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Conservation set-asides improve carbon storage and support associated plant diversity in certified sustainable oil palm plantations

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ABSTRACT

Maintaining forest conservation set-asides is a key criterion of sustainability certification of many crops that drive tropical deforestation, but their value for carbon storage and associated biodiversity is unclear. We conducted vegetation measurements to examine the benefits of set-asides for aboveground carbon stocks (AGC) in certified oil palm plantations on Borneo, and whether their AGC is positively associated with plant diversity. The mean estimated AGC of live trees and palms ≥10 cm diameter in set-asides in certified oil palm plantations (52.8 Mg ha^{-1}) was > 1.5-times that of oil palm (30.3 Mg ha^{-1}), with some plots supporting similar AGC to primary forest. For lowland Borneo, we estimate that the average AGC of oil palm plantations with 10% coverage of set-asides is up to 20% greater than the average AGC of oil palm plantations without set-asides, newly demonstrating carbon storage as a benefit of conservation set-asides. We found positive relationships between AGC and plant diversity, highlighting the carbon–biodiversity co-benefits of set-asides. However, set-asides had a lower density of tree seedlings than continuous primary forest, indicating potential suppression of future tree regeneration and AGC. Our findings support the application of zero-deforestation during agricultural development, to conserve areas of remaining forest with high AGC and high biodiversity. We recommend management practices that boost regeneration in existing set-asides (e.g. enrichment planting), which would be most effective in larger set-asides, and could substantially increase the AGC of agricultural landscapes without removing land from production, and help conserve forest-dependent biodiversity.

1. Introduction

If global food demand continues to increase without substantial shifts in diet and food distribution, global crop production will need to double by 2050, causing large-scale land-use change (Ray et al., 2013; Shepon et al., 2018). This risks considerable environmental damage because land-use change for commodity production is the largest driver of forest loss globally, mostly occurring in the tropics (Curtis et al., 2018), where forests harbour exceptional biodiversity and contribute critically to global carbon cycling (Baccini et al., 2012; Gibson et al., 2011). Moreover, reducing greenhouse gas (GHG) emissions from tropical agriculture and associated deforestation is fundamental to limiting climate change in line with the Paris Agreement (Griscom et al., 2020; United Nations, 2015), because global land-use accounts for nearly a quarter of recent anthropogenic GHG emissions, primarily through agriculture and deforestation (IPCC, 2019).

To reduce the environmental impacts of tropical agriculture, many corporations have made commitments to reduce deforestation in their

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supply chains, and 'zero-deforestation' commitments now cover two-thirds of global palm oil production (Haupt et al., 2018). If successfully implemented, such commitments have the potential to considerably reduce the negative environmental impacts of oil palm agriculture, given the high GHG emissions and biodiversity loss from extensive deforestation associated with recent oil palm expansion in Southeast Asia (Haupt et al., 2018; Pendrill et al., 2019; Wilcove et al., 2013). 'Zero-deforestation' commitments are frequently put into effect through voluntary certification schemes for sustainable commodity production, such as the Roundtable on Sustainable Palm Oil (RSPO) (Chagas et al., 2018). A key criterion of many of these schemes is the maintenance of conservation set-asides of natural habitat within agricultural landscapes (RSPO, 2018; Senior et al., 2015). Since its inception in 2005, RSPO certification has required natural habitat (largely primary or logged forest) with 'High Conservation Values' (HCVs) to be set-aside for conservation within oil palm concessions (RSPO, 2018). These HCV set-aside sites are identified according to their value for biodiversity, ecosystem services and local communities (Brown et al., 2013; Senior et al., 2015). Oil palm plantations developed before 2005, and certified subsequently, also contain HCV set-asides identified retrospectively, such as remaining areas of natural habitat with low suitability for oil palm cultivation. More recently in 2018, the RSPO strengthened their criteria for sustainability and adopted a 'no deforestation' policy, to align with 'zero-deforestation' commitments of consumer-goods corporations. These commitments require new planted areas to follow a combined HCV-High Carbon Stock Approach (HCV-HCSA) to identify forest areas for protection, based on vegetation structure (such as carbon stocks and tree density) in addition to HCVs (Rosoman et al., 2017; RSPO, 2018). The HCV-HCSA includes protection of low aboveground carbon stocks (AGC) forest, enabling regeneration of set-aside trees and AGC (Rosoman et al., 2017). By protecting forest set-asides, the RSPO aims to increase the extent of forest within certified oil palm plantations, and minimise biodiversity loss and carbon emissions from land-use change (Rosoman et al., 2017; RSPO, 2018). 4.2 M ha of oil palm plantations are currently RSPO-certified globally (RSPO, 2020), so the recent requirements for set-aside conservation could have considerable implications for AGC and biodiversity. To better understand these implications, it is therefore important to examine the benefits of existing conservation set-asides in oil palm.

The benefits of maintaining conservation set-asides for ecosystem services and biodiversity are not well established (Edwards and Laurance, 2012; Senior et al., 2015). Forest set-asides in Southeast Asian oil palm landscapes can support 60–70% of primary forest biodiversity and high seedling survival rates, but this depends on their size (Lucey et al., 2017; Yeong et al., 2016). The fragmented nature of many set-asides (Scriven et al., 2019) is likely to negatively impact their biodiversity and carbon storage capacity (Laurance et al., 2011). For example, within 100 m of the forest edge, elevated tree mortality substantially reduces AGC, favouring regeneration of pioneer species with low wood density (Laurance et al., 2011; Ordway and Asner, 2020; Qie et al., 2017), and these negative edge-effects on AGC can extend up to 1.5 km from the forest edge (Chaplin-Kramer et al., 2015). In addition to edge-effects associated with fragmentation, set-asides have frequently undergone commercial selective logging prior to plantation development, like much of the remaining forest in Southeast Asia (Flint, 1994; Gaveau et al., 2016). Selective logging reduces AGC through timber extraction, and is likely to cause long-term impacts in set-asides through reduced tree regeneration, particularly under additional disturbances such as drought and increasing temperatures (Jucker et al., 2018a; Pillay et al., 2018; Qie et al., 2019). Nevertheless, recent studies based on LiDAR surveys of AGC in Malaysian Borneo found that selectively logged forests contain 60–140 Mg AGC ha^{-1}, which decreases to c. 40–100 Mg ha^{-1} at forest edges (Asner et al., 2018; Ordway and Asner, 2020), suggesting that conservation set-asides of logged forest fragments could still substantially improve the AGC of plantations, given that the AGC of oil palm is c. 30 Mg ha^{-1} (Kho and Jepsen, 2015). However, the AGC of set-asides is likely to vary substantially with local context such as disturbance history (Austin et al., 2017), soil and topography (Jucker et al., 2018a; Quesada et al., 2012). It is also unclear whether set-aside AGC contributes to the conservation of biodiversity, because relationships between AGC and biodiversity in tropical forests are frequently found to be positive but are variable and scale-dependent (Deere et al., 2018; Strassburg et al., 2010; Sullivan et al., 2017). At large spatial scales, the 'land-sharing' approach of retaining conservation set-asides within agricultural landscapes may be less effective for conserving AGC and biodiversity than the 'land-sparing' approach of conserving continuous tracts of forest, because the conservation value of continuous primary forest for biodiversity and AGC is unparalleled (Gibson et al., 2011; Watson et al., 2018).

In this study, we collect new field data on vegetation in forest conservation set-asides in oil palm plantations on Borneo, to establish the value of set-asides for increasing plantation AGC, and whether conservation of AGC in set-asides can have co-benefits for plant diversity. We compare plot-level AGC in set-asides with that of continuous forest (logged and primary sites) and the oil palm planted area, and compare differences in their vegetation structure, including assessing regeneration potential by examining variation in seedling density. We examine potential drivers of variation in set-aside AGC (topography, degree of fragmentation, and soil parameters), and relationships between AGC and plant diversity. We scale up our estimates of set-aside AGC to predict average AGC of oil palm plantations, and use our findings to make policy recommendations on the establishment and management of set-asides for optimizing AGC storage and conserving biodiversity.

