber, oil palm,
rubber bush and other. Jungle rubber and rubber plantation were combined because
they could not be well distinguished, and this combination resulted in significant
improvements in the accuracy of the overall classification. On the basis a
ground-truth validation with 298 samples of systematically selected points, the
overall accuracy of the classification was 78.2%. A change matrix was derived for
the acquisitions of 1990 and 2011 by overlaying the LUTC maps. The changes
between the two acquisitions were expressed in percentage of the total area.

Experimental design of core plots for the ecological studies. The study region
(Supplementary Fig. 1) was delineated into two main landscapes that are both on
heavily wooded soils but mainly differed in texture: loam and clay Acrisols soils. In
each landscape, four land-use systems were studied: rainforest, jungle rubber, and
smallholder monoculture plantations of rubber (7–17 years old) and oil palm (9–16
years old). The landscape (between 1.94° S, 103.24° E and 2.19° S, 103.36° E) is located ∼60 km south of Jambi city, and the clay Acrisols landscape (between 1.94° S, 102.58° E and 02.14° S, 102.85° E) is located ∼110 km
west of Jambi city. Acrisols are characterized by clay translocation in the soil profile,
low-effective cation exchange capacity (ECEC; <24 cmol charge kg
−1 of clay within 0.5 m depth) and low saturation (<50%) of the 0.5–1.0 m depth. The mean annual temperature was 26.7 ± 0.2 °C and mean annual precipitation was
2235 ± 385 mm (1991–2011; data from the Indonesian Meteorological,
Climatological and Geophysical Agency at a meteorological station located at the
Sultan-Thaha Airport in Jambi). For each land use in each landscape, four replicate
plots of 50 × 50 m were selected. Minimum distance between plots was 116 m, and
altitude varied between 35 and 95 m above sea level. Forests are selectively
logged-over old-growth forest, which is equivalent to ‘primary degraded forest’
as classified by Marongo et al.19 Jungle rubber represents a smallholder rubber
agroforest system established by planting rubber trees into secondary rainforest. Its
implementation dates back to the early 20th century before rubber and oil palm
plantations were smallholder plantations, meaning that they were owned and
managed by small farm households, as opposed to large-scale company
plantations. The implicit assumption of our experimental design, comparing the changes in
converted land-uses to the reference land use (that is, forest) with assess effects of
land-use change, is that the initial soil conditions were comparable before conversion.
To test this assumption, we statistically compared land-use independent soil
characteristics (that is, texture at depth >50 cm) among land uses within each
landscape. We did not detect significant differences in soil texture between the
reference and converted land uses within a soil landscape, suggesting that soil
conditions were previously similar. The measurements in these 32 core plots are
described in detail below and summarized in Supplementary Table 5.

Trees and understory vegetation. Within each core plot, all trees with a diameter at breast height (DBH) ≥10 cm were identified and measured (height, DBH, crown structure). All vascular plant individuals growing within five 5 × 5 m
subplots were identified and measured (height). Whenever possible, herbarium
specimens were prepared of three individuals per species for identification and later
deposition at several Indonesian herbaria (Herbarium Bogoriense, BIOTROP
Herbarium, UNJA Herbarium, Harapan Rainforest Herbarium). To calculate the
naturalness of agroforest systems, all cores were identified for the presence and
abundance of the ten most common weed species on plot level (specimens deposited at
Herbarium Bogoriense).

Birds. Birds were sampled with point counts as well as automated sound recordings.
The point counts were located in the centre of each plot and all birds within the
plot were recorded for 20 min between 6:00 and 10:00 in June–July 2013. The timing of
bird data collection alternated between early and late morning and all plots were
visited three times. Individuals flying above the canopy were excluded, and unfamiliar
bird calls were recorded using a directional microphone. The recordings were com-
pared with the Xeno-Canto online bird call database (http://xeno-canto.org/) for
confirmation. In addition, we recorded sound at 44,100 Hz using stereo recorders
(SMX-II microphones, SM2 + recorder, Wildlife acoustics) which were attached to
the central core plot of each landscape. Eight photographs, so sampling all 32 plots took four days (10th and 13th of May, and the 3rd and
7th of June 2013). The first 20 min from sunset were uploaded to a website
(http://soundeforts.uni-goettingen.de/) where two independent ornithologists tagged
all audible bird calls (within an estimated 35 m radius) with the corresponding species
name. Owl bird species were identified by both ornithologists, and if uncertainties persisted, they were removed. Finally, all bird habitat preference was classified based on Beukema et al.44 to detect forest
specialists. Missing bird information was looked up in the online Handbook of the
Birds of the World (http://www.bbw.com/).

