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Do high carbon stock forests provide co-benefits for tropical biodiversity?

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Standard Paper

Do high carbon stock forests provide co-benefits for tropical biodiversity?

Running head: Biodiversity co-benefits of high carbon areas

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Summary

1. Carbon-based policies provide powerful opportunities to unite tropical forest conservation with climate change mitigation. However, their effectiveness in delivering biodiversity co-benefits is dependent on high levels of biodiversity being found in high carbon areas. Previous studies have focussed solely on the co-benefits associated with Reducing Emissions from Deforestation and forest Degradation (REDD+) over large spatial scales, with few empirically testing carbon-biodiversity correlations at management unit scales appropriate to decision-makers. Yet, in development frontiers, where most biodiversity and carbon loss occurs, carbon-based policies are increasingly driven by commodity certification schemes, which are applied at the concession-level.
2. Working in a typical human-modified landscape in Southeast Asia, we examined the biodiversity value of land prioritised via application of REDD+ or the High Carbon Stock (HCS) Approach, the emerging land-use planning tool for oil palm certification. Carbon stocks were estimated via low- and high-resolution datasets derived from global or local-level biomass. Mammalian species richness was predicted using hierarchical Bayesian multi-species occupancy models of camera-trap data from forest and oil palm habitats.
3. At the community level, HCS forest supported comparable mammal diversity to control sites in continuous forest, while lower carbon strata exhibited reduced species occupancy.
4. No association was found between species richness and carbon when the latter was estimated using coarse-resolution data. However, when using high-resolution, field-validated biomass data, diversity demonstrated positive relationships with carbon for threatened and disturbance-sensitive species, suggesting sensitivity of co-benefits to carbon data sources and the species considered.
5. *Policy implications.* Our work confirms the potential for environmental certification and REDD+ to work in tandem with conservation to mitigate agricultural impacts on tropical

forest carbon stocks and biodiversity, especially if this directs development to low carbon, low biodiversity areas.

Keywords: High Carbon Stock Approach; REDD+; mammals; occupancy modelling; oil palm; mitigation; certification.

Introduction

Agricultural expansion has emerged as a pervasive threat to tropical forests and biodiversity (Wilcove *et al.* 2013), and has been implicated in the loss of ~150 million ha of tropical forest over the last three decades (Gibbs *et al.* 2010; Hansen *et al.* 2013). A key driver of recent deforestation has been rising demand for cheap vegetable oil such as that from oil palm (*Elaeis guineensis*), which now covers 16 million ha across 43 countries, often at the expense of tropical forest (Pirker *et al.* 2016).

The potential economic and social benefits associated with oil palm (Potter 2015) contrast with severe and well-documented ecological impacts. Conversion of forest to oil palm plantation results in major biodiversity decline, which disproportionately affects forest specialists and species of conservation concern, resulting in assemblages dominated by disturbance-tolerant generalists (Fitzherbert *et al.* 2008; Yaap *et al.* 2010). With around 19% of land suitable for oil palm coinciding with areas of high biodiversity (Pirker *et al.* 2016), across forested Asia, Africa and South America, the full ecological impact of this commodity crop is yet to be fully realised. Mitigation measures that reconcile environmental sustainability, biodiversity conservation and production of crops such as oil palm are therefore essential in tropical regions.

Retaining native habitat in oil palm estates is known to enhance the biological value of plantation landscapes by providing ecological refugia and improved connectivity (Gillies & St Clair 2010; Struebig *et al.* 2011). However, in practice, the designation of conservation set-asides can be hindered by agricultural profitability, with income exceeding US\$11,240 ha^{-1} over a 25 year growing cycle (Fisher *et al.* 2011). Thus, conservation efforts seeking to preserve forest within plantations may be more successful when economic incentives are provided to offset the opportunity costs associated with foregoing development. Amongst several mitigation tools available, two incentive-driven policies based on carbon stocks have gained traction in tropical regions: (1) REDD+ (United Nations Reducing Emissions from Deforestation and forest Degradation) and related carbon credit schemes, and (2) improved land-use planning via commodity certification (Yaap *et al.* 2010).