2. Materials and methods

2.1. Study sites

We undertook vegetation surveys in Sabah, Malaysian Borneo, between July and November 2017, in conservation set-asides within RSPO-certified oil palm plantations ($n = 14$ sites) across Eastern Sabah, and within a single, large tract of continuous forest for comparison ($n = 4$ sites; Fig. 1a), part of a network of forest reserves between East Sabah and the central Borneo highlands (Asner et al., 2018). The majority of set-asides (12 of 14) were in oil palm plantations planted prior to the establishment of the RSPO in 2005, so were generally in locations unsuitable for planting, and had subsequently been classified for conservation under RSPO Principles and Criteria (RSPO, 2018). Whilst these set-asides were not all initially conserved specifically for AGC or biodiversity value, they provided variation in degree of forest fragmentation (from isolated fragments to sites contiguous with forest outside the plantation, such as state forest reserves), set-aside age (oil palm plantations aged 8–26 years since first planting), and vegetation structure representative of the likely variation in conservation set-asides designated during plantation development (e.g. under the RSPO's, 2018 'no deforestation' policy (RSPO, 2018)). We sampled in fully-protected primary continuous forest ($n = 2$ sites), which has never been selectively logged. We also sampled sites in once-logged ($n = 1$ site, logged in 1988) and twice-logged ($n = 1$ site, logged in mid-1980s and 2005/6) continuous forest, to include sites spanning a range of commercial selective logging intensities likely to represent logging in set-asides prior to plantation development (Reynolds et al., 2011). All sites were ≥1.5 km apart to minimise issues of spatial autocorrelation and pseudoreplication in our analyses. The dominant soil types across our sites were orthic acrisols and dystric cambisols, which are common across lowland Sabah (Land Resources Division, 1974).

2.2. Vegetation surveys

In each of the 18 sites (14 set-asides and 4 continuous sites) we estimated aboveground biomass and AGC in 2–3 circular plots

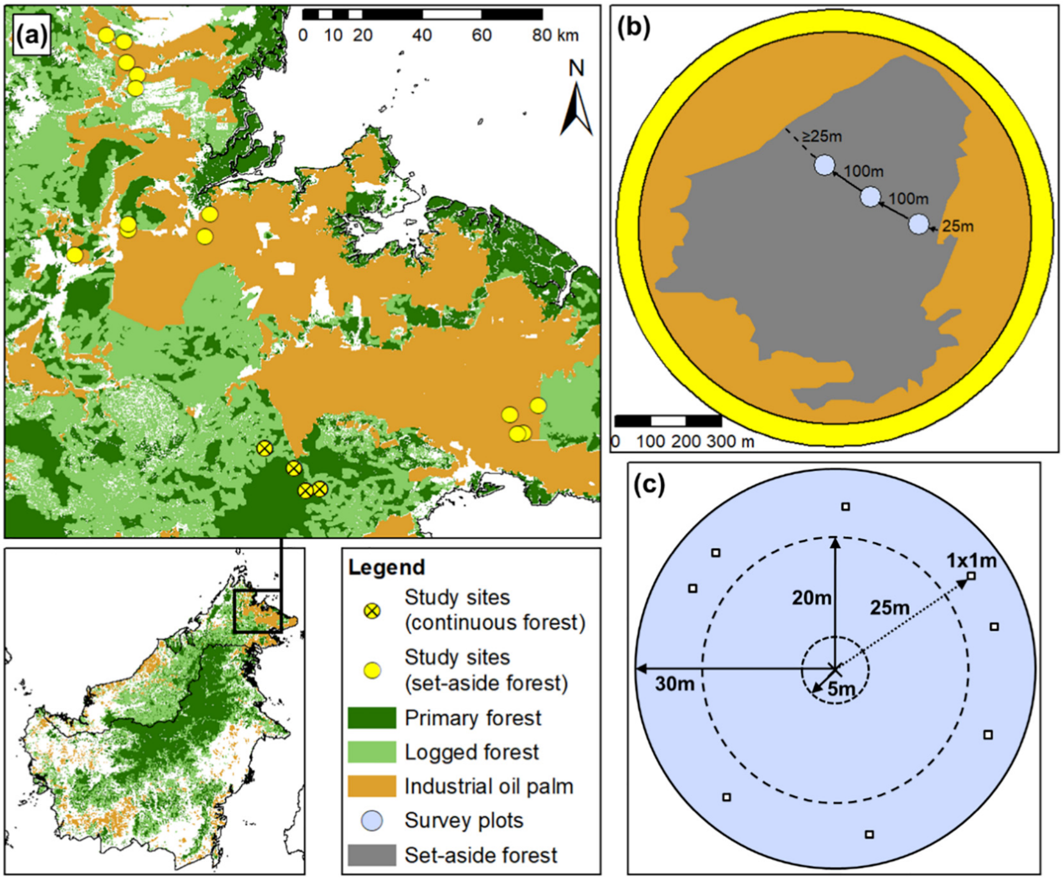

Fig. 1. (a) Map of the sampling sites across Sabah, Malaysian Borneo ($N = 18$ sites). 14 of the sites were in set-asides in RSPO-certified oil palm plantations, and four sites were in a large tract of continuous forest (Danum Valley and Malua Forest Reserves). Forest cover and industrial oil palm plantation maps were obtained from CIFOR (Gaveau et al., 2016, 2014). (b) Transect design (shown for a set-aside site). We placed two or three circular plots 100 m apart, with the first plot boundary 25 m from the nearest forest edge, and the boundaries of subsequent plots at least 25 m from any forest edge. (c) Nested plot design for vegetation sampling. In the main plot of 30 m radius, we recorded live trees and palms ≥25 cm dbh; in the subplot of 20 m radius, we recorded live trees and palms ≥10 cm and < 25 cm dbh; and in the subplot of 5 m radius, we recorded live trees ≥2 cm and < 10 cm dbh. We sampled seedlings (< 2 cm dbh) rooted within eight 1 × 1 m quadrats, on random bearings 25 m from the plot centre.

(depending on set-aside size) of 30 m radius (plot size 0.28 ha; $N = 49$ plots in total). In set-asides, we placed the first plot boundary 25 m from the nearest forest edge to include edge effects, and subsequent plots 100 m apart and ≥25 m from any edge (Fig. 1b). We defined forest edge as the boundary of continuous woody vegetation over 2 m height and canopy closure > 20%, in line with HCSA guidelines, although boundaries between set-asides and oil palm were usually well-defined along minor plantation roads (Rosoman et al., 2017). We used a nested survey design for live trees and palms (Fig. 1c), following standard protocols (Marthews et al., 2014; Phillips et al., 2016). We identified live trees ≥2 cm dbh to genus, and to species when known, in the field, and identified remaining specimens and all seedlings at the herbaria at Danum Valley and Forest Research Centre, Sepilok. We also surveyed lianas and deadwood but these contributed only 6% of the variation in total AGC, so we do not include them in the main article (Appendix A2).

2.3. Estimating tree height for tree biomass estimation

One person (AJ) estimated tree height by eye (in m; 'eye estimates') for a subset of trees ≥10 cm dbh in each plot (30.9% of stems, spanning 10–130 cm dbh), stratified by dbh, and for all palm stems, to improve the accuracy of our AGC estimates (Chave et al., 2014). Eye estimates and clinometer height estimates ('tangent method') (Larjavaara and Muller-Landau, 2013) were closely correlated ($r = 0.754$, $df = 48$, $p < 0.001$, based on 5% of stems with eye estimates), giving us confidence in our eye estimates (Fig. A1). Both of these methods are subject to error, so we did not systematically correct eye estimates according to the clinometer estimates; thus we used the eye estimates to predict height for all remaining stems (Larjavaara and Muller-Landau, 2013). We selected a second-order log-log model to predict remaining tree heights from the eye estimates, which had the lowest relative standard error of the four candidate models we compared using the function 'modelHD' in the BIOMASS package in R (Table A1) (Réjou-Méchain et al., 2017). We compared our field-based estimates of tree height, and resulting AGC estimates, to height and AGC estimates derived from established allometric equations, and found that the method for estimating heights did not alter our conclusions (Appendix A1). Here, we present AGC estimates derived from field-based height estimates because these have previously been found to outperform regional and pan-tropical allometric estimates of tree height (Sullivan et al., 2018).

2.4. Plant diversity and carbon stock estimation for study plots

For seedlings (< 2 cm diameter), saplings (≥2 cm and < 10 cm dbh) and adult trees (≥10 cm dbh), we calculated genus richness, and Fisher's alpha (based on genera; a measure of diversity robust to differences in stem density), per plot. We estimated the biomass of live tree stems ≥10 cm dbh using a pantropical allometric equation (Chave et al., 2014) in the R BIOMASS package (Réjou-Méchain et al., 2017), which outperforms regional models for Bornean forest (Rutishauser et al., 2013). We checked all tree identifications against a database of plant taxonomy (The Plant List, 2013), and assigned wood density values at the finest taxonomic level available, from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). For trees ≥10 cm dbh, we assigned wood density to 20.5% of stems by species, 78.2% by genus, 1.25% by family, and 0.032% by plot-level mean wood density (a single unidentified individual). We used a mixed-species model to estimate palm biomass, to cover the multiple palm species in our surveys, based on dry mass fraction (which we assumed to be 0.37, the mean value for multiple species), diameter and stem height (Goodman et al., 2013). We assumed a carbon content of 47.1% for all biomass (Thomas and Martin, 2012).

