

Enhancing the ecological value of oil palm agriculture through set-asides

Received: 23 February 2021

Accepted: 8 December 2022

Published online: 6 February 2023

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Agricultural expansion is the primary driver of ecological degradation across the tropics. Set-asides—uncultivated parts of agricultural landscapes, often on steep slopes and alongside rivers—may alleviate environmental impacts but can reduce the area cultivated. Here we model an approach to configuring set-asides aimed at optimizing ecological outcomes (biodiversity, above-ground carbon storage and nutrient cycling) without reducing net cultivation area. We compare set-asides in an oil palm landscape where all plantations adopt the same configuration ('uniform' approach) with a scenario where there can be variation in configuration among plantations ('variable' approach). We find that all set-aside configurations support substantial ecological values but that the best strategies involve set-asides, particularly alongside rivers, that are spatially targeted and variable among plantations. This 'variable' approach can increase ecological outcomes twofold over the 'uniform' approach without reducing net cultivation area. Our findings underscore the potential importance of well-planned set-asides for enhancing agricultural sustainability.

Agricultural expansion is the primary driver of habitat loss^{1,2}. With crop demand predicted to double by 2050³, 1 billion hectares of new agricultural land will be needed^{4,5}, much of it replacing tropical forest^{6–8}. Over the past three decades, more than 150 million hectares (Mha) of tropical forest have been cleared for agriculture^{4,9,10}. This expansion drives biodiversity losses^{11–13} and climate change (contributing 7–14% of global CO₂ emissions^{14–17}), and has negative impacts on multiple ecosystem functions and services¹⁸. Consequently, the challenge of reconciling rising resource requirements while safeguarding critical ecosystems is dependent on the manner in which tropical agricultural landscapes are established.

Oil palm (*Elaeis guineensis*) is one of the world's fastest expanding crops, now occupying ~28 Mha (4% of agricultural land in the tropics¹), mostly (82%) in Southeast Asia (faostat.org). Since 1980, there has been a 15-fold upsurge in production, with increasing intensification (Supplementary Fig. 1). Today, half of the world consume palm oil, and it is a key ingredient in animal feed, cosmetics and biofuels^{19,20}. It is predicted that oil palm agriculture could double in area by 2050^{19,21}, with associated deforestation anticipated to negatively affect 54% and 64% of threatened mammals and birds globally¹⁹, and release ~330 MtCO₂ each year^{22,23}, equivalent to almost half the average annual CO₂ emissions from global aviation²⁴.

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Pressure is mounting on supply chains to improve sustainability standards, or risk continued calls for palm oil to be boycotted^{25–27}; however, switching to alternatives could exacerbate the problem^{19,25} because palm oil is more efficient than other vegetable oils^{19,28}. To try to alleviate environmental concerns, over 4,000 companies have now adopted voluntary commitments to source, produce and sell certified sustainable palm oil, which is cultivated conforming to social, environmental and agricultural best-practice standards^{23,29,30}. Included in these best-practices are set-asides, which are uncultivated parts of the agricultural landscape that can reduce environmental impacts³¹. However, because set-asides remove areas from agricultural production, this could result in further agricultural expansion to meet production demands, with knock-on negative impacts for biodiversity (reviewed in ref.³²). Consequently, it is important to consider set-aside strategies that reduce the environmental impacts of crop production without compromising agricultural productivity.

Here we aimed to model an approach to set-aside that could improve the ecological value of set-asides in various oil palm landscape settings without reducing net cultivation area (Fig. 1). We test this by taking a landscape-scale approach in the global epicentre of palm oil production^{31,32}, the carbon- and biodiversity-rich island of Borneo.

Set-aside in oil palm agriculture

In oil palm agriculture, set-aside is often incorporated into national regulations, as well as being required by voluntary sustainability certification including the Roundtable on Sustainable Palm Oil (RSPO), which certifies 19% of all palm oil (a further 2% is certified by other bodies). Set-aside standards are determined by policymakers and certification bodies, and companies are required to adhere to these. However, due to varying approaches, set-asides come in an array of shapes and sizes and are not necessarily informed by scientific evidence³³. Nevertheless, set-asides offer important biodiversity refugia, can enhance habitat connectivity^{33–36}, help maintain ecosystem functions and services including nutrient cycling and carbon stores^{34,36–40}, and support livelihoods⁴¹.

Set-asides are frequently determined by (1) the need to maintain natural habitat on steep slopes (commonly those that are greater than 25°; hereafter ‘maximum slope for cultivation’) to protect soils and watersheds, and (2) the retention of natural habitat near rivers (hereafter ‘riparian reserve width’) to maintain hydrological systems (see Supplementary Note 1 for current voluntary and mandatory regulations determining set-asides in most oil palm plantations). Most riparian reserve regulations in industrial oil palm estates stipulate fixed widths (for example, 20 m or 50 m) of forest to be retained on either side of the river, depending on the country/state. Conversely, some approaches, including those of RSPO, vary on the basis of river width and local context. For example, 5 m of forest is retained on either side of very small rivers, but up to 100 m of forest on either side of larger rivers, or in areas considered to be particularly important for wildlife or habitat connectivity (Supplementary Note 1 and Table 1). Maximum slope for cultivation is often 25°, but this is dependent on local climate and soil (Supplementary Note 1).

A framework to optimize set-aside in oil palm landscapes

To appraise the impacts of varying set-aside approaches, we modelled ecological outcomes for a real-world 119,000 ha production landscape in Sabah, Malaysian Borneo, comprising four industrial-scale plantations and an array of remnant forest in set-asides (Supplementary Figs. 2 and 3). Across this landscape, the agricultural matrix comprised oil palms planted 12–15 years before data collection (Methods). Remnant logged forest fragments occur on steep slopes and in riparian forests alongside many of the rivers, with a median of ~53 m on either side of the river, but ranging from 0 to 470 m. Each of the four plantations across this landscape has a distinct topographic profile, varying in ruggedness

from 18 to 56% of the plantation above 15° slope (for further detail see Methods, and Supplementary Figs. 2–7 and Table 2). Most of the forest remnants have been logged two to four times over the last 30 years⁴², but some still contain ‘high carbon stocks’ determined by a minimum of 35 carbon tonnes per hectare (Ct ha⁻¹) (Supplementary Note 1). As a result, species assemblages in the landscape have undergone ~15 years of edge effects and accompanying extinction debts. Throughout this landscape, we empirically sampled biodiversity, nutrient cycling and above-ground carbon in forests, and used these data to appraise ecological outcomes associated with various set-aside configurations (Methods).

Before evaluating the impacts of set-aside approaches, we consulted major producers across the palm oil industry to ensure that our analyses focused on maximum slopes for cultivation and riparian reserve widths that could be implemented feasibly in a real-world context (Methods). We then spatially modelled all set-aside configurations, encompassing combinations of 20 riparian reserve widths (in 5 m increments, ranging from 5 to 100 m, on both sides of rivers) and 11 maximum slope angles (ranging from 15 to 25°) per plantation, equating to 880 combinations across the four plantations (220 in each). Therefore, areas with slopes steeper than 25° were always in set-aside, and likewise for land within 5 m of a river (Fig. 1). In each configuration, we assumed that all land outside of set-asides is otherwise suitable for cultivation.

Impacts of set-aside on cultivation area

We first assessed the impacts of our different set-aside configurations on cultivation area. Larger riparian reserve widths and lower maximum slopes for cultivation both mean that there is a greater area of set-aside in the landscape and, correspondingly, less area available for cultivation. Across all possible set-aside configurations modelled, 61–92% of our landscape remained available for cultivation (Fig. 2). To put this into context, and for baseline comparison, current regulations for Sabah (Malaysia) and Indonesia require 20 and 50 m riparian reserve widths, respectively, and 25° maximum slopes for cultivation. This would leave 89–91% of our landscape available for cultivation and is consistent with plantations in peninsular Malaysia where, on average, 89% of industrial-sized plantations are cultivated⁴³.

To explore the relative impacts of set-asides determined by riparian reserve widths and maximum slope for cultivation separately on area available for cultivation, we also quantified the impact of fixing maximum slope for cultivation and riparian reserve widths in turn. At maximum slopes fixed at 25° (the current common approach in Malaysia, Indonesia and RSPO standards), the percentage of the landscape available for cultivation varied from 84% (100 m riparian reserve) to 93% (5 m riparian reserve; Fig. 2a). With maximum slopes fixed at 20°, land available for cultivation varied from 77 to 86%, and at 15°, land available for cultivation varied from 62 to 70% (Fig. 2a). Consequently, in our landscape, the resulting set-aside from 15° maximum slopes is far beyond current practices, regardless of riparian reserve width (see also Supplementary Note 2). On the other hand, at riparian reserves widths fixed at 5 m, percentage of the landscape available for cultivation varied from 70% (15° maximum slope for cultivation) to 93% (25° maximum slope for cultivation; Fig. 2b). At widths of 20 m (common guideline in Malaysia), the percentage of the landscape available for cultivation varied from 68 to 91%; at 50 m (common guideline in Indonesia), land available for cultivation varied from 66 to 88%; and at 100 m widths, land available for cultivation varied from 62 to 84% (Fig. 2b).