Litter invertebrates. Litter invertebrate sampling took place between
October and November 2012. In each core plot, we sampled 1 m² in each of three
5 × 5 m subplots. This sampling was done by sieving the complete leaf litter layer from
the 1m² sample through a coarse sieve with a mesh width of 2 cm. A total of
7,742 macro-invertebrates were then hand-collected from the sieved samples and
stored in 65% ethanol. Specimens were identified to morphospecies based on
consistent morphological characteristics.

Terms. Termitite sampling was conducted in 10 × 50 m transects bisecting each
plot. Along each transect, termite tubes were searched for on the soil surface, leaf litter and
trees (Fig. 3). Baits made from rubber wood with the volume of 3 × 3 × 50 cm
were installed on each of the five 5 × 5 m subplots. Wood baits were inserted into
the soil up to half of their length. Baits were harvested after four weeks and the
termites collected. Termite tubes removed from transects and baits were stored in 70%
ethanol, labelled, and identified.

Ants. Ants were collected using direct sampling and baiting. Direct sampling
was carried out in three stratum, leaf litter, soil, and tree trunk, and lasted 5–10 min per
stratum per subplot. Leaf litter was separated into coarse and fine litter and ants
were taken from the fine leaf litter. For the soil and tree strata, ants were collected directly
from the ground and trunk with forceps. The baiting method used plastic observation
plugs of 2 cm³ of a mixture of baits (2 cm³ of the bait mixture) with 70% sugar
solution attached to sample ants. One plate was laid at breast height on each of the
two trees in each subplot. If there were not two trees in a subplot (often the case in oil
palm plantations), the closest trees to the subplot were chosen. The plates were
collected at 15, 30, 45 and 60 min after placing the plates on the trees. Specimens were
collected from each ant species present where possible without disrupting recruitment.
All sampling was completed between 9:00 and 11:00 and never during or immediately
after rain due to a reduction in ant activity in wet conditions. Direct sampling was
conducted once every four months (February–March 2012, February–March 2013, October–November 2013, February–March 2014). All
ants collected were identified to species/morphospecies level.

Testate amoebae (protists). Samples from the litter/fermentation layer were
taken in October–November 2013, using a core of a diameter of 5 cm. Testate amoebae
were extracted by washing 1 g litter sample from each core plot over a filter of 500 μm mesh
and then back-sieving the filtrate through 10 μm. Microscopic slides were prepared from the
final filtrate and testate amoebae were identified to morphospecies.

Prokaryotic soil community. Soil sampling (top 5–7 cm) was carried out in 2012
for three subplots within each core plot. All samples were stored at –80°C until
further use. Subsequently, deoxyribonucleic acid (DNA) was isolated using the
PowerSoil DNA isolation kit (Dianova, Hamburg, Germany). Subsequently, 16S RNA gene
amplifications of bacteria and archaea were generated from DNA. The resulting 16S rRNA
gene data sets were processed and analysed using QIIME 1.8 (ref. 45). Initially, sequences shorter than 300 base pairs (bp), containing
unsolved nucleotides, exhibiting an average quality score lower than 25, harbouroing mismatches longer than 3 bp in the forward primer (Supplementary
Data 1), or possessing homopolymers longer than 8 bp, as well as primer sequences,
were removed. Subsequently, sequencing noise and potential chimeric
sequences were resolved by using Acacia46 and UCHIME47 with RDP48 as reference data set
(trainset10_082014_rmdup.fasta). Operational taxonomic unit (OTU)
determination was performed at a genetic divergence of 3% by using the software
tool picc_open_reference_otus.py of the QIIME 1.8 package using the Silva NR
SSU 119 database version as refs 45 and 49. Taxonomic classification was
performed with parallel_assign_taxonomy_blast.py against the same database.
OTUs representing singletons, chloroplasts, extrinsic domains, and unclassified
were removed. OTU tables were subsampled and comparisons were performed at
the same surveying effort (Bacteria 6.800 sequences and Archaea 2.000 sequences).
Diversity estimates were generated employing alpha_rarefaction.py.