2.5. Estimation of oil palm AGC

Since oil palm is replanted in a regular 25–30 year cycle, we estimated time-averaged AGC stocks of oil palm (mean and 95% confidence intervals (CIs) for a 30-year planting cycle) from oil palm age-AGC functions which model carbon sequestration during oil palm growth (Carlson et al., 2013, 2012). We used mean value theorem to calculate average oil palm AGC (average height of curve) for the oil palm growth curves between 0 and 30 years, providing us with mean and 95% CI estimates of time-averaged oil palm AGC for a 30-year planting cycle. We did not estimate oil palm AGC for the ages of the plantations specific to the set-asides in this study, but for unspecified industrial plantations under a 30-year planting cycle, in order to maintain general relevance of our results for the oil palm industry. To include oil palm in our statistical model comparing AGC of forest types (continuous primary, continuous logged, and set-aside) and oil palm, we simulated oil palm AGC data points following a Normal distribution with the mean and standard deviation of the time-averaged oil palm AGC ($n = 15$, following number of data points used to derive the oil palm growth curves in Carlson et al. (2013, 2012)).

2.6. Topographic measurements

To examine the influence of topography on variation in set-aside AGC, we measured slope (°) and elevation (m above sea level) in each plot. We took the maximum absolute value of four slope measurements in the cardinal directions from the plot centre as our measure of plot slope. We obtained elevation measurements from the barometric altimeter of a handheld GPS (Garmin 64s), which we had calibrated at sea level.

2.7. Degree of forest fragmentation in the landscape

To examine whether the degree of forest fragmentation surrounding plots in set-asides affected their AGC, we used UAV imagery provided by an oil palm company to determine surrounding land cover (forest or oil palm). Within a 1 km radius from the centre of each plot, we calculated total forest area (km^2) and edge index (number of 5 m-resolution grid cells containing forest–oil palm boundary, divided by total forest area; higher values signify that a greater proportion of forest is adjacent to oil palm). For each plot, we also quantified straight-line distance (m) to nearest forest–oil palm edge, and time since fragmentation (years since first adjacent oil palm establishment, obtained from the oil palm company; see Fig. A7 for boxplots of these predictors, and scatterplots with AGC). These four variables (surrounding forest area, edge index, distance to forest, time since fragmentation) were correlated (absolute r values ranged 0.39–0.82; Fig. A8), so we combined them using principal components analysis (PCA). We extracted the first principal component (PC1; which explained 68% of total variation) as a 'fragmentation index', with higher values representing greater forest fragmentation (Fig. A9; Table A4). We tested the impact of varying the buffer size for calculating forest area and edge index on our results (for buffers of 0.2–2 km), but it did not affect our conclusions (Table A6).

2.8. Soil parameters

We used seven soil parameters (moisture, pH, available P, total P, total N, organic C and C:N ratio) to test the influence of soil properties and nutrients on AGC in set-asides (see Fig. A10 for boxplots of these variables, and scatterplots with AGC). In each plot, we collected, bulked and subsampled five topsoil cores (0–20 cm depth; see Appendix A3 for details of soil analyses, which were conducted at the Forest Research Centre, Sepilok). Because these seven parameters were correlated (Fig. A11), we combined them by PCA and extracted the first two PCs (which explained 55% and 21% of the variation) as major gradients in soil nutrients and moisture (Fig. A12; Table A5).

2.9. Statistical analyses

We conducted all analyses in R version 3.6.2 (R Core Team, 2017; see Fleiss, 2020 for the R code). We compared plot-level AGC between set-asides ($n = 37$ plots), continuous forest (logged forest, $n = 6$; primary forest, $n = 6$) and oil palm (simulated data points, $n = 15$), using a Bayesian linear mixed effects model (LMM). We fitted site as a random intercept (15 simulated oil palm sites and 18 field sites) with an uninformative gamma prior for the random effect variance, using the blmer function in the R package 'blme' (Dorie, 2011). We found that model convergence was more robust under our low random effect replication using Bayesian parameter estimation than using conventional methods for parameter estimation (which was also the case for the Bayesian models described below). The model structure sufficiently accounted for spatial autocorrelation as the residuals were not spatially autocorrelated (Moran's I of residuals $= -0.19$, $p = 0.20$). We conducted post-hoc Tukey pairwise comparisons on the LMM using the glht function in the R package 'multcomp' (Hothorn et al., 2008).

We assessed differences in vegetation structure among forest types, including to obtain an indication of regeneration potential from seedlings and saplings in set-asides (from abundance, measured as stem density; and mean wood density, which indicates the likely wood density of larger trees in future, and thus the potential for AGC regeneration). We fitted three Bayesian LMMs with each of stem density, mean dbh and wood density as response variables, forest type and tree size class as fixed effects with an interaction term, and site as a random intercept with an uninformative gamma prior for its variance. We log-transformed stem density and mean dbh to remove heteroscedasticity of residuals. For models with significant main effects, we conducted post-hoc Tukey pairwise comparisons on a single categorical predictor of all pairwise combinations of forest type and size class.

To assess potential drivers of variation in AGC within set-asides, we ran generalized additive mixed models (GAMMs) using the R package 'gamm4' (Wood and Scheipl, 2017), with AGC in set-aside plots ($n = 37$) as the response variable, and a Gaussian family and identity link. We included the 'fragmentation index' (fragmentation PC1), two soil variables (soil PC1 and PC2) and slope as main effects; site as a random intercept; and elevation as a penalized cubic regression spline. We initially included both slope and elevation as splines, because the relationships between these and AGC can be non-linear (Jucker et al., 2018b), but we fitted slope as a main effect owing to insufficient variation for model computation.

To test the relationship between plant diversity and AGC, we conducted Bayesian general linear mixed effects models (GLMMs), with total AGC and size class fitted as fixed effects with an interaction term, and site as a random intercept, using the function bglmer in the R package 'blme' (Dorie, 2011). We fitted the model explaining Fisher's alpha with a Gamma family and identity link, excluding four data points (three seedling and one sapling) because their Fisher's alpha values were over seven orders of magnitude greater than the other data, owing to a small number of stems of unique genera in those plots. We fitted the model explaining genus richness with a Poisson family and log link.

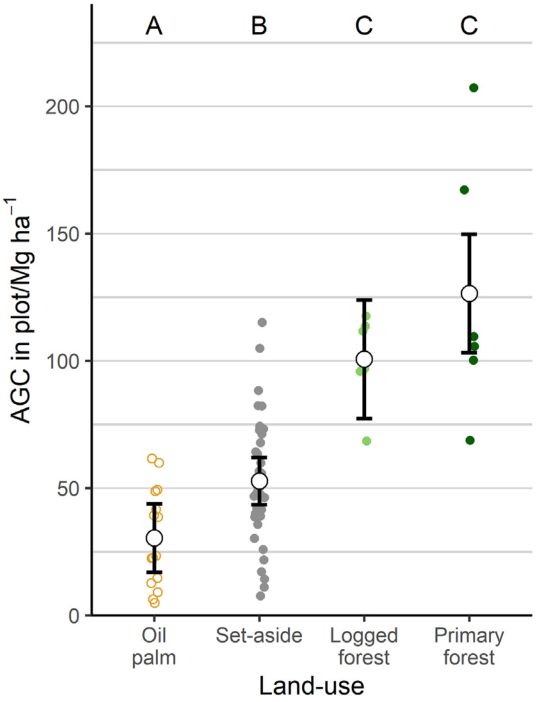

Fig. 2. Estimated plot-level AGC by land-use type (mean ± 95% CI), for all study plots ($n = 49$, closed circles), and estimated time-averaged AGC of oil palm ($n = 15$ simulated data points derived from Carlson et al. (2013, 2012), open circles). Estimates of AGC for field plots comprise AGC of live trees and palms ≥10 cm dbh. Model $\chi^2 = 38.4$, $p < 0.001$ in comparison to null model (site as random intercept only). Different letters (A, B, C) denote significant difference between the land-use types at $p < 0.05$, derived from post-hoc Tukey pairwise comparisons (Table A2); where two land-use types have the same letter, their estimated AGC is not significantly different. See Fig. A3 for a comparison of this model using different methods of tree height estimation; and Fig. A4 for AGC values including deadwood and lianas.