Trade-offs between cultivation area and ecological outcomes

To assess the trade-off between the land available for cultivation (as a result of set-aside area) and ecological outcomes (biodiversity, an ecosystem function and an ecosystem service), we combined our set-aside configurations with field-derived ranges for 247 species (150 birds,

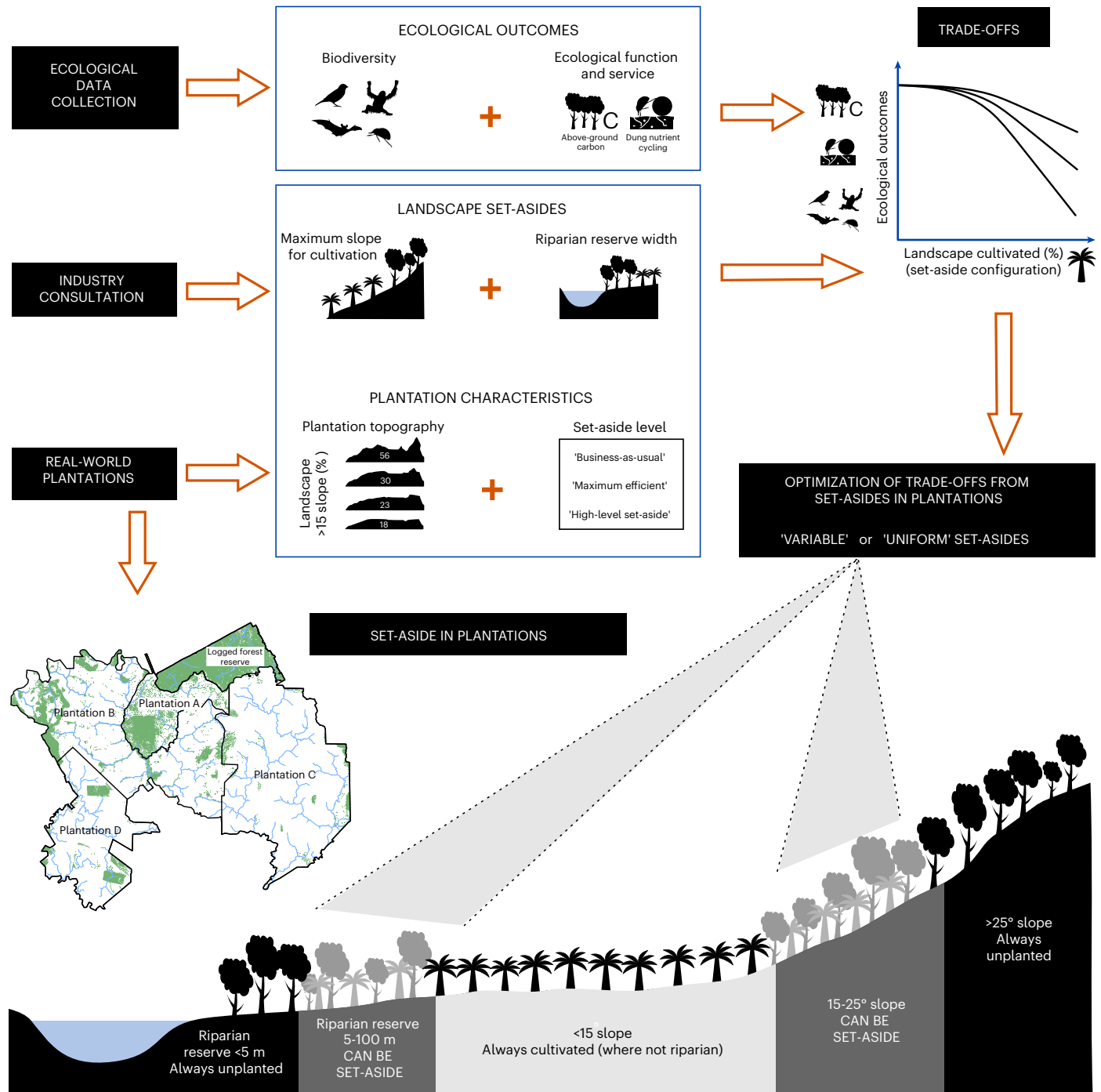


Fig. 1 | Study workflow. Study workflow, showing the steps described in Methods. Inset map indicates the study landscape (see Supplementary Fig. 1 for larger map with further details). Our ecological dataset was empirically measured at the study landscape in Borneo, comprising 247 species, above-ground carbon biomass in forests and dung nutrient cycling. We consulted with representatives from eight of the world’s largest palm oil producers to identify the set-asides

tested. The potential set-aside configurations included riparian reserve widths ranging from 5 to 100 m and maximum slopes for cultivation ranging from 15 to 25°. Under the ‘uniform’ approach, all plantations in the landscape apply the same riparian reserve width and maximum slope for cultivation, whereas they can vary between plantations under the ‘variable’ approach. Animal silhouettes were reproduced from <https://en.silhouette-ac.com/>.

19 non-volant mammals, 21 bats and 57 dung beetles), dung nutrient cycling using regression kriging of field measurements, LiDAR-derived above-ground forest carbon storage in the study landscape at timepoint zero, and predictions of carbon stored following 20 years of natural regeneration and active restoration (Methods).

We first draw curves of the relationship between ecological outcomes and the percentage of the total landscape cultivated across all of

our 220 configurations of the landscape (Fig. 3a–c and Supplementary Fig. 8), also showing ecological outcomes at 10% steps in cultivated area (Fig. 3d). We then draw curves separately across our 11 different maximum slopes for cultivation (Fig. 4a–c) and 20 different riparian reserve widths (Fig. 4d–f). These demonstrate a linear increase in ecological outcomes for every increase in riparian reserve width, while there is a nonlinear reduction in outcomes for every increase in the maximum

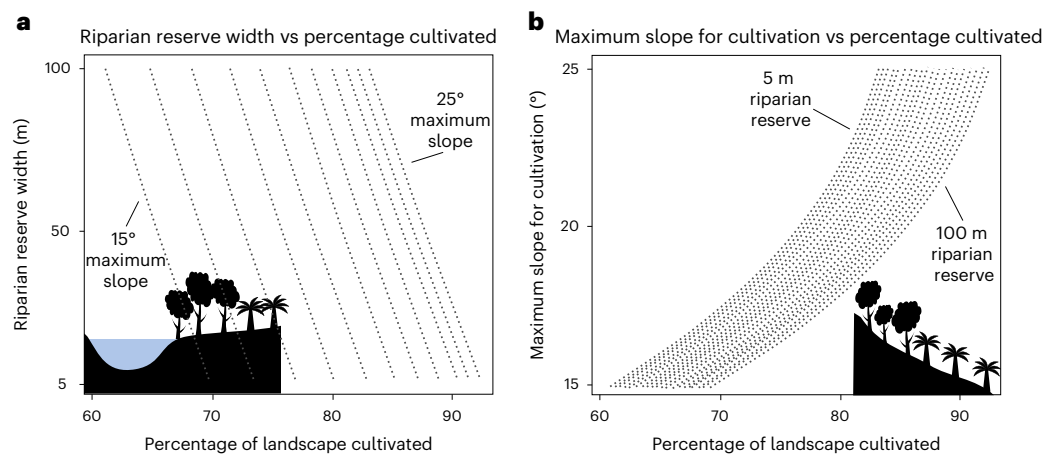


Fig. 2 | Relationship between set-aside configurations and landscape cultivated. **a**, Relationship between riparian reserve widths ranging from 5 to 100 m and proportion of the landscape cultivated. Dashed lines show all set-aside configurations across 11 different maximum slopes for cultivation ranging from

15 to 25°. **b**, Relationship between maximum slope for cultivation and proportion of the landscape cultivated. Dashed lines show all set-aside configurations across the 20 different riparian reserve widths ranging from 5 to 100 m.

slope for cultivation (Fig. 4), corresponding to the relationship with the percentage of the landscape cultivated seen in Fig. 2.

Optimizing trade-offs in cultivation and ecological outcomes

In optimizing the trade-off between cultivation area and ecological outcomes, we express ecological outcomes in terms of net and relative percentage comparisons of percentage species occurrence in set-aside, as well as percentage comparisons of total above-ground forest carbon storage and dung nutrient cycling. Therefore, net changes in species occurrence in set-aside are calculated as the percentage change in relation to the landscape area, but we also report relative changes calculated as a percentage change in relation to maximum possible species area/ecosystem function/service. For example, if a species occurred in 20% of the landscape in one set-aside configuration and then 30% in another, this would equate to a 10% net increase and a 33% relative increase. This dual approach enables interpretation of the effects of set-asides on widespread species as well as those with smaller ranges, but also a more general appraisal of how this may translate into other landscapes.