REDD+, a payment for ecosystem services tool to mitigate climate change, aims to compensate stakeholders in developing nations for conservation initiatives and sustainable management practices that protect and restore the carbon sequestered by forests (Venter & Koh 2012). If REDD+ were to achieve its economic potential, payments generated could make forest conservation financially competitive compared to oil palm cultivation (Butler, Koh & Ghazoul 2009). REDD+ is also attractive to conservation because it may deliver co-benefits, whereby safeguarding high carbon areas also protects biodiversity at no additional cost (Gardner *et al.* 2012). However, this assumes spatial congruence between areas of high carbon and biodiversity. In reality it is difficult to generalise on the nature, strength and extent of these co-benefits because outcomes vary both within and between spatial scales (e.g. global: Naidoo *et al.* 2008 vs. Strassburg *et al.* 2010; national: Egoh *et al.* 2009 vs. Murray *et al.* 2015; landscape: Ruiz-Jean and Potvin, 2010 vs. Kessler *et al.* 2012). The extent to which carbon-biodiversity co-benefit assumptions hold at management unit scales appropriate to decision-makers remains an open question.

REDD+ is largely implemented at sub-national levels. While an increasing number of studies are recognising the importance of fine-scale assessments (e.g. Magnago *et al.* 2015; Beaudrot *et al.* 2016; Sollmann *et al.* 2017), most information on biodiversity co-benefits is derived from global- and national-scale studies that demonstrate overreliance on coarse-grained, secondary data sources. Carbon data are typically derived from global maps (e.g. Baccini *et al.* 2012; Avitabile *et al.* 2016), which have limited application at local-scales pertinent to management (Mitchard *et al.* 2014). Furthermore, field-based species data are widely underrepresented in the co-benefits literature due to the costs associated with biodiversity surveys in the tropics (Gardner *et al.* 2008). Researchers predominantly rely on coarse species range delineations (e.g. Murray *et al.* 2015), which are fraught with uncertainty (Rodríguez-Castañeda *et al.* 2012) and may not account for localised extirpation due to anthropogenic pressure (Harrison *et al.* 2016). Despite statistical advances that account for imperfect detection in biodiversity indices (Royle & Dorazio 2008), these methods have received relatively limited application in a co-benefits context (but see Gilroy *et al.* 2014; Sollmann *et al.* 2017), resulting in possible underestimates of species assemblages. Consequently, biodiversity co-benefits assessments at local-scales, using primary, fine-grained data would provide valuable policy insights.

While the potential importance of REDD+ cannot be overstated, agricultural certification schemes show promise to ensure sustainable practices as companies benefit from greater access to environmentally conscious markets and increased price premiums of certified products (Yaap *et al.* 2010). The Roundtable on Sustainable Palm Oil (RSPO) is often seen as an exemplar scheme within the agricultural sector, currently certifying 21% of the global palm oil market across 2.48 million ha of land (RSPO 2017). RSPO certification prohibits the conversion of high conservation value habitat in oil palm estates. However, associated assessment procedures have attracted criticism, raising concerns that current methodologies do not afford adequate biodiversity protection (Yaap *et al.* 2010; Edwards, Fisher & Wilcove 2012).

The High Carbon Stock (HCS) Approach has emerged as a land-use planning tool to demarcate conservation priority areas based on carbon value, and is being explored within the RSPO architecture and that of other certification schemes. The HCS methodology seeks to conserve biodiverse and ecologically functional forest networks within agricultural concessions by directing conversion towards heavily degraded land of low carbon value

(Rosoman *et al.* 2017). This is achieved by stratifying land into discrete classes according to vegetation density and structure, which are then adopted as proxies for above-ground carbon stocks and assumed to support varying levels of biodiversity. These strata are subsequently validated using ground-based above-ground carbon estimates, before land parcels are prioritised for conversion based on area and connectivity (Rosoman *et al.* 2017).