2.10. *Extrapolating our AGC estimates to oil palm plantations*

To examine the benefits of set-asides for AGC at the plantation scale, we estimated the average AGC of oil palm plantations (average carbon stocks in Mg ha^{-1} across a plantation of unspecified size) without set asides, and with set-asides (for varying set-aside coverage; 1–100% of the plantations), as well as of continuous forest sites for comparison. We define oil palm plantations as containing oil palm monoculture and set-aside forest patches (or oil palm monoculture alone), as in many industrial oil palm plantations in Southeast Asia (Gaveau et al., 2014; Wicke et al., 2011). We calculated total AGC mean and 95% PIs (prediction intervals) for each of the three land-use types (oil palm, set-aside and continuous forest) to determine average landscape-scale AGC (for plantations with and without set-asides, and continuous forest). We derived the 95% PIs for time-averaged oil palm AGC from the mean and 95% CIs for oil palm described above. We derived the mean and 95% PIs for set-aside and continuous forest sites from site-level estimates of set-aside AGC ($N = 18$, mean AGC of all plots at a site). We combined continuous primary and logged forest for this analysis because their plot-level AGC did not differ significantly (Fig. 2). We estimated the average AGC of oil palm plantations with set-asides as the sum of the proportion of the plantation occupied by each land-use type (oil palm and set-aside) multiplied by the AGC (mean, lower 95% PI and upper 95% PI). We did not incorporate any effect of forest fragmentation on expected set-aside AGC (i.e. our estimates of AGC of oil palm plantations with set-asides assume that set-aside AGC is directly proportional to set-aside coverage) because we found no effect of fragmentation on set-aside AGC in this study (Fig. A13; Table A6). To compare the average AGC of oil palm plantations with set-asides for different values of AGC stored in set-asides, we also calculated the average AGC of oil palm plantations with set-asides for set-aside AGC of 2.5th and 97.5th percentiles of our set-aside sites (and mean oil palm AGC; for 1–100% of the plantation occupied by set-asides). It is unlikely that variation in topographic and soil parameters was sufficient to limit set-aside AGC in this study, particularly because set-asides had undergone selective logging (Asner et al., 2018; Quesada et al., 2012); therefore we assume that set-aside AGC could be 'improved' to the 97.5th percentile value for sites in this study.

3. Results

Across 49 0.28-ha plots in 18 sites, we measured 3120 live tree stems (10–140 cm dbh), 33 live palm stems (11–47.2 cm dbh), 989 saplings (2–9.8 cm dbh) and 1076 seedlings (< 2 cm dbh).

3.1. *Comparison of plot-level AGC between set-asides, continuous forest and oil palm*

The mean plot-level AGC of live trees and palms in set-asides (52.8 Mg ha^{-1}) was > 1.5-times the mean simulated time-averaged AGC of oil palm (30.3 Mg ha^{-1}), about half the mean AGC of continuous logged forest (101 Mg ha^{-1}), and considerably lower than that of continuous primary forest (126 Mg ha^{-1}; Fig. 2; Table A2). AGC of plots in set-asides was highly variable (7.8–115 Mg ha^{-1}), spanning values lower than the time-averaged AGC of oil palm to values greater than some continuous forest plots (68.4–207 Mg ha^{-1}). The variation of AGC within forest types arises from considerable variation both within and between sites (Fig. A5).

3.2. *Comparison of vegetation structure among forest types*

The mean dbh of the largest tree size class (medium-large trees, ≥25 cm dbh) was significantly lower in set-asides (mean 34.7 cm) than in continuous forest (logged forest: 41.7 cm; primary forest: 48.7 cm), but there were no differences in stem density or mean wood density for size classes included in AGC estimates (small trees and medium-large trees) (Fig. A6; Table A3). However, mean seedling density was significantly lower in set-asides (1.63 m^{-1}) than primary continuous forest (5.83 m^{-1}).

3.3. *Drivers of variation in set-aside AGC*

Variation in set-aside AGC was partly explained by elevation, but we found no effect of fragmentation, soil or slope (Table A6, Fig. A13). Our final model included elevation alone ($F = 0.14$, $p = 0.039$) and explained 15% of variation in AGC (adjusted R^2).

3.4. *Relationship between set-aside AGC and diversity*

Genus richness of seedlings, saplings and adult trees were positively associated with AGC in set-asides (Fig. 3; AGC $\chi^2 = 22.9$, $p < 0.001$). Fisher's alpha was positively associated with AGC for saplings and trees, implying that the positive relationship between diversity and AGC is independent of stem density for these size classes. In contrast, there was a weak negative association between Fisher's alpha and AGC for seedlings (Fig. 3; size class-AGC interaction term $\chi^2 = 6.18$, $p = 0.046$).

3.5. *Impact of set-asides on oil palm plantation AGC*

Our estimates of average site-level AGC in set-asides (mean AGC of all plots at a site) range from 28.1 to 96.6 Mg ha^{-1}. For each additional 10% coverage of set-asides in an oil palm plantation, average plantation AGC increases by 2.34 Mg ha^{-1}, when set-aside AGC is estimated as the average site-level AGC of set-asides in this study (53.8 Mg ha^{-1}; Fig. 4). When set-aside AGC is at the 97.5th percentile of site-level set-aside