To optimize set-asides, we evaluated two approaches: (1) ‘uniform’ set-asides where all plantations in the landscape adopt the same riparian reserve widths and maximum slopes for cultivation, reflecting most national/state-scale regulations (for example, Indonesia, Sabah and peninsular Malaysia). This analysis included all 11 potential maximum slopes for cultivation and 20 riparian reserve widths as detailed above (a total of 220 different landscape combinations). (2) ‘variable’ set-asides where there can be variability in riparian reserve widths and maximum slopes for cultivation between plantations (220 possible configurations ‘per’ plantation), aiming to enhance ecological outcomes without impacting the cultivated area. We used a multi-objective optimization model with two objectives: enhance ecological outcomes (objective one) and maximize area of the landscape available for oil palm cultivation (objective two) (see Methods and Supplementary Note 3).

Under the ‘uniform’ approach, in our landscape, each 10% of the area in set-aside results in a net increase in species occurrence of 3–30% across all 247 species (mean of 10% net increase, but up to 248% relative increase), a 6% net increase in above-ground carbon storage at time-point zero (estimated to rise by 46 or 74% after 20 years of natural regeneration or active restoration, respectively; Supplementary Fig. 9) and a 9% net increase in dung nutrient cycling (Fig. 3d), demonstrating

that even with these very simple approaches, the potential importance of set-asides in delivering ecological gains in tropical agricultural landscapes becomes clear.

Compared to a ‘uniform’ approach, ‘variable’ set-asides offer higher levels of species occurrence and above-ground carbon storage for any given percentage of the landscape cultivated. Therefore, by adopting ‘variable’ set-aside configurations, ecological outcomes can be improved for no net loss in cultivation at the landscape level. Alternatively, the ‘variable’ approach achieves specified levels of species occurrence and above-ground carbon storage at lower overall set-aside area than in the equivalent ‘uniform’ approach (Figs. 5 and 6). The greatest gains from the ‘variable’ approach are obtained when set-aside configurations result in 80–88% of the landscape being cultivated (upper quartile of the difference between ‘uniform’ and ‘variable’ approaches; Fig. 5a). The most efficient of these is achieved when 85% of the landscape is cultivated (‘maximum efficient’). In this scenario, compared with the ‘uniform’ approach, net species occurrence within set-asides rises by 8.8% (range: –8.1 to 17% net change in occurrence across all species) from an average across species of 53% for the ‘uniform’ approach to an average of 62% for the ‘variable’ approach, and 3.8% more above-ground carbon stored (Supplementary Tables 3 and 4, and Fig. 6b,d,e). By comparison, achieving the same gain in ecological outcomes with the ‘uniform’ approach would require a reduction in cultivation area of 8.5% (Supplementary Table 3, and Figs. 5a and 6b). At maximum efficient cultivation levels, all ecological outcomes increase under the ‘variable’ approach compared with the ‘uniform’ approach (Fig. 5a–g, and Supplementary Figs. 10–13 and Note 4), with the greatest average gains among the birds (Fig. 5b), including endemic and threatened species. We also find that at 90% (hereafter ‘business-as-usual’; broadly equivalent to regulations in Indonesia and Malaysia, which are our baseline for comparison) and 70% (‘high-level set-aside’) of the landscape cultivated, the ‘variable’ approach enhances ecological outcomes, albeit to a lesser degree than when 85% of the landscape is planted (Figs. 5 and 6a,c, and Supplementary Table 3 and Note 4).

With 85% of the landscape cultivated, the corresponding set-aside (15% of the landscape) can be achieved through a range of ‘uniform’ set-aside configurations of riparian reserve widths (mean = 61 m) and maximum slope for cultivation (mean = 19°; Supplementary Table 5). However, the flexibility of the ‘variable’ approach allows for more spatially targeted set-asides to be distributed heterogeneously across the landscape to maximize ecological outcomes. As a result,

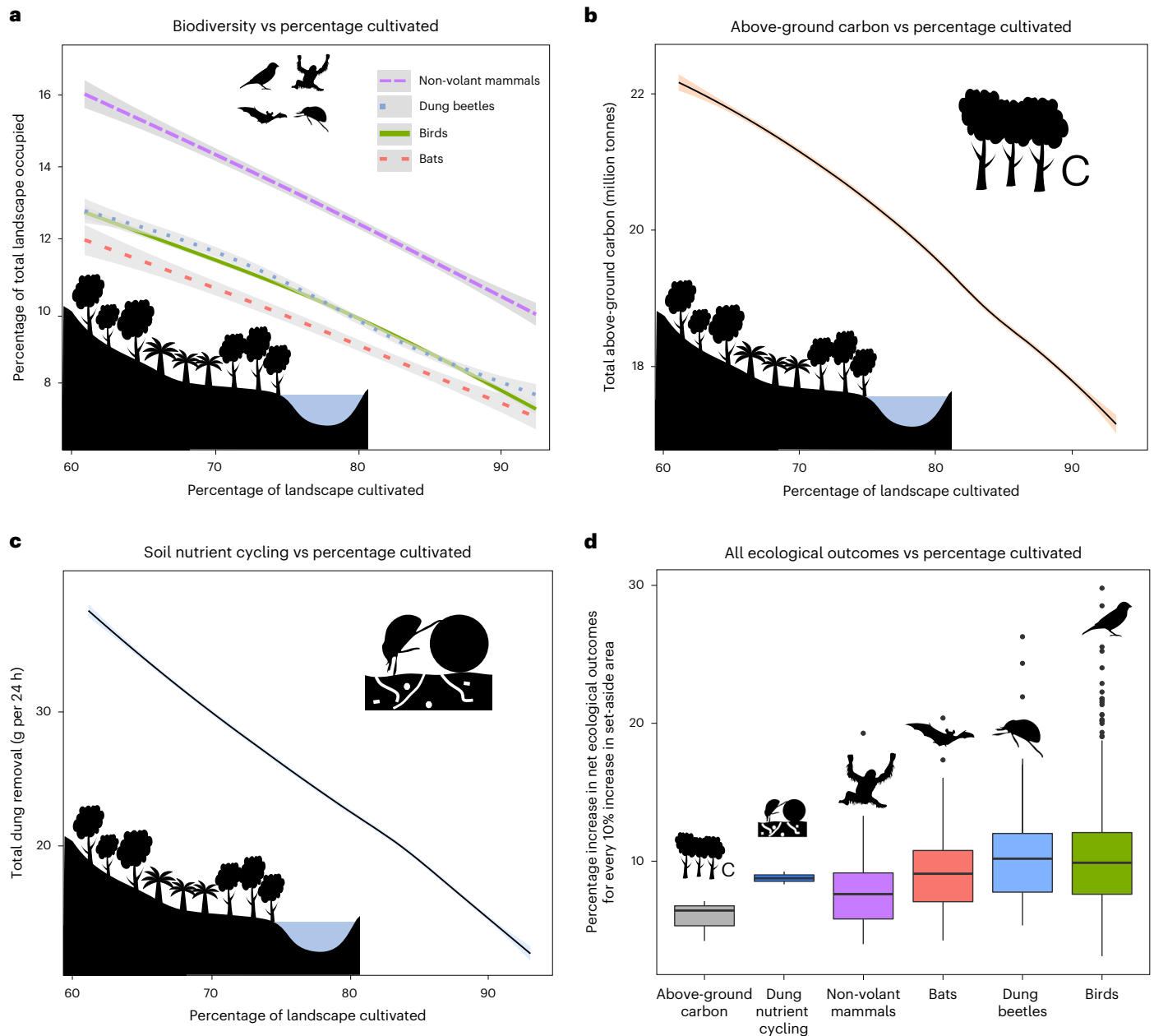


Fig. 3 | Relationship between ecological outcomes and percentage of the landscape cultivated. **a–c**, Curves for biodiversity (per taxon) **(a)**, above-ground carbon storage (at timepoint zero excluding sequestration that would be expected to occur with recovery) **(b)** and dung nutrient cycling **(c)** vs predicted proportion of the landscape cultivated as determined by different combinations of maximum slope for cultivation and riparian reserve widths. Shading shows 95% confidence interval (CI). In **a**, the Y axis shows species occurrence in set-aside as a percentage of the total landscape. All curves use local polynomial regression for locally estimated scatterplot smoothing (LOESS). **d**, Percentage increase in

net ecological outcomes for each 10% ‘uniform’ increase in set-aside area under the ‘uniform’ approach (for landscape configurations that range from 61 to 92% cultivated; comparing incremental 10% steps of 62–72%, 72–82% and 82–92% cultivated). Bold horizontal line, median across 10% steps, and across species (for taxonomic groups); box, 25th and 75th percentiles; whiskers, largest and smallest values within 1.5 times the interquartile range. Biodiversity (including taxa in **d**) based on 247 species (150 birds, 21 bats, 19 non-volant mammals and 57 dung beetles). Animal silhouettes were reproduced from <https://en.silhouette-ac.com/>.

the ‘variable’ approach could have lower overall set-aside with a mean riparian reserve width of 49 m and mean maximum slope for cultivation of 23° to achieve the same overall ecological outcome. This is particularly pertinent for the ‘variable’ set-aside configurations used in most certification schemes (Supplementary Note 1) because they should translate into improved ecological outcomes without the need to reduce net cultivation area.