Genetic diversity of plants. In each of the core plots, ten vascular plant species
(woody species and herbaceous plants including ferns), selected based on their
dominance in terms of above-ground biomass (AGB), were selected using a
modified angle count technique (‘Bitterlich–Method’). From each selected species,
leaf material of ten individual plants belonging to the same species was sampled.
In total, 40 plant species × 10 samples = 400 samples were collected. Due to different dominance of species in each plot, a total number of 112 species
were sampled. Using the DNeasy 96 Plant kit and its protocol (Qiagen, Hilden,
Nutrient leaching fluxes. We installed at random two suction cup lysimeters (P80 ceramic, maximum pore size 1 mm; CeramTeC AG, Markteditz, Germany) in each of the eight replicate plots of forest, jungle rubber and rubber, and one suction cup lysimeter in each of the eight replicate plots of oil palm. Lysimeters in the oil palm plots were placed at 1.3–1.5 m distance from the palm trunk. In all plots, lysimeters were installed into the soil at 1.5 m depth, which was well below the rooting depth. This was ascertained from the fine and coarse root distribution with depth, which we measured at 0.1 m depth interval down to 1 m and showed a strong exponential decrease of root mass with depth. Before installation, lysimeters, sample tubes and collection containers were acid-washed and rinsed with copious amounts of deionized water. Lysimeters were installed three months before the first sampling to allow resetting of natural soil conditions before measurement. The collection containers (dark glass bottles) were placed in plastic buckets with lid and buried in the ground far from the lysimeters. Soil water was sampled biewise to monthly, depending on the frequency of rainfall, from February to December 2013. Soil water was withdrawn by applying suction to the sample tubes, which represents soil water at natural potential and slowly draining pores. The collected soil water was transferred into 100 ml plastic bottles and was frozen immediately on arrival at the laboratory. All frozen soil water samples were transported by air to the laboratory of Soil Science Tropical and Sub-tropical Ecosystems (SSTSE), University of Goettingen, Germany, and remained frozen until analysis. Total dissolved N was determined using continuous flow injection analysis, and roughed N mineralization was carried out with the GeneMapper 4.1 (Applied Biosystems). We calculated Shannon Index/genetic diversity with 10 individuals of each species in every plot. Based on the 1–9 matrices, we calculated Shannons information index (I).

Soil processes and functioning. Litterbags (20 × 20 cm with 4 mm mesh size), containing 10 g dry leaf litter mixture of three tree species from one of the forest plots, were incubated in situ with one litterbag in each of the 32 plots from October 2013 to March 2014. The composition of the litter reflected that of fallen litter at the plot of origin: 4 g from Garcinia sp., 3 g from Gironniera nervosa, 3 g from C. Swartia lagivaga. Mass loss was calculated as the difference between the initial litter dry mass and litter dry mass remaining after 6 months and expressed as percentage of the initial leaf litter mass. In addition, soil samples down to a depth of 0.3 m were taken for each replicate plot in 2013 to 2014. The composition of the litter reflected that of fallen litter at the plot of origin: 4 g from Garcinia sp., 3 g from Gironniera nervosa, 3 g from C. Swartia lagoitiva. Mass loss was calculated as the difference between the initial litter dry mass and litter dry mass remaining after 6 months and expressed as percentage of the initial leaf litter mass. In addition, soil samples down to a depth of 0.3 m were taken with a corer (5 cm diameter) at three subplots in each of the 32 plots, from which soil samples were composited, finely ground and analyzed with one AFLP primer combination for all species. We calculated Shannon Index/genetic diversity with 10 individuals of each species in every plot. Based on the 1–9 matrices, we calculated Shannons information index (I).