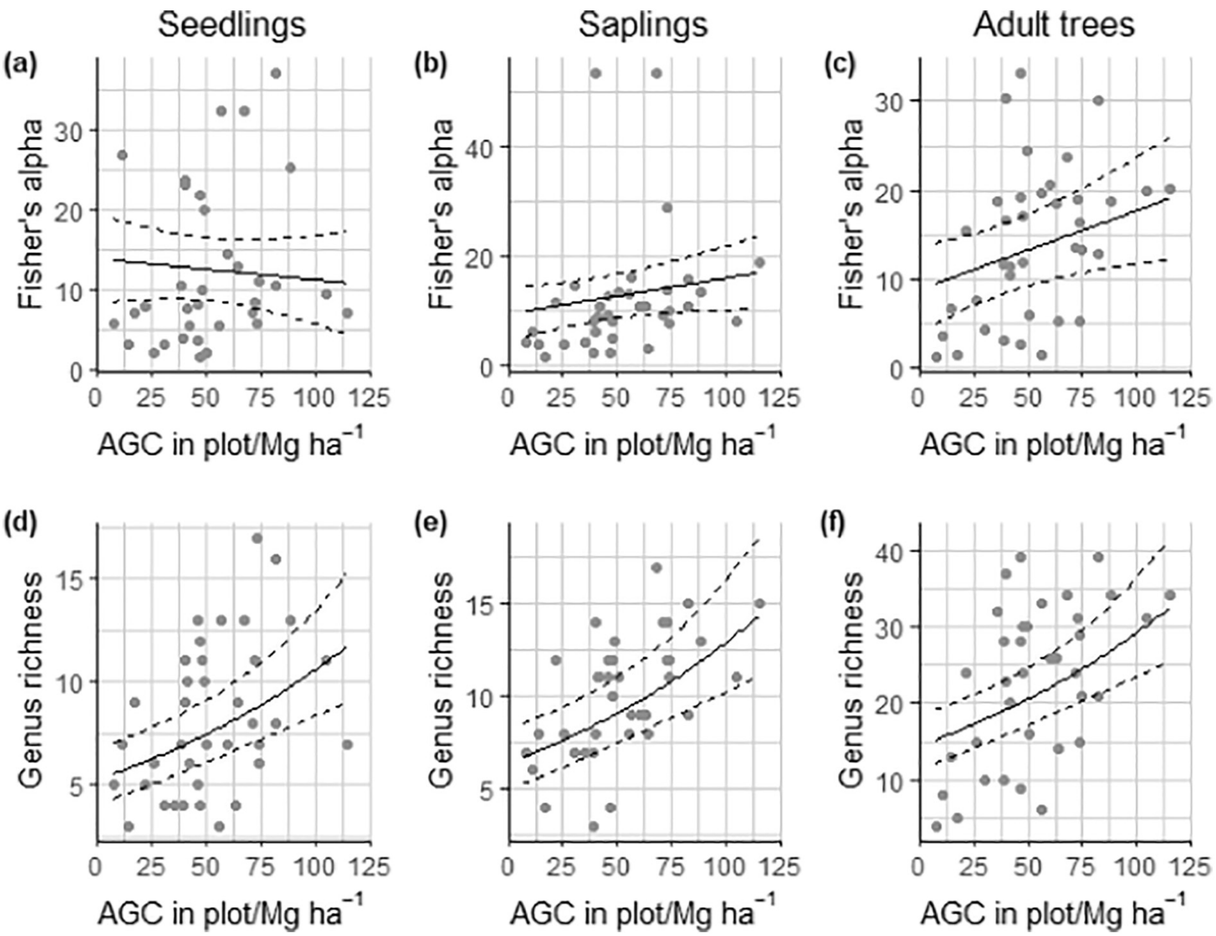

Fig. 3. Results of Bayesian GLMMs modelling the relationship between plot-level AGC and plant diversity, for seedlings (< 2 cm diameter), saplings (≥2 cm and < 10 cm dbh) and adult trees (≥10 cm dbh). (a–c) Fisher's alpha was significantly predicted by the full model (Gamma GLMM, identity link) including the AGC-size class interaction term ($\chi^2 = 6.18, p = 0.046$ for inclusion of the interaction term). (d-f) Genus richness was significantly predicted by AGC and size class (Poisson GLMM, log link; $\chi^2 = 22.9, p < 0.001$ for inclusion of AGC; $\chi^2 = 318.9, p < 0.001$ for inclusion of size class), but including the AGC-size class interaction term did not improve model fit ($\chi^2 = 0.94, p = 0.62$). Dashed lines denote 95% confidence intervals. Note variation in y axes.

AGC (91.6 Mg ha^{-1}), each additional 10% coverage of set-asides increases average plantation AGC by 6.13 Mg ha^{-1}. Thus a plantation with 10% set-aside cover and average set-aside AGC has 7.7% greater AGC than a plantation without set-asides, and a plantation with 10% set-aside cover and 97.5th percentile set-aside AGC has 20.2% greater AGC than a plantation without set-asides.

For a plantation with existing set-asides, improving the AGC of all set-asides can substantially increase average plantation AGC, although the degree for potential improvement depends on current AGC in the set-asides (Fig. 4). For example, in a plantation with 10% set-aside cover, increasing the set-aside AGC from mean set-aside AGC to the 97.5th percentile would increase average plantation AGC by 3.8 Mg ha^{-1} (11.6%), whereas increasing the set-aside AGC from the 2.5th percentile to the 97.5th percentile would increase average plantation AGC by 6.3 Mg ha^{-1} (20.7%).

4. Discussion

4.1. Value of set-asides for increasing the AGC of oil palm plantations

Mean plot-level AGC of set-asides in lowland Sabah was more 1.5-times that of oil palm (Fig. 2), with upper values roughly equivalent to those in continuous forest. We estimate that plantations with 10% cover of set-asides support up to ~20% more AGC than oil palm plantations without such set-asides (Fig. 4). Thus set-asides contribute substantially to carbon storage, in addition to supporting biodiversity (Lucey et al., 2017), connectivity (Scriven et al., 2019), and water quality (Luke et al., 2017); and can therefore contribute to mitigating the GHG emissions of oil palm agriculture (Burton et al., 2017). We highlight the importance of conserving the largest trees for AGC, as shown previously (Slik et al., 2013), because the mean diameter of the largest tree size class in set-asides was significantly smaller than that in continuous forest, resulting in significantly lower AGC in set-asides. Positive relationships between AGC and genus richness of seedlings, saplings and adult trees in set-asides demonstrate co-benefits of conserving set-asides for high AGC and plant diversity (Fig. 3), which we expect to hold true for other taxonomic groups (Ferreira et al., 2018). The positive value of set-asides for improving AGC of oil palm plantations is likely to hold in other croplands, because oil palm has unusually high AGC for a crop (Bonini et al., 2018). However, the value of set-asides for plantation-scale AGC is likely to vary between crop types; for example, negative edge effects on AGC may be stronger for perennial crops (e.g. soy) than oil palm, because of a greater contrast in vegetation structure and microclimate at edges (Laurance et al., 2011), creating a more hostile environment for tree growth and recruitment.

4.2. Unparalleled value of continuous forest for AGC

Mean AGC in continuous forest plots was over double that of set-asides, highlighting the unparalleled importance of continuous forest for AGC storage (Asner et al., 2018), as for biodiversity (Gibson et al., 2011). Furthermore, it is likely that we under-estimated the AGC of

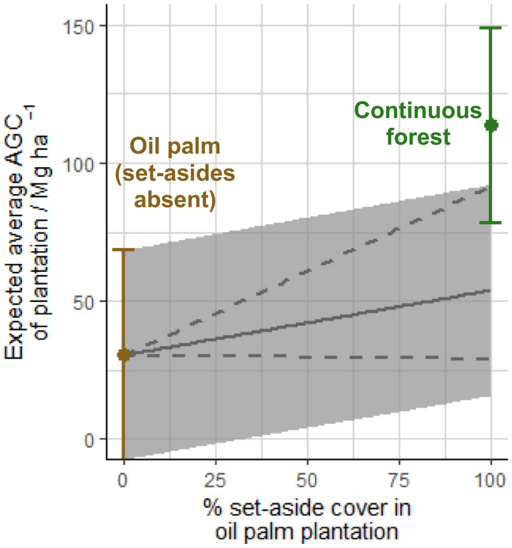

Fig. 4. Predicted average AGC for oil palm plantations with set-asides (grey solid line and shading; mean ± 95% PI), based on estimates of AGC of set-aside sites ($n = 14$). We also show the predicted average AGC (mean ± 95% PI) for plantations without set-asides (i.e. oil palm monoculture only; brown point and error bars; derived from Carlson et al. (2013, 2012)) and in continuous forest landscapes (green point and error bars; based on estimates of AGC in continuous forest sites ($n = 4$)) for comparison. We assume that plantations comprise only oil palm and forest set-asides (when present; i.e. no water bodies, infrastructure, open areas, etc.), and that average plantation AGC increases in direct proportion to the percentage cover of set-asides. Upper and lower dashed lines are predicted AGC when the set-aside AGC is the 97.5th and 2.5th percentiles of the site-level set-aside AGC, rather than the mean (solid line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

continuous forest (Asner et al., 2018; Tangki and Chappell, 2008) because our small plot size (0.28 ha) likely under-sampled the largest stems (Clark and Clark, 2000), and our continuous forest AGC values are low for the region (e.g. Asner et al., 2018), although some previous estimates are similar (Berry et al., 2010, using 1 ha plots; Saner et al., 2012, using 0.25 ha transects). Our continuous forest sampling design was pseudoreplicated at the spatial scale of our forest types (all continuous forest plots were spatially clustered in comparison to the spread of set-asides across Eastern Sabah), although we did not detect spatial autocorrelation in our statistical model residuals. Therefore we may have under-sampled variation for continuous forest AGC across Eastern Sabah (Ramage et al., 2013). However, an improved sampling design with less clustering would not likely alter our conclusion that continuous forest has unparalleled AGC value in comparison to set-asides, because this holds true for previous estimates of continuous forest AGC in Sabah, collected using both field and LiDAR sampling (Asner et al., 2018; Kho and Jepsen, 2015).

4.3. Substantial variation in set-aside AGC

AGC in plots in set-asides varied substantially (7.8–115 Mg ha^{-1}), with values ranging from less than the time-averaged AGC of oil palm (mean 30.3 Mg ha^{-1}) to greater than some continuous forest plots (68.4–207 Mg ha^{-1}). This variation in set-aside AGC is similar to existing estimates of the variation in AGC of logged (continuous and fragmented) forests across Sabah (mostly 20–120 Mg ha^{-1}; Asner et al., 2018). Elevation accounted for some variation in set-aside AGC, but we were unable to explain most of the variation. The high variability of AGC in tropical primary forests is driven by multiple factors such as rainfall, soil, elevation and local plant diversity (Asner et al., 2018; Poorter et al., 2015), and it is likely that these also contribute to variation in the AGC of logged forest. However, we expect that variation in forest disturbance prior to or during plantation development (e.g. from commercial selective logging) is the primary driver of variation in set-aside AGC. All the set-aside sites in this study were logged at least once during plantation development, and it is highly likely that logging intensities would have varied considerably across study plots (e.g. variation in the volumes of timber extracted, and techniques used) (Putz et al., 2001; Reynolds et al., 2011), depending on the volume of commercial timber present, accessibility, and regulations implemented during logging operations. Negative edge effects on AGC in Sabah vary with topography and soil type, and are correlated with edge effects on other aspects of ecosystem functioning, such as foliar phosphorus content, canopy gap area, and leaf mass per area (Ordway and Asner, 2020). Given that our sample size in set-asides was relatively small (37 plots in 14 sites), variation in local disturbance and ecosystem functioning may have masked any effects of fragmentation and edge effects on set-aside AGC in this study, which have been found in other studies in the region (Ordway and Asner, 2020). Much of the existing literature on forest fragmentation does not address the impacts of additional disturbances such as logging (e.g. Laurance et al., 2011), even though most forests across the tropics have been selectively logged as well as fragmented (Asner et al., 2009). Understanding the combined effects of multiple disturbances on the carbon storage, dynamics, biodiversity and potential for recovery of forest set-aside areas would provide insight into the potential conservation value of set-asides in the long-term, and should be a priority for future studies.