We also conducted our set-aside optimizations of ecological outcomes with ‘uniform’ maximum slopes of 25°, 20° and 15° but letting

riparian reserve width vary. We did this because the palm oil industry told us that varying maximum slope for cultivation would be less favourable from an operational perspective. To mirror this, we conducted set-aside optimizations of ecological outcomes with ‘uniform’ riparian reserve widths of 5, 20, 50 and 100 m, but letting maximum slope for cultivation vary. In all cases, the ‘variable’ approach resulted in ecological gains, albeit with reduced benefit compared with varying both riparian reserve width and maximum slope for cultivation (Supplementary Figs. 14 and 15). In doing so, we additionally observed

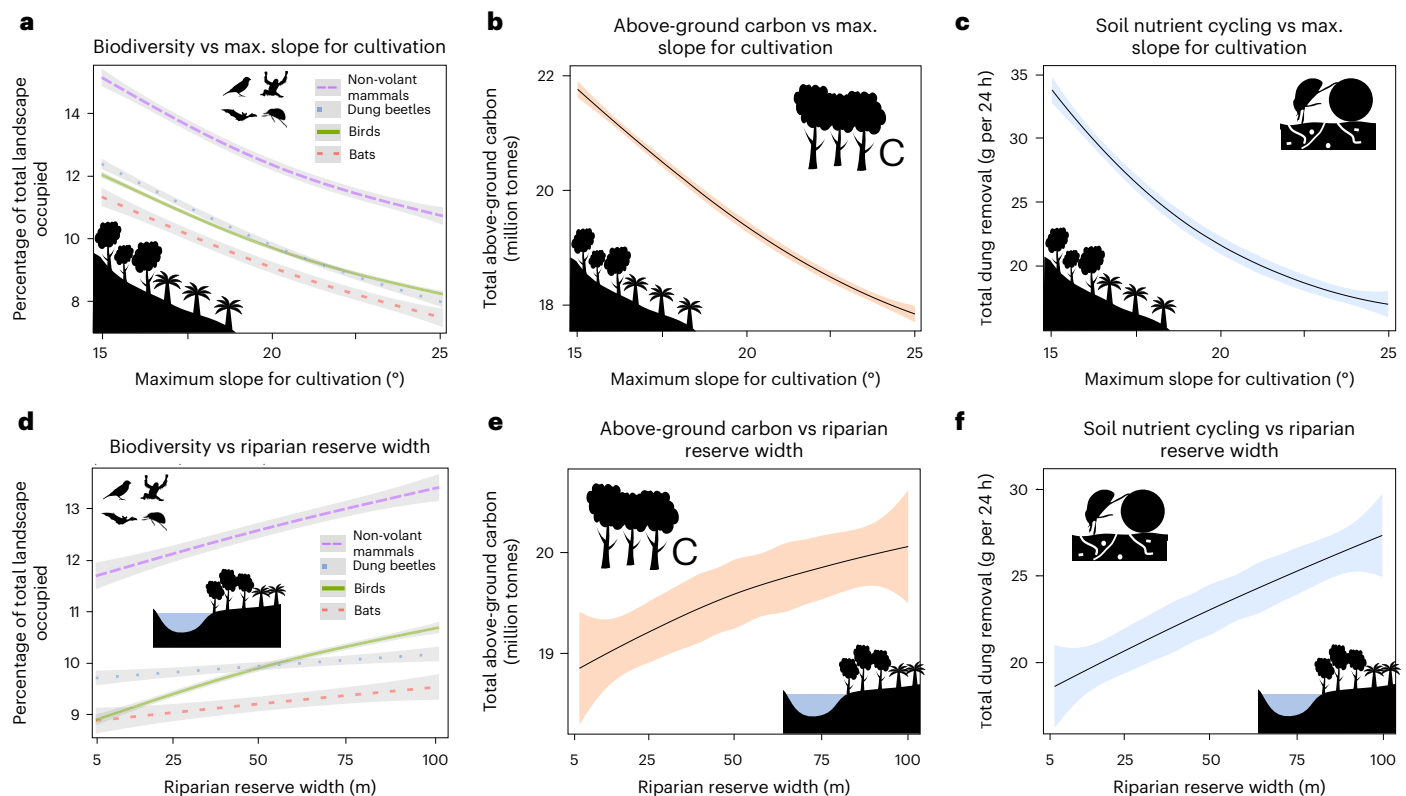


Fig. 4 | Relationship between ecological outcomes, maximum slope for cultivation and riparian reserve width. **a–c**, Curves for biodiversity (per taxon) (**a**), above-ground carbon storage (at timepoint zero excluding the carbon that could accumulate as a result of forest recovery) (**b**) and dung nutrient cycling (**c**) for different maximum slopes for cultivation, independent of width of riparian reserves. **d–f**, Curves for biodiversity (per taxon) (**d**), above-ground carbon

storage (**e**) and dung nutrient cycling (**f**) for different riparian reserve widths, independent of maximum slope for planting. In **a** and **d**, the Y axis shows species occurrence as a percentage of the total landscape. Shading shows 95% CI. All curves use local polynomial regression for LOESS. Animal silhouettes were reproduced from <https://en.silhouette-ac.com/>.

that when more than ~85% of the landscape is cultivated, the impact of changes to maximum slope for cultivation diminish, and riparian reserve width primarily drives changes in the amount of set-aside and, consequently, ecological outcomes (Figs. 2 and 3, Supplementary Figs. 14 and 15, and Note 5). We therefore conclude that at typical cultivation levels (for example, 85–90% of the landscape), ‘variable’ riparian reserves are more important than maximum slope for enhancing ecological outcomes.

Optimizing set-aside in oil palm landscapes across Borneo

On Borneo, an additional 30 Mha (40% of the island) is bioclimatically suitable for oil palm cultivation and falls outside of protected areas⁴⁴. Of this, we estimate that 8 Mha (11% of the island) could be potential set-aside in future plantations, as this is the area of forested slopes of 15–25° and within 100 m of a river (Methods). Therefore, compared with existing plantations, for no net decrease in ecological outcomes, future plantations with spatially optimized ‘variable’ set-asides (that is, ‘variable’ compared with ‘uniform’ approaches) could represent a potential increase in cultivated area of up to 8.5%, yielding 216 million tonnes of crude palm oil over 20 years (Supplementary Table 6).

Discussion

Our study demonstrates that locally optimized set-aside configurations could augment carbon storage, nutrient cycling and biodiversity with little or no reduction in net cultivated area. As such, the ‘variable’ approach we modelled can inform plantation planning and could contribute to voluntary certification standards. Practically, this would be

undertaken during environmental impact assessments (common in oil palm expansion), which might use more straightforward procedures and commonly available datasets than those we tested here. This may result in smaller ecological gains than we estimate but would still be an improvement over ‘uniform’ set-aside configurations. For example, the high carbon stock approach (Supplementary Note 1) utilizes a simple decision tree to determine forest patches that meet criteria for protection and is primarily informed by freely available remote sensing data and local knowledge (<http://highcarbonstock.org/>). A similar, voluntary approach for planning ‘variable’ riparian reserves would improve ecological outcomes in oil palm landscapes, whereby the most ecologically important rivers receive wider riparian reserve widths. Such an approach could prioritize rivers (and their riparian forests) with high carbon stocks and rivers that are well connected to larger forest patches or continuous forests, or those known to harbour species of conservation importance. For example, this could happen where a particular plantation is located in an area of exceptional ecological value where large set-asides are deemed necessary to benefit a migration route for a species with large habitat requirements (as illustrated in ref.⁴⁵ for the case of Bornean elephants). However, where a given plantation experiences losses in cultivation area as a result, this would need to be accompanied by appropriate compensation payments. Alongside this, less ecologically important rivers would receive smaller riparian reserve widths (although sufficient to maintain hydrological processes as a minimum). This has some overlap with that required under RSPO certification but places more emphasis on ecological value than on river width, although these often coincide^{35,36,38,46}. Consequently, guidance under voluntary certification schemes could be adapted to consider