Soil sampling and fertility characteristics. In each core plot, a 10 × 10 m grid was established and we randomly selected 10 grid points as subplots that were at least 5 m distance from the plot’s border for soil sampling22. Soil samples were taken within an area of 0.4 × 0.4 m in each grid point. The soil had no organic layer. We used a soil auger to determine the soil horizon and its biogeochemical soil properties. Soil samples were taken at several depth intervals (0–0.1, 0.1–0.3, 0.3–0.5, 0.5–1.0, 1.0–1.5 and 1.5–2.0 m), and we report here the changes in soil characteristics for the top 0.1 m, except for net N mineralization (which was for the top 0.05 m) and SOC (which was for the entire 2 m). Soil samples were air-dried and sieved (2 mm sieve) at the University of Jambi, Indonesia and sent to SSTSE laboratory, University of Goettingen, Germany for analysis. From the air-dried, sieved soil samples, pH was analysed in a 1:4 soil-to-water ratio, and ECEC was determined by percolating the soils with unbufflered 1 mol L−1 NH4Cl and the percolation cation concentrations (exchangeable bases, Al, Fe and Mn) were measured using ICP-AES. Soil pH was calculated as soil hydrogen ion concentration (Ca, Mg, K and Na) of the ECEC. Extractable P was determined using the Bray 2 method, and analysed using ICP-AES. For soil 15N natural abundance signature, the 10 sub-samples from each replicate plot was composited, finely ground and analysed using isotope ratio mass spectrometry (Delta Plus, Finnigan MAT, Bremen, Germany), and the 15N isotopic signature was determined using the 15N standards (Supplementary Data 1). Two samples of each species were repeated from DNA extraction onwards for reproducibility testing. Fragment determination was carried out with the GeneMapper 4.1. (Applied Biosystems). We calculated Shannon Index/genetic diversity with 10 individuals of each species in every plot. Based on the 1–9 matrices, we calculated Shannons information index (I).
Net primary productivity. We measured above-ground litterfall, pruned oil palm fronds, rubber latex harvest, oil palm fruit harvest, and stem increment from March 2013 to April 2014. Fronds were collected in 16 replicates (75×75 cm) from cows,直径为25 cm, pruned from the upper canopy, which were subsequently oven-dried for 72 h at 60°C until constant mass was attained. In the oil palm plantations, all pruned oil palm fronds on each plots were counted. The average dry weight per frond, obtained from 16 harvested fronds, was used for the calculation of litter productivity. Oil palm fruit harvest was done every two weeks, while rubber was harvested every 70–87 days at frequencies depending on season and expected productivity. The yield of oil palm fruits and rubber latex (in Mg ha−1) was recorded by weighing the harvested fresh material for all trees in each plot. A similar procedure was followed for litterfall data. Litterfall was collected from March 2013 and April 2014, based on the allometric equations used for biomass estimation as described above. For a plot-based estimation of above-ground tree biomass, we applied mean increment rates per plot and tree species for the remaining tree individuals. An in-growth core measurement was conducted to estimate fine-root productivity in all plots, using the method described by Powell and Day. Sixteen in-growth cores per plot were installed at random locations (at 30 cm distance from the litter traps) and re-sampling of the cores was done after 8–10 months. The extracted soil cores were processed in the same manner as done for the fine-root inventory. The fine-root growth in the cores was extrapolated to one year and expressed in g dry mass produced per m² area surface per year, representing the annual fine-root production. To determine carbon stocks and carbon sequestration, the C concentration in stem wood, fine roots, dead wood, and litter fractions was analysed with a CN Analyzer (Vario EL III, Hanau, Germany) at the University of Goettingen. For all methodological details see Kotowska et al. Statistical methods. Data were standardized by subtracting the mean and dividing by the standard deviation. Species richness, nutrient flux and yield data were log10-transformed before standardization to avoid heteroscedasticity. When a single response was indicated by a single measured indicator variable, we used general linear models for ecological data, and linear mixed models with village as a random grouping factor for household-based data. When a single response was indicated by multiple measured indicator variables, we used linear mixed models with plot (ecological data), or household nested in village (household data), as a grouping variable. In addition, when including an indicator variable expected to negatively affect the response, we used its additive inverse (see soil fertility and stability in climatic conditions). The significance of the transformation system effect and its interaction with the identity of the indicator variables was assessed using F/Wald-tests on models fitted using Maximum-likelihood. For the household data we also included these tests for the type of land use (transplant vs. non-transplant) and its interaction with the transformation system. Differences among transformation systems are assessed using Tukey post-hoc tests. Analyses were done in R 3.1.2 (ref. 69) with packages ‘nlme’ v.3.1-118 (ref. 70) and ‘multcomp’ v.1.3-8 (ref. 71).

Data availability. Data is archived at EFForTs, with openly accessible, keyword-searchable metadata and data holder contact details for data requests. Datasets used in this study have the identification numbers 11250, 11253, 11254 and 11257 (household survey), 11411 and 11460 (attitudes to risk), 12027, 12028, 12029 and 12030 (land-use/cover), 11611 (soil processes), 12014 (leaching), 11481, 11482 and 11484 (yields), 12002 (biomass and productivity), 11485 (tree structure), 12221 and 12200 (plant genetic diversity), 11922, 11923, 11924 and 11925 (plant diversity), 11720, 11723 and 13061 (birds), 11780, 11966, 12266 and 12300 (macro-invertebrates), 12180, 12324, 12341, 12342 and 12343 (invasive plants), 12322 (decomposition), 12321 (testate amoebae), 12013 (microbial biomass and basal respiration) 11742 (16S rRNA gene based analysis of soil archaeal communities, DNA), 11740 and 12264 (16S rRNA gene based analysis of soil bacterial communities, DNA), 11660 (meteorological data). For the prokaryotic 16S rRNA gene sequences deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under study accession number SRP056374.

References
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References


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43. Author contributions

44. Acknowledgements

45. Additional information

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