4.4. Regeneration of trees and AGC in set-asides

Set-asides had fewer seedlings than continuous primary forest, suggesting that without management intervention (see below), regeneration of trees and thus future AGC may be reduced in set-asides. The relationships between Fisher's alpha (i.e. diversity accounting for abundance) and genus richness (i.e. diversity not accounting for abundance) for seedlings with set-aside AGC were contrasting, suggesting that seedling abundance is positively correlated with set-aside AGC, driving this pattern. The reduced seedling abundance in plots with low AGC may have reduced the negative density-dependence acting on seedling recruitment, resulting in slightly higher seedling Fisher's alpha-values in set-asides with low AGC (LaManna et al., 2017). This recruitment of more diverse seedlings in set-asides with low AGC could enhance AGC in these set-asides in future (Poorter et al., 2015), although the relationship was weak so the effect may be minimal. Furthermore, the seedling genus richness in set-aside plots with the lowest AGC was very low (~5 genera), suggesting reduced resilience of seedlings to disturbances such as drought, which are poorly buffered in forest fragments (Ewers and Banks-Leite, 2013). Therefore we expect that the overall reduced seedling abundance in set-asides (and particularly in those with low AGC, as suggested by the diversity relationships) will have a greater negative impact on AGC regeneration in the medium-term than any positive impact of increased seedling diversity.

4.5. Relevance of findings to current conservation policy

Within the first seven months of RSPO implementation of the HCV-HCSA, over 300,000 ha of conservation set-asides were identified within 1.6 m ha of land-holdings proposing new land clearance (RSPO, 2019, p. 39), indicating that conservation set-asides will be an increasingly significant component of certified oil palm plantations. All the set-asides in this study were in RSPO-certified oil palm plantations, but were formed prior to the adoption of the HCV-HCSA by the RSPO (RSPO, 2018). Our set-aside site-level AGC (mean of all plots in a site; 28.1–96.6 Mg ha^{-1}) ranged from below the lower threshold for protection under the HCV-HCSA to much higher quality forest. It is therefore likely that set-asides in new plantations developed under the HCV-HCSA will span a similar or greater range of AGC than in our study sites. Thus, many set-asides designed under HCV-HCSA are likely to require management to improve their AGC and biodiversity benefits (see below).

4.6. Designing sustainable oil palm landscapes to conserve carbon

Our findings contribute new evidence to support the design of set-asides for AGC in line with the HCV-HCSA (Rosoman et al., 2017; RSPO, 2018):

(a) *Maximising set-aside area where possible*. We estimate that plantations with greater cover of set-asides have higher AGC. Although we found no effect of fragmentation on set-aside AGC, fragmentation often negatively affects AGC and biodiversity, particularly in the tropics and specifically in this region (Betts et al., 2019; Laurance et al., 2011; Lucey et al., 2017; Ordway and Asner, 2020; Qie et al., 2017); thus we recommend maintaining large forest patches where possible (> 200 ha 'core area', habitat at least 100 m from the forest edge, is recommended by Lucey et al., 2017) and designing set-asides to minimise edge effects.

(b) *Prioritising forest with the highest AGC for conservation* (*alongside other conservation values*). We estimate that set-asides with the highest AGC (and therefore a high density of the largest trees, ≥25 cm diameter) confer over double the benefit to average plantation AGC as the same area of set-asides with average AGC, and that set-asides with higher AGC support greater plant diversity. Given the trade-off between total area of set-asides and cultivated area, prioritising high-AGC forest for conservation is preferable for minimising loss of crop area, as recommended for Gabon (Burton et al., 2017).

(c) *Protecting low AGC sites*. The majority of our set-aside sites fall within the lowest AGC category of HCSA ('Young Regenerating Forest') (Rosoman et al., 2017), considerably below the maximum AGC of set-aside sites (97 Mg ha^{-1}, corresponding to HCSA 'Medium Density Forest'). Nonetheless, these low-AGC set-asides provide considerable opportunity for increasing plantation AGC through management for regeneration (see below).

4.7. Management of set-asides for improved carbon stocks and plant diversity

Low seedling density in set-asides highlights the potential need for management to support tree regeneration and maintain or improve set-aside AGC and plant diversity in the long-term. Forest restoration such as enrichment planting (Yeong et al., 2016) and liana cutting (Marshall et al., 2016) may accelerate AGC gains in set-asides, and planting fruiting trees may attract seed dispersing birds and mammals, further enhancing forest regeneration (Meijaard et al., 2005) and benefitting forest biodiversity. Focusing management on larger set-asides would likely produce greater increases in AGC and biodiversity because restoration is more likely to be successful (Crouzeilles et al., 2016), and because larger sites can support greater total AGC and biodiversity.

5. Conclusion

Conservation set-asides in oil palm plantations can support high AGC stocks, and improve the average AGC of oil palm plantations, thereby helping to mitigate GHG emissions from oil palm agriculture. Set-aside AGC and plant diversity are positively associated, so conserving set-asides for high AGC has co-benefits for conserving high plant diversity. Our findings support the HCV-HCSA guidelines for set-aside conservation, such as prioritising conservation of locations which are large in size and/or support high AGC, as well as conserving forest areas of relatively low AGC to enable future regeneration of AGC and biodiversity. We recommend management of set-asides to improve tree and AGC regeneration, which would increase the AGC of oil palm plantations without removing land from crop production, and prevent future declines in AGC and tree diversity due to poor regeneration from the current low abundance of seedlings in set-asides.

Data availability

Data collected for this study are available to download (see Waddell et al., 2020).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors' contributions

SF, JKH and HK conceived the ideas. SF, JKH, CJM, EHW, LFB, DSC, SB, KLY, ABS and AJ designed methodology; SF, EHW, AJ and ABS collected the data; AJ and BBO led plant identification; SF analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and approved the final version for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108631.

References

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., Emerson, R., 2009. A contemporary assessment of change in humid tropical forests. Conserv. Biol. 23 (6), 1386–1395. https://doi.org/10.1111/j.1523-1739.2009.01333.x.

Asner, G.P., Brodrick, P.G., Philipson, C., Vaughn, N.R., Martin, R.E., Knapp, D.E., ... Coomes, D.A., 2018. Mapped aboveground carbon stocks to advance forest conservation and recovery in Malaysian Borneo. Biological Conservation 217, 289–310. https://doi.org/10.1016/J.BIOCON.2017.10.020.

Austin, K.G., Lee, M.E., Clark, C., Forester, B.R., Urban, D.L., White, L., ... Poulsen, J.R., 2017. An assessment of high carbon stock and high conservation value approaches to sustainable oil palm cultivation in Gabon. Environmental Research Letters 12 (1), 014005. https://doi.org/10.1088/1748-9326/aa5437.

Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., ... Houghton, R.A., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nature Climate Change 2 (3), 182–185. https://doi.org/10.1038/nclimate1354.

Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., ... Hamer, K.C., 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodiversity and Conservation 19 (4), 985–997. https://doi.org/10.1007/s10531-010-9779-z.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B., ... Ewers, R.M., 2019. Extinction filters mediate the global effects of habitat fragmentation on animals. Science 366 (6470), 1236 LP–1239. https://doi.org/10.1126/science.aax9387.

Bonini, I., Hur Marimon-Junior, B., Matricardi, E., Phillips, O., Petter, F., Oliveira, B., Marimon, B.S., 2018. Collapse of ecosystem carbon stocks due to forest conversion to soybean plantations at the Amazon-Cerrado transition. For. Ecol. Manag. 414, 64–73. https://doi.org/10.1016/J.FORECO.2018.01.038.