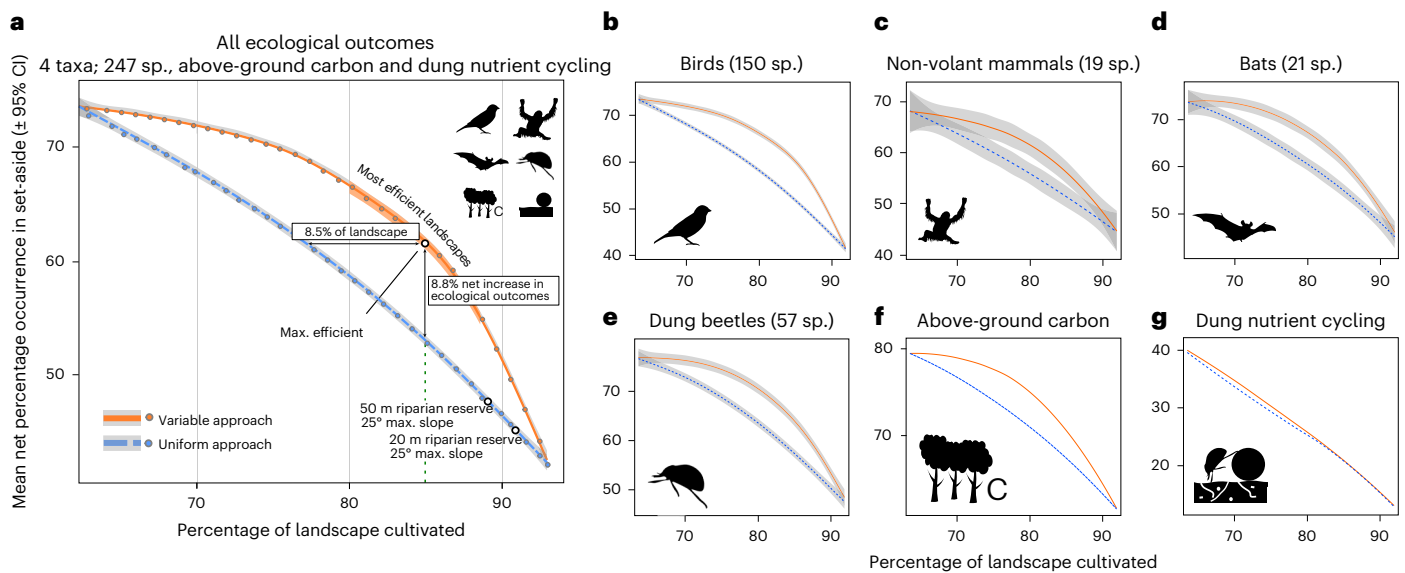


Fig. 5 | Ecological outcomes under ‘variable’ and ‘uniform’ set-aside approaches across all landscape configurations that lead to varying levels of the landscape cultivated. **a–g**, Percentage of maximum possible net ecological outcomes (species occurrence, above-ground carbon storage and dung nutrient cycling) against the percentage of the landscape cultivated under ‘variable’ (orange line) and ‘uniform’ (blue line) approaches. Under the ‘uniform’ approach, all plantations in the landscape apply the same riparian reserve width and maximum slope for cultivation, whereas they can vary between plantations under the ‘variable’ approach. Grey shading shows 95% CI. The ‘most efficient landscapes’ show gains from the ‘variable’ approach that are obtained when set-

aside configurations result in 77–87% of the landscape being cultivated (upper quartile of the difference between ‘uniform’ and ‘variable’ approaches), with the largest difference achieved when 85% of the landscape is cultivated (‘max. efficient’ black and white dot and green dashed vertical line). The regulations in Sabah, Malaysia (25° maximum slope for cultivation, 20 m riparian reserve width) and Indonesia (25° maximum slope for cultivation, 50 m riparian reserve width), which are our baseline for comparison, are shown with labelled dots. Curves use local polynomial regression for LOESS. **a** shows all ecological outcomes combined, and **b–g** show the curves per taxon/service/function. Animal silhouettes were reproduced from <https://en.silhouette-ac.com/>.

ecological enhancements from landscape-scale variable approaches to set-aside configuration.

In our study, we compared ‘variable’ and ‘uniform’ approaches to planning set-asides at the spatial unit of the plantation. This was sufficient to illustrate the potential gains of varying set-aside configuration and demonstrated an important rule-of-thumb; spatially targeted set-aside configurations will improve ecological outcomes. Our ‘variable’ optimization could have been conducted with higher-resolution spatial units, such as those used in precision agricultural systems, which would enhance the ecological outcomes even more than we estimated, shifting our pareto optimization curves further to the right. In the case of oil palm production, such precision planting is rare, particularly for smallholders who are highly unlikely to have access to such data, technology and/or capacity. Nonetheless, it could be feasible for some producers to implement set-aside optimization at the level of drainage basins within plantations, which again specifically underscores the importance of riparian set-asides. This question of the size/definition of a spatial unit is also key to jurisdictional approaches to RSPO certification⁴⁵, which are currently being piloted in Sabah, Kalimantan and Ecuador. In such cases, guidance is set at the estate level, so it is likely that individual landholdings will contribute differently to overall landscape-scale sustainability objectives.

Our analysis can guide planning and management of both current and future plantations. To enhance ecological values, where cultivated parts of contemporary plantations require larger set-aside than currently prescribed, practically, this would probably require restoration or natural recovery to bring back forests and important habitat. In our study landscape, total above-ground carbon stored in forest was estimated to increase by up to 39 and 74% (depending on the approach and cultivation area) after 20 years of natural regeneration and active restoration, respectively (Supplementary Table 4). While these figures are probably overestimates due to edge effects, they

illustrate the potential value of recovering set-asides for climate change mitigation^{14–17}. As such, the RSPO provides standards on restoration of set-aside in oil palm. Realistically, this would need to be done after a growing cycle, when palms are replaced—typically around 20–25 years from establishment⁴⁴. There are an estimated 5–10 Mha of oil palm due for a crop rotation over the next decade (based on Supplementary Fig. 1 and the data therein), yielding an opportunity to bring back lost ecological values through recovery planned using spatial optimization of set-aside.

Implementing a ‘variable’ approach to maximum slopes for cultivation may be more difficult than for riparian reserve widths, and this could, in part, explain why our stakeholder consultations revealed less willingness to see changes in maximum slopes for cultivation. Nonetheless, at cultivation levels between ~83% and ~91% with fixed slopes between 20 and 25° (that is, within current cultivation levels and approaches to maximum slopes for cultivation), varying riparian reserve widths alone would still lead to substantial ecological gains, even without the need for changes in net cultivation area (Supplementary Figs. 14 and 15). As such, our study not only shows the importance of riparian reserves but also the importance of a varied approach to determining their widths. In the same study landscape, riparian reserves have clear value for biodiversity across multiple terrestrial and aquatic taxa, with widths of 40–100 m supporting broadly equivalent levels of biodiversity to continuous logged forest³⁶. Compared with the current 20 m prescription in Sabah, 40 m widths would lead to substantial ecological gains, yielding 28% and 14% more bird and mammal species, respectively, but with some strictly forest-dependent species needing much larger widths (for example, ≥100 m). Therefore, a one-size-fits-all approach to set-aside planning is poorly supported even when considering only ecological values (for example, refs. ^{33,34,36,47}) and not the trade-off with cultivation as demonstrated here.

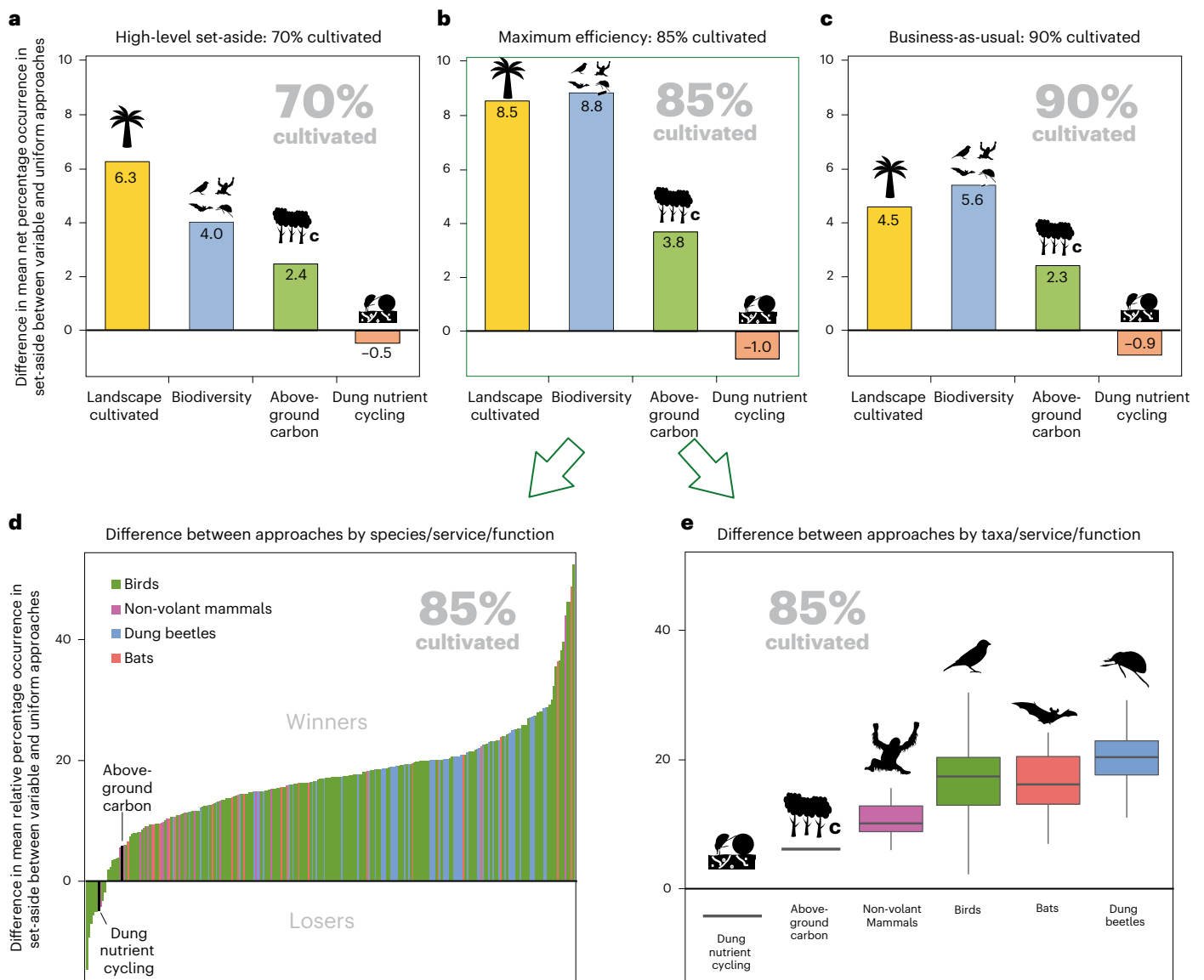


Fig. 6 | Differences in ecological outcomes under ‘variable’ and ‘uniform’ set-aside approaches. **a–c**, Possible net percentage gains in net occurrence in set-aside from adopting the ‘variable’ approach at 70 (**a**), 85 (**b**) and 90% (**c**) landscape cultivation compared to the ‘uniform’ approach, for landscape cultivated, biodiversity (mean net species occurrence), above-ground carbon storage and dung nutrient cycling. Under the ‘uniform’ approach, all plantations in the landscape apply the same riparian reserve width and maximum slope for cultivation, whereas they can vary between plantations under the ‘variable’

approach. **d,e**, Difference between approaches at the ‘maximum efficient’ level (85% of the landscape cultivated) in terms of relative percentage occurrence in set-aside by species/service/function (**d**) and by taxa/service/function (**e**). For boxplots in **e**: bold horizontal line, median; box, 25th and 75th percentiles; whiskers, largest and smallest values within 1.5 times the interquartile range. Biodiversity (including taxa in **e**) based on 247 species (150 birds, 21 bats, 19 non-volant mammals and 57 dung beetles). Animal silhouettes were reproduced from <https://en.silhouette-ac.com/>.

We show that landscape topography is a key attribute affecting how set-asides impact area available for cultivation. This is important because historically, tropical agricultural plantations are less likely to occur on steep slopes due to their being more expensive to deforest and harder to cultivate successfully^{6,43,44}. However today, much of the undeveloped land remaining in the tropics comprises forest on steep slopes⁶. Future set-aside planning will therefore be affected by the fact that landscapes with high proportions of steep areas also have more rivers and riparian areas, and therefore more potential set-aside. This again suggests that concentrating set-aside planning at ‘variable’ riparian reserves may be the best approach because slopes represent a more limiting factor for cultivation, and sticking with the fixed approach to maximum slope for cultivation may be more realistic. Nonetheless even riparian

planning must consider that yields can often be poor close to rivers⁴⁶ and estates that do cultivate these areas often suffer economic losses⁴⁸. This is again more acute in rugged landscapes where riparian zones can be very steep, and so are either not cultivated or can suffer increased soil stability-related mortality. By contrast, if palms are planted in riparian zones in lower lying flat areas, palms sometimes suffer flooding-related mortality⁴⁶.

Our analysis shows that the implementation of variable set-asides would help to improve ecological values without having to compromise net cultivation area. This is critical because perceived losses to production may disincentivize growers from adopting best-practice set-aside measures anyway. Our findings are consequently important for both conservation and agricultural planning. To this end, our study shows that locally tailored riparian set-asides may be the best way to boost

the biodiversity and ecosystem service value of tropical agricultural systems such as oil palm landscapes.

Methods

Study workflow

We aimed to optimize trade-offs between oil palm cultivation area and ecological outcomes provided by set-asides. We modelled an approach to set-aside placement that could improve the ecological value of set-asides without reducing net cultivation area.

To do so, we:

1. Collected ecological data regarding 247 species of animals (biodiversity), an ecosystem function (dung nutrient cycling) and ecosystem service (above-ground carbon storage) from a real-world oil palm landscape made up of four plantations that vary in their actual set-aside levels.
2. Created landscape level spatial data of our ecological outcomes. We used the biodiversity data to generate species distribution models that represent the maximum possible species occurrence across the landscape (see full Methods below). We measured above-ground carbon biomass in forest across the landscape using LiDAR (see full Methods below), and we predicted dung nutrient cycling across the landscape (see full Methods below).
3. Reviewed the regulations that determine set-aside in oil palm landscapes (see Supplementary Note 1) and undertook questionnaires with oil palm growers to determine the attributes of those set-asides that could be explored as potentially relevant to appraise the trade-off between oil palm cultivation and ecological outcomes determined by configurations of different set-asides.
4. Generated spatial layers of 220 combinations of set-asides determined by riparian reserve widths and maximum slope for cultivation across our study landscape. When broken down at the plantation level, we appraised 880 spatial combinations across all four plantations in our study landscape.
5. Determined the potential cultivation area available under all set-aside configurations, as well as explicitly under current regulations in Malaysia and Indonesia (where >80% of oil palm is grown).
6. Drew trade-off curves of the relationship between percentage of the landscape cultivated (inverse of set-aside area) and area occupied by each species for all set-aside configurations, and then assessed the ecological outcomes for each 10% increase in set-aside under a 'uniform' approach, where each plantation in the landscape adopts the same riparian reserve widths and maximum slope for cultivation. Specifically, we compared landscape configurations that range from 61 to 92% cultivated in incremental 10% steps of 62–72%, 72–82% and 82–92% cultivated. Our mathematical notation to estimate trade-off curves is given in Supplementary Note 5.
7. Optimized the trade-off between cultivation area and ecological outcomes in set-aside by comparing a 'uniform' approach to set-aside placement with a 'variable' approach. Under the uniform approach, all plantations in the landscape apply the same riparian reserve widths and maximum slope for cultivation, whereas under the variable approach, these two components can vary among plantations to maximize the trade-off between ecological outcomes and net cultivated area. Our optimization framework and mathematical notation are given in Supplementary Note 3.
8. Optimized the trade-off between cultivation area and ecological outcomes in set-aside by comparing a 'uniform' approach to set-aside placement with a 'variable' approach, but this time the maximum slope and riparian reserve widths were fixed in turn, with the other able to vary.

9. Specifically compared ecological outcomes from 'uniform' and 'variable' approaches at 70%, 85% ('maximum efficient') and 90% of the plantation available for cultivation.
10. Using values from the 'maximum efficient' level, we predicted the potential impact of optimized set-asides in oil palm landscapes across Borneo.

Study landscape

Our study landscape is made up of four oil palm plantations and a logged forest reserve in Sabah, Malaysian Borneo (Supplementary Figs. 2–4). One of the plantations lies within the Stability of Altered Forest Ecosystems (SAFE) project (<https://www.safeproject.net/>; ref. 49). The other three are commercial plantations owned by two Malaysian palm oil producers. Together, the study area covers 119,000 ha of plantation and forest. Most of the forest has been logged two to four times over 30 years and contains few mature trees⁴², although some areas are less disturbed and are now formally protected. The surrounding agricultural matrix comprises oil palms, which were planted 12–15 years before our data collection. Remnant logged forest areas are found on steep slopes and alongside rivers, with widths of 0–470 m on either side of the river (median 53 m). The area of a plantation within 100 m of a river varies by 12–23% (Supplementary Table 2). Each plantation has a distinct topographic profile, varying in ruggedness in 18–56% of the landscape above 15° slope. This topographic variability makes our study landscape particularly suitable for appraising the impacts of set-asides because much of tropical agricultural expansion is expected to be in currently undeveloped rugged landscapes⁶ where set-asides have the greatest impact on potential cultivation area (as described in the main text). Another benefit of this real-world landscape and the accompanying ecological dataset is that it already reflects the fragmented and degraded nature of set-asides in oil palm estates. It includes both tiny and very large fragments (up to ~2,000 ha), and the species assemblages in the riparian forests and steep fragments have already experienced -15 years of edge effects⁵⁰. Therefore, the biodiversity and associated ecosystem functions and services measured in our study landscape incorporate multiple generations of extinction debts⁵¹. Consequently, the effects of fragmentation are integrated in our species distribution models. It is therefore an appropriate study system for assessing the increases/decreases in set-asides that we appraise in our modelling framework. If our approach was used to model set-asides that are substantially smaller/larger than those within our landscape, then edge effects (which become more critical as patch area declines) could lead to under- or overestimation of biodiversity and forest functioning.