Brown, E., Dudley, N., Lindhe, A., Muhtaman, D.R., Stewart, C., Synnott, T., 2013. Common Guidance for the Identification of High Conservation Values. (HCV Resource Network).

Burton, M.E.H., Poulsen, J.R., Lee, M.E., Medjibe, V.P., Stewart, C.G., Venkataraman, A., White, L.J.T., 2017. Reducing carbon emissions from forest conversion for oil palm agriculture in Gabon. Conserv. Lett. https://doi.org/10.1111/conl.12265.

Carlson, K.M., Curran, L.M., Ratnasari, D., Pittman, A.M., Soares-Filho, B.S., Asner, G.P., ... Rodrigues, H.O., 2012. Committed carbon emissions, deforestation, and community land conversion from oil palm plantation expansion in West Kalimantan, Indonesia. In: Proceedings of the National Academy of Sciences of the United States of America, https://doi.org/10.1073/pnas.1200452109.

Carlson, K.M., Curran, L.M., Asner, G.P., Pittman, A.M., Trigg, S.N., Marion Adeney, J., 2013. Carbon emissions from forest conversion by Kalimantan oil palm plantations. Nat. Clim. Chang. 3 (3), 283–287. https://doi.org/10.1038/nclimate1702.

Chagas, T., Streck, C., Galt, H., Zwick, S., Schulte, I., Kroeger, A., Thompson, A., 2018. Impacts of Supply Chain Commitments on the Forest Frontier. Retrieved from. https://www.tfa2020.org/wp-content/uploads/2018/06/Impacts-of-Supply-Chain-Commitments-on-the-Forest-Frontier.pdf.

Chaplin-Kramer, R., Ramler, I., Sharp, R., Haddad, N.M., Gerber, J.S., West, P.C., ... King, H., 2015. Degradation in carbon stocks near tropical forest edges. Nature Communications 6. https://doi.org/10.1038/ncomms10158.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12 (4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C.C., ... Goodman, R.C., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20 (10), 3177–3190. https://doi.org/10.1111/gcb.12629.

Clark, D., Clark, D., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manag. 137 (1–3), 185–198. https://doi.org/10.1016/S0378-1127(99)00327-8.

Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E.V., Rey Benayas, J.M., 2016. A global meta-analysis on the ecological drivers of forest restoration success. Nat. Commun. 7 (1), 11666. https://doi.org/10.1038/ncomms11666.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361 (6407), 1108–1111. https://doi.org/10.1126/science.aau3445.

Deere, N.J., Guillera-Arroita, G., Baking, E.L., Bernard, H., Pfeifer, M., Reynolds, G., ... Struebig, M.J., 2018. High Carbon Stock forests provide co-benefits for tropical biodiversity. Journal of Applied Ecology 55 (2), 997–1008. https://doi.org/10.1111/1365-2664.13023.

Dorie, V., 2011. blme: Bayesian Linear Mixed-Effects Models. *http://CRAN.R-Project.Org/Package=Blme*.

Edwards, D.P., Laurance, S.G., 2012. Green labelling, sustainability and the expansion of tropical agriculture: critical issues for certification schemes. Biol. Conserv. https://doi.org/10.1016/j.biocon.2012.01.017.

Ewers, R.M., Banks-Leite, C., 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. PLoS One 8 (3), e58093. https://doi.org/10.1371/journal.pone.0058093.

Ferreira, J., Lennox, G.D., Gardner, T.A., Thomson, J.R., Berenguer, E., Lees, A.C., ... Barlow, J., 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature Climate Change 8 (8), 744–749. https://doi.org/10.1038/s41558-018-0225-7.

Fleiss, S., 2020. R code to reproduce analyses of aboveground carbon stocks and associated plant diversity in fragmented and continuous forest sites in Sabah, Malaysian Borneo, 2017. NERC Environmental Information Data Centrehttps://doi.org/10.5285/9ff5cdca-b504-4994-8b07-5912ee6aff47.

Flint, E.P., 1994. Changes in land use in South and Southeast Asia from 1880 to 1980: a data base prepared as part of a coordinated research program on carbon fluxes in the tropics. Chemosphere 29 (5), 1015–1062. https://doi.org/10.1016/0045-6535(94)90166-X.

Gaveau, D.L.A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N.K., ... Wielaard, N., 2014. Four decades of forest persistence, clearance and logging on Borneo. PloS One 9 (7), e101654.

Gaveau, D.L.A., Sheil, D., Husnayaen, A., Salim, M.A., Arjasakusuma, S., Ancrenaz, M., ... Meijaard, E., 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. Scientific Reports 6, 32017. https://doi.org/10.1038/srep32017.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., ... Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478 (7369), 378–381. https://doi.org/10.1038/nature10425.

Goodman, R.C., Phillips, O.L., Del Castillo Torres, D., Freitas, L., Cortese, S.T., Monteagudo, A., Baker, T.R., 2013. Amazon palm biomass and allometry. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2013.09.045.

Griscom, B.W., Busch, J., Cook-Patton, S.C., Ellis, P.W., Funk, J., Leavitt, S.M., ... Worthington, T., 2020. National mitigation potential from natural climate solutions in the tropics. Philosophical Transactions of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rstb.2019.0126.

Haupt, F., Bakhtary, H., Schulte, I., Galt, H., Streck, C., 2018. Progress on Corporate Commitments and their Implementation. Retrieved from. https://www.tropicalforestalliance.org/en/insights/publications/.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. https://doi.org/10.1002/bimj.200810425.

IPCC, 2019. IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems. Summary for Policymakers. Retrieved from. https://www.ipcc.ch/site/assets/uploads/2019/08/Edited-SPM_Approved_Microsite_FINAL.pdf.

Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., ... Coomes, D.A., 2018a. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Global Change Biology. https://doi.org/10.1111/gcb.14415.

Jucker, T., Bongalov, B., Burslem, D.F.R.P., Nilus, R., Dalponte, M., Lewis, S.L., ... Coomes, D.A, 2018b. Topography shapes the structure, composition and function of tropical forest landscapes. Ecol. Lett. 21 (7). https://doi.org/10.1111/ele.12964.

Kho, L.K., Jepsen, M.R., 2015. Carbon stock of oil palm plantations and tropical forests in Malaysia: A review. Singapore Journal of Tropical Geography. https://doi.org/10.1111/sjtg.12100.

LaManna, J.A., Mangan, S.A., Alonso, A., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S., ... Myers, J.A., 2017. Plant diversity increases with the strength of negative density dependence at the global scale. Science. https://doi.org/10.1126/science.aam5678.

Land Resources Division, 1974. The soils of Sabah. British Government's Overseas Development Administration (Land Resources Division) United Kingdom, for the Sabah Government.

Larjavaara, M., Muller-Landau, H.C., 2013. Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. Methods Ecol. Evol. 4 (9), 793–801. https://doi.org/10.1111/2041-210X.12071.

Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., ... Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation 144 (1), 56–67. https://doi.org/10.1016/J.BIOCON.2010.09.021.

Lucey, J.M., Palmer, G., Yeong, K.L., Edwards, D.P., Senior, M.J.M., Scriven, S.A., ... Hill, J.K., 2017. Reframing the evidence base for policy-relevance to increase impact: a case study on forest fragmentation in the oil palm sector. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.12845.

Luke, S.H., Barclay, H., Bidin, K., Chey, V.K., Ewers, R.M., Foster, W.A., ... Aldridge, D.C., 2017. The effects of catchment and riparian forest quality on stream environmental conditions across a tropical rainforest and oil palm landscape in Malaysian Borneo. Ecohydrology 10 (4), e1827. https://doi.org/10.1002/eco.1827.

Marshall, A.R., Coates, M.A., Archer, J., Kivambe, E., Mnendendo, H., Mtoka, S., ... Njilima, F.M., 2016. Liana cutting for restoring tropical forests: a rare palaeotropical trial. African Journal of Ecology. https://doi.org/10.1111/aje.12349.

Marthews, T., Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., ... Cain, R., 2014. Measuring Tropical forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v3.0). Manual. pp. 121. Retrieved from. http://gem.tropicalforests.ox.ac.uk/.

Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., ... O'Brien, T., 2005. Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo. In: Life After Logging: Reconciling Wildlife Conservation and Production Forestry in Indonesian Borneo, https://doi.org/10.17528/cifor/001663.