Across the study area, we sampled multiple taxonomic groups, above-ground carbon storage and dung nutrient cycling. Methods, locations and sample sizes varied, but all encompassed roughly equal proportions of set-asides in the form of forest fragments, heavily degraded forest (twice logged and then salvage logged), riparian forest (through oil palm and through contiguous forest), contiguous 'logged forest reserve' and in some cases oil palm (details for each are provided below). Species occurrence data from the logged forest reserve were used to improve our estimates of species distributions but were not used in the trade-off analyses.

We obtained plantation boundaries for the study landscape directly from plantation owners. We mapped rivers across the landscape using a combination of geographic information system (GIS) data from the Sabah Department of Irrigation and Drainage (DID) and the Shuttle Radar Topography Mission (STRM) (<http://srtm.usgs.gov>) digital elevation model at a resolution of 30 × 30 m. The DID data included the location of rivers but did not include hydrological information such as flow, which is used to estimate channel width. To estimate flow, we first used the *r.watershed* module in GRASS GIS to create raster files for flow accumulation and drainage direction, which were

then inputted into the `r.stream.extract` module to create a raster and vector of channels using the flow accumulation and direction layers. We added network information to the raw vector channels using an R script to find links between channels (https://www.safeproject.net/dokuwiki/safe_gis/stream_networks). The STRM-generated data matched very closely with the governmental DID data, so we used the STRM river network in our analysis, which allowed us to exclude small streams predicted to be under 5 m in channel width, as these were very rare or no longer actually present on the ground due to cultivation. These tiny rivers are not normally considered for set-asides in Sabah regulations, so this size of river rarely receive riparian reserves. We ground-truthed 20 rivers to ensure that predictions of channel width were broadly accurate (Supplementary Table 8). To estimate and map slope across the landscape, the SRTM data were further processed using the `gdaldem_slope` function (<https://gdal.org/programmes/gdaldem.html>) in Python to generate a raster of slope angles measured in degrees.

Palm oil producer consultations. Before undertaking our landscape analyses, we consulted palm oil producers to inform the range of set-asides to be tested and to ensure that they were feasible to implement from an industry perspective. We spoke to nine representatives from eight of the world's largest palm oil companies. Collectively they manage about 9% of the world's industrial oil palm plantations, an area of land covering over 1.7 Mha, with plantations located in nine different countries across Southeast Asia and West Africa.

We used semi-structured interviews to assess company support for set-asides. We asked respondents to rank ('Not supportive', 'Neutral', 'Supportive') the implementation potential and importance of changes to regulations that determine riparian reserves, areas with steep slopes, forest reserves (for example, high conservation value areas – see Supplementary Note 1) and wildlife corridors. Two key set-aside components emerged as plausible and important: riparian reserve widths and maximum slope for cultivation. Eight of the nine respondents felt that increasing riparian reserve width was both feasible and important for meeting goals relating to enhancing sustainability and ecological outcomes in their plantations. Additionally, all respondents indicated that they would support the establishment of wildlife corridors within plantations, with riparian reserves being the main way to achieve this. We additionally asked respondents for plausible riparian reserve widths to achieve these wildlife corridors, with responses ranging from 2–100 m, with two companies also commenting that riparian reserve widths of over 100 m could be implemented in exceptional circumstances, but therefore not routinely. Four out of the nine respondents were supportive of changes to maximum slope for cultivation but explained that they rarely cultivate slopes steeper than 20°. Combined, this led us to model the set-asides and their limits that we applied in our analyses (5–100 m riparian reserve widths and 15–25° maximum slopes for cultivation).

Set-aside configurations used in the analyses. Set-aside configurations of maximum slopes for cultivation and riparian reserve widths were assessed in a GIS. We created 20 different riparian reserve width layers by adding buffers of 5–100 m (in 5 m increments) around the river network. We created polygons for 11 different thresholds for maximum planting slope ranging from 15–25° (in 1° increments). These two sets of layers were subsequently merged to produce 220 combined riparian reserve width and maximum slope for cultivation layers and then clipped to each plantation (but not the forest reserve) to produce 880 plantation-specific set-aside layers. Across the four plantations, this resulted in 220⁴ or 2,342,560,000 unique ways to configure the landscape. The landscape configurations were overlaid with estimated species distributions, above-ground carbon storage (only considering forest above 35 Ct ha⁻¹) (for further details, see Supplementary Note 1) and dung nutrient cycling layers. These allowed us to examine and optimize trade-offs between the amount of land available for cultivation and the ecological outcomes.

Bird biodiversity field methods. We sampled bird communities via point counts at 376 sample locations across the landscape, spaced at a minimum of 200 m apart. Our point count locations covered all habitat types across the landscape. During each point count, a single experienced observer (S.L.M.) recorded all bird species heard or seen within a 50 m radius of the point for 15 min, including fly-overs. We conducted point counts between 05:50–11:00 in clear weather and these were repeated on three separate occasions at each site between 2014 and 2016 (for further details, see ref. ³³).

Non-volant mammal biodiversity field methods. Camera traps (HC500 Hyperfire, Reconyx) were deployed at 121 locations across the landscape between May and September 2015. Locations were separated by a mean distance of 1.4 km and were stratified to capture the heterogeneity of the landscape. The camera traps were positioned at a standardized height of 30 cm and were deployed for 42 consecutive nights per location, yielding a total survey effort of 4,669 camera nights (for further details, see ref. ⁵²).

Bat biodiversity field methods. We sampled bat communities via harp trapping at 294 sampling points across the landscape from 2015 to 2016. Sampling locations included fragmented forests, riparian forests and secondary regrowth adjacent to oil palm but not directly in oil palm. At each sampling location, traps were positioned to maximize captures, for example, in gaps in the understory. At each site and each year, we performed 10 nights of trapping using 6 four-bank harp traps (60 harp trap nights per site in total) from 20:30–08:30 (for further details, see ref. ⁵³).

Dung beetle biodiversity field methods. We sampled dung beetle (*Scarabidae* sp.) communities via baited pitfall traps at 310 sampling points covering all habitat types across the landscape from 2015 to 2016. Traps were plastic containers 14 cm deep and 13 cm in diameter, part-filled with a mixture of water, salt, detergent and chloral hydrate. These were placed flush with the soil surface. A muslin bag of human faeces (~25 g) was suspended 5 cm above the trap. Each trap was protected from rain by a plastic plate held 20 cm above it. Traps were set in the morning and left for 48 h before collection (for further details, see refs. ^{36,54–56}).

Biodiversity species distribution predictions. We generated presence–pseudo absence species distribution models (SDMs) for 247 species (150 birds, 21 bats, 19 non-volant mammals and 57 dung beetles) using the SSDM package in R (<https://www.r-project.org/>). For each species, we set the model parameters to construct an ensemble model of six algorithms: generalized linear models (GLMs), generalized boosted models (GBMs), random forests (RFs), support vector machines (SVMs), multivariate adaptive regression splines (MARSs) and artificial neural networks (ANNs), with five repetitions of each algorithm. Ensemble predictions were used because they can improve evaluation metrics and minimize biases associated with any single SDM⁵⁷. Accuracy of each model was assessed using cross-validation with a 70–30 split of the occurrence data into training and evaluation sets, repeating the procedure to combine the ensemble using the highest AUC (area under curve) weighted by summing the probabilities of the habitat suitability maps. Relative variable importance was computed on the training dataset using Pearson's correlations between predictions of the full model and with each variable iteratively removed. A presence–absence prediction was then made using the sensitivity-specificity (SES) equality metric as recommended in ref. ⁵⁸. We did not use bioclimatic variables as predictors because we were working at a fine-resolution landscape scale and there was not enough variability. Instead, we used location and landcover predictors (elevation, slope, distance to river and soil type), which are static and do not change with the configuration of the study landscape. As such,

our estimated species distributions represent the maximum possible predicted distribution for each species across the landscape.

Dung nutrient cycling predictions. Dung removal is an important soil nutrient cycling process and reduces greenhouse gas emissions⁵⁹. We measured dung removal at 309 sampling points across the landscape. At each location, 700 g of dung were placed under a rain cover and 24 h later, any remaining dung was collected and weighed. We also used three evaporation/precipitation controls, comprising 700 g piles which were not accessible to fauna (for further details of the approach, see ref. ⁵⁵). To estimate dung removal across the entire landscape, we used residual corrected ordinary regression kriging between our point estimates and landscape-level predictors implemented in SAGA GIS. We predicted \log_{10} dung removal using the same predictors as for the species distribution models (elevation, slope, distance to river and soil type), plus dung beetle richness and non-volant mammal richness (summed from our species distribution models) due to the positive relationship between non-volant mammal and dung beetle richness^{60,61}. The final model represented 38% of the variation in dung removal and retained dung beetle richness and elevation as significant predictors ($R^2 = 0.38, P < 0.001$).

Above-ground carbon storage in forest predictions. To estimate above-ground carbon stored in forest across the landscape, we used data from the Carnegie Airborne Observatory-3. The dataset combines airborne Light Detection and Ranging (LiDAR) with satellite imaging and other geospatial data to map forest above-ground carbon density at 30 m resolution throughout the Malaysian state of Sabah, Borneo. On the basis of a combination of data from the Government of Sabah, ground truthing and assessment of the LiDAR pattern, oil palm was masked from the data (for further details, see refs. ^{62,63}). In our trade-off analyses that included above-ground carbon storage, we considered pixels above a threshold of 35 Ct ha⁻¹ to ensure we were only considering high carbon stock forests. Where the area of set-aside increased, we report the above-ground carbon stored in forests at timepoint zero in the study landscape and the additional carbon accumulated after 20 years if the degraded forest naturally regenerates or undergoes active restoration. To do so, we used the best available values from logged but less fragmented forest in Sabah, where above-ground carbon is accumulated at a rate of 2.9 Ct ha⁻¹ yr⁻¹ for natural regeneration and 4.4 Ct ha⁻¹ yr⁻¹ for active restoration⁶⁴. However, as edge effects are likely to impact carbon sequestration in small forest patches^{51,65}, these accumulation rates may be overestimates for our landscape.

Estimating enhancements to future cultivation on Borneo. To calculate the area of Borneo suitable for oil palm cultivation, we clipped the dataset of global oil palm suitability created by ref. ⁴⁴ to Borneo and then extracted and summed the area of 'Suitable', 'High' and 'Perfect' categories across the island. We then revised this figure by removing existing protected areas (from <https://protectedplanet.net/>) and existing oil palm plantations (from <https://atlas.cifor.org/>). We then intersected the remaining area with all areas falling between 15° and 25° slopes (at a 90 m resolution), by following the same procedure described above for assessing slopes across the study landscape. We estimated the area of Borneo within 100 m of a perennial river using river networks created by Milieux Environnementaux, Transferts et Interactions dans les Hydrosystèmes et les Sols (METRIS; <https://www.metis.upmc.fr/en/node/375>). To calculate the potential average additional oil palm trees across Borneo from optimizing set-aside configuration within plantations, we applied a value of 125 oil palm trees per planted hectare on the basis of data from plantations C and D (Supplementary Table 6). To calculate the potential average additional crude palm oil (CPO) yield over 20 years, we applied an average yield value of 4.1 metric tonnes CPO ha⁻¹ yr⁻¹ assuming an oil extraction rate of 25%, and average fresh fruit bunch yield of 16.4 tonnes ha⁻¹ yr⁻¹ (data from plantations C and D

and close to the average for Malaysia which is 4.2 tonnes CPO ha⁻¹ yr⁻¹) (fao.org/faostat/ and ref. ⁶⁶).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Analyses are based on the following datasets. Dung beetle assemblage: <https://doi.org/10.5281/zenodo.3247494>, <https://doi.org/10.1002/fee.2473>, <https://doi.org/10.1111/1365-2664.13784>, <https://doi.org/10.1111/1365-2664.14049> and <https://doi.org/10.1111/1365-2656.13655>; dung nutrient cycling: <https://doi.org/10.5281/zenodo.3247494>; bat community: <https://doi.org/10.5281/zenodo.3247465> and <https://doi.org/10.1111/mec.16153>; non-volant mammal community: <https://doi.org/10.5285/62774180-ae72-4873-9482-e8be3935f533> and <https://doi.org/10.1002/fee.2473>; bird community: <https://doi.org/10.5061/dryad.kn251r8>, <https://kar.kent.ac.uk/76185/> and <https://doi.org/10.1002/fee.2473>; above-ground carbon LiDAR: <https://doi.org/10.1016/j.biocon.2017.10.020>. DOIs for the ecological and ecosystem service/function data are also listed in Supplementary Table 7.

Code availability

The study workflow is included in the Methods and shown in Fig. 1. Calculations for the optimizations are provided in the Supplementary Information. Analyses conducted in R do not use custom code; as such, they use standard approaches for that package and the name of the package is listed in the Methods. Custom code used to estimate river flow and links between river channels is available at https://www.safeproject.net/dokuwiki/safe_gis/stream_networks.

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Acknowledgements

We thank the numerous field assistants for help with fieldwork, and SAFE Project for extensive support; the Carnegie Airborne Observatory and Sabah Forestry Department for use of the above-ground carbon LiDAR data; R. Nathan, M. Y. Abdullah, V. Moduying, D. Aloysius, M. Ationg, J. Lucey and S. Lord for involvement in the oil palm producer consultations; and D. Orme for developing the code used to extract slope values from SRTM data. The research was supported by UK Natural Environment Research Council (NERC) grants NE/K016407/1, NE/K016261/1 and NE/K016148/1 as part of the LOMBOK consortium of the Human Modified Tropical Forests (HMTF) programme.

Author contributions

J.E.B. led manuscript writing; conducted the landscape and Borneo-wide set-aside analyses, species, above-ground carbon storage and dung nutrient cycling modelling; created the figures; and undertook the oil palm producer consultations. Z.G.D. and M.J.S. conceived the study concept and analytical framework, contributed to the research design and co-wrote the manuscript. J.R.O., with J.E.B., developed and ran the optimization framework. P.R.A. advised on the study concept and optimization methodology. E.M.S., N.J.D., S.L.M.,

D.H.-B. and V.K. provided biodiversity data, and E.M.S. additionally provided nutrient cycling data. A.L.A., Z.G.D., E.M.S. and G.R. helped with the design and delivery of the oil palm producer consultations. D.A.C. contributed towards the estimates of above-ground carbon. S.J.R. and O.T.L. contributed to research design and helped secure funding. All authors provided editorial input on the manuscript.

Competing interests

Authors declare no competing interests.

Ethics statement

Ethics approval was granted by the University of Kent School of Anthropology and Conservation Ethics Committee (reference number 001-ST-17).

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41893-022-01049-6>.

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Peer review information *Nature Sustainability* thanks Susannah Fleiss and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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Software and code

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Data collection N/A

Data analysis ArcGIS Pro; R Studio; Python; SAGA GIS; QGIS; CPLEX studio version 12.9

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DOIs for the ecological data are listed in Supplementary Table 7.

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Study description	Data collection was conducted under multiple studies, as summarized in the Methods, Supplementary Information, and linked to in Supplementary Table 7.
Research sample	Data collection was conducted under multiple studies, as summarized in the Methods, Supplementary Information, and linked to in Supplementary Table 5.
Sampling strategy	Data collection was conducted under multiple studies, as summarized in the Methods, Supplementary Information, and linked to in Supplementary Table 7.
Data collection	Data collection was conducted under multiple studies, as summarized in the Methods, Supplementary Information, and linked to in Supplementary Table 7.
Timing and spatial scale	Across the landscape detailed in the manuscript, and within the papers listed in Supplementary Table 7. All data were collected during 2014-2015.
Data exclusions	No data were excluded
Reproducibility	Standard methods were used for field surveys.
Randomization	Field data collection sites were stratified random, ensuring spatial independence via taxon specific spacing.
Blinding	Not applicable
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	Tropical forests and oil palm plantations in Sabah, Malaysia.
Location	SAFE project in Sabah Malaysia and surrounding plantations. Centred on 4.678198, 117.564159. For further details see https://www.safeproject.net/
Access & import/export	Various field research permits each detailed under the DOIs shown in Supplementary Table 7
Disturbance	No disturbance other than human presence

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Methods

n/a	Involved in the study
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<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

Animals and other organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research

Laboratory animals	N/A
Wild animals	We collected abundance data of 247 species. Bird and non-volant mammal data was non-intrusive and observational. Bats were trapped and released at the study site in Sabah. Dung beetles were collected using lethal pit-fall traps.
Field-collected samples	N/A
Ethics oversight	Ethical approval was granted by the University of Kent School of Anthropology and Conservation ethics committee: reference number 001-ST-17.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Human research participants

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Population characteristics	We conducted semi-structured interviews with nine representatives from seven palm oil producers. We did not collect data on age (apart from ensuring they were over 18) or gender (although our sample included both men and women).
Recruitment	All oil palm companies attending an oil palm conference were invited to conduct a semi-structured interview
Ethics oversight	Ethical approval was granted by the University of Kent School of Anthropology and Conservation ethics committee: reference number 001-ST-17.

Note that full information on the approval of the study protocol must also be provided in the manuscript.