Ordway, E.M., Asner, G.P., 2020. Carbon declines along tropical forest edges correspond to heterogeneous effects on canopy structure and function. Proc. Natl. Acad. Sci. https://doi.org/10.1073/pnas.1914420117.

Pendrill, F., Persson, U.M., Godar, J., Kastner, T., Moran, D., Schmidt, S., Wood, R., 2019. Agricultural and forestry trade drives large share of tropical deforestation emissions. Glob. Environ. Chang. 56, 1–10. https://doi.org/10.1016/j.gloenvcha.2019.03.002.

Phillips, O., Baker, T., Feldpausch, T., Brienen, R., 2016. RAINFOR Field manual for plot establishment and remeasurement. Retrieved from. http://www.rainfor.org/upload/ManualsEnglish/.

Pillay, R., Hua, F., Loiselle, B.A., Bernard, H., Fletcher, R.J., 2018. Multiple stages of tree seedling recruitment are altered in tropical forests degraded by selective logging. Ecology and Evolution. https://doi.org/10.1002/ece3.4352.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., ... Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Global Ecology and Biogeography. https://doi.org/10.1111/geb.12364.

Putz, F.E., Blate, G.M., Redford, K.H., Fimbel, R., Robinson, J., 2001. Tropical forest management and conservation of biodiversity: an overview. Conserv. Biol. https://doi.org/10.1046/j.1523-1739.2001.00018.x.

Qie, L., Lewis, S.L., Sullivan, M.J.P., Lopez-Gonzalez, G., Pickavance, G.C., Sunderland, T., ... Phillips, O.L., 2017. Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects. Nature Communications 8 (1), 1966. https://doi.org/10.1038/s41467-017-01997-0.

Qie, L., Telford, E.M., Massam, M.R., Tangki, H., Nilus, R., Hector, A., Ewers, R.M., 2019. Drought cuts back regeneration in logged tropical forests. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/ab0783.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., ... Lloyd, J., 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences. https://doi.org/10.5194/bg-9-2203-2012.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Retrieved from. http://www.r-project.org/.

Ramage, B.S., Sheil, D., Salim, H.M.W., Fletcher, C., Mustafa, N.Z.A., Luruthusamay, J.C., ... Potts, M.D., 2013. Pseudoreplication in Tropical Forests and the Resulting Effects on Biodiversity Conservation. Conservation Biology. https://doi.org/10.1111/cobi.12004.

Ray, D.K., Mueller, N.D., West, P.C., Foley, J.A., 2013. Yield trends are insufficient to double global crop production by 2050. PLoS One 8 (6), e66428. https://doi.org/10.1371/journal.pone.0066428.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an r package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. 8 (9), 1163–1167. https://doi.org/10.1111/2041-210X.12753.

Reynolds, G., Payne, J., Sinun, W., Mosigil, G., Walsh, R.P.D., 2011. Changes in forest land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum Valley region. Philosophical Transactions of the Royal Society B-

Biological Sciences 366 (1582), 3168–3176. https://doi.org/10.1098/rstb.2011.0154.

Rosoman, G., Sheun, S.S., Opal, C., Anderson, P., Trapshah .E., R., 2017. In: Rosoman, R., Sheun, G., Opal, S.S., Anderson, C., Trapshah, P. (Eds.), The HCS Approach Toolkit, Singapore. Retrieved from. http://highcarbonstock.org/wp-content/uploads/2017/05/HCSA-Toolkit-v2.0-Module-1-Introduction-190917-web.pdf.

RSPO, 2018. Roundtable on Sustainable Palm Oil Principles & Criteria for Sustainable Palm Oil. Retrieved from. https://rspo.org/resources/certification/rspo-principles-criteria-certification.

RSPO, 2019. RSPO Impact Update 2019. pp. 15. Retrieved from. https://rspo.org/impact.

RSPO, 2020. Impact| RSPO-Roundtable on Sustainable Palm Oil. Retrieved May 6, 2020, from. https://www.rspo.org/impact.

Rutishauser, E., Noor'an, F., Laumonier, Y., Halperin, J., Rufi'ie, Hergoualch, K., Verchot, L., 2013. Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia. For. Ecol. Manag. 307, 219–225. https://doi.org/10.1016/j.foreco.2013.07.013.

Saner, P., Loh, Y.Y., Ong, R.C., Hector, A., 2012. Carbon stocks and fluxes in tropical lowland dipterocarp rainforests in Sabah, Malaysian Borneo. PLoS One 7 (1), e29642. https://doi.org/10.1371/journal.pone.0029642.

Scriven, S.A., Carlson, K.M., Hodgson, J.A., McClean, C.J., Heilmayr, R., Lucey, J.M., Hill, J.K., 2019. Testing the benefits of conservation set-asides for improved habitat connectivity in tropical agricultural landscapes. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13472.

Senior, M.J.M., Brown, E., Villalpando, P., Hill, J.K., 2015. Increasing the scientific evidence base in the "high conservation value" (HCV) approach for biodiversity conservation in managed tropical landscapes. Conserv. Lett. 8 (5), 361–367. https://doi.org/10.1111/conl.12148.

Shepon, A., Eshel, G., Noor, E., Milo, R., 2018. The opportunity cost of animal based diets exceeds all food losses. Proc. Natl. Acad. Sci. U. S. A. 115 (15), 3804–3809. https://doi.org/10.1073/pnas.1713820115.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., ... Zweifel, N., 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Global Ecology and Biogeography. https://doi.org/10.1111/geb.12092.

Strassburg, B.B.N., Kelly, A., Balmford, A., Davies, R.G., Gibbs, H.K., Lovett, A., ... Rodrigues, A.S.L., 2010. Global congruence of carbon storage and biodiversity in terrestrial ecosystems. Conservation Letters 3 (2), 98–105. https://doi.org/10.1111/j.1755-263X.2009.00092.x.

Sullivan, M.J.P.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., ... Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. Scientific Reports 7 (1), 39102. https://doi.org/10.1038/srep39102.

Sullivan, M.J.P., Lewis, S.L., Hubau, W., Qie, L., Baker, T.R., Banin, L.F., ... Phillips, O.L., 2018. Field methods for sampling tree height for tropical forest biomass estimation. Methods in Ecology and Evolution 9 (5), 1179–1189. https://doi.org/10.1111/2041-210X.12962.

Tangki, H., Chappell, N.A., 2008. Biomass variation across selectively logged forest within a 225-km2 region of Borneo and its prediction by Landsat TM. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2008.07.018.

The Plant List, 2013. The Plant List Version 1.1. Retrieved March 8, 2018, from. http://www.theplantlist.org.

Thomas, S.C., Martin, A.R., 2012, June 19. Carbon content of tree tissues: a synthesis. In: Forests. Molecular Diversity Preservation International, https://doi.org/10.3390/f3020332.

United Nations, 2015. Paris Agreement. Retrieved from. https://unfccc.int/sites/default/files/english_paris_agreement.pdf.

Waddell, E.H., Fleiss, S., Bala Ola, B., Bin Sailim, A., Jelling, A., Yeong, K.L., Tangah, J., Benedick, S., King, H., Hughes, M., McClean, C.J., Chapman, D.S., Hill, J.K., Banin, L.F, 2020. Vegetation and habitat data for fragmented and continuous forest sites in Sabah, Malaysian Borneo, 2017. NERC Environmental Information Data Centrehttps://doi.org/10.5285/c67b06b7-c3f6-49a3-baf2-9fc3a72cb98a.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. Nature Ecology and Evolution. https://doi.org/10.1038/s41559-018-0490-x.

Wicke, B., Sikkema, R., Dornburg, V., Faaij, A., 2011. Exploring land use changes and the role of palm oil production in Indonesia and Malaysia. Land Use Policy. https://doi.org/10.1016/j.landusepol.2010.06.001.

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. Trends in Ecology and Evolution. https://doi.org/10.1016/j.tree.2013.04.005.

Wood, S., Scheipl, F., 2017. gamm4: Generalized Additive Mixed Models using "mgcv" and "lme4". R package version 0.2-5. Retrieved from. https://cran.r-project.org/package=gamm4.

Yeong, K.L., Reynolds, G., Hill, J.K., 2016. Enrichment planting to improve habitat quality and conservation value of tropical rainforest fragments. Biodivers. Conserv. 25 (5), 957–973. https://doi.org/10.1007/s10531-016-1100-3.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., ... Chave, J., 2009. Global wood density database. https://doi.org/10.5061/dryad.234.