The HCS Approach has attracted widespread interest amongst agricultural industries with 10 million ha of land being evaluated across five oil palm producing countries (Rosoman, unpublished data). As a model scheme, the successful integration of the HCS Approach within the RSPO framework may encourage uptake across other certifiable agricultural commodities, such as rubber and soya. Nevertheless, the extent to which HCS strata correspond to areas of high biodiversity value is dependent on the accurate partitioning of vegetation classes according to their carbon value, as well as the underlying association between carbon and biodiversity. Before the HCS Approach is formally adopted within certification standards, these assumptions should be tested to understand the conservation merit of the tool.

Here, we determine the effectiveness of incentive-driven carbon-based mechanisms to safeguard biodiversity, and provide the first validation of both the carbon and biodiversity credentials of the HCS land-use planning tool. Our appraisal focuses on a landscape undergoing conversion from forest to oil palm in Borneo, a region characterised by high deforestation and forest degradation (Gaveau *et al.* 2014; Struebig *et al.* 2015) that is typical of most HCS applications. First, we validate the accuracy of the HCS classification procedure and quantify the biodiversity value of the vegetation strata. We then assess the potential for REDD+ to deliver biodiversity co-benefits using primary and high-resolution data sources. To assess the influence of spatial grain on the nature of co-benefit relationships, we compare global- and local-scale measures of carbon. Throughout, we employ biodiversity indices that explicitly account for imperfect detection to provide a more accurate representation of species assemblages than simple species counts. Our work evaluates the extent to which policy options that attach greater economic significance to conservation protect vulnerable tropical forests and safeguard biodiversity.

Materials and Methods

Study system

The study was conducted over a 13,153 ha development area comprising the Stability of Altered Forest Ecosystems project (SAFE; www.safeproject.net) and surrounding plantations in Kalabakan Forest Reserve, Sabah, Malaysian Borneo (4° 46'N, 116° 57' E; Fig. 1). SAFE is a landscape-scale forest modification experiment (Ewers *et al.* 2011) comprising highly disturbed lowland and hill dipterocarp forest that was logged multiple times between 1978 and 2008. The wider landscape includes forest in Brantian-Tatulit Virgin Jungle Reserve, twice-logged forest in Ulu Segama Forest Reserve, and plantations (primarily oil palm).

HCS classification and validation

The HCS Approach uses high-resolution remotely-sensed images to stratify concessions into six vegetation classes, each with unique structural characteristics (in descending order of carbon value): (1) 'High Density Forest'; (2) 'Medium Density Forest'; (3) 'Low Density Forest'; (4) 'Young Regenerating Forest'; (5) 'Scrub'; and, (6) 'Open Land' (see Appendix S1 in Supporting Information). In practice, the High, Medium and Low Density Forest strata are aggregated as 'Dense Forest' and earmarked for conservation. Young Regenerating Forest can also comprise valuable carbon stocks and is also spared from development. The threshold for allocating land for production rests on distinguishing these strata from heavily degraded Scrub and Open Land. Therefore, we mapped Dense Forest, Young Regenerating Forest, Scrub and Open Land as separate classes.

All spatial data processing was implemented in ArcGIS 10.2.1 (ESRI). We used Landsat 8 and SPOT5 satellite imagery (15 m and 2.5 m resolution respectively; temporal range: 2012-2014) to stratify forest habitat using HCS assessment protocols (see Appendix S1). Multiple data sources were chosen to minimise classification difficulties associated with cloud cover and haze. We undertook a supervised classification of satellite images, supplemented with visual interpretation techniques to correct for the potentially confounding effects of topographic shadow (Wulder *et al.* 2004). The resulting classes were then calibrated using above-ground carbon values derived from forest inventory data (N=139), collected as part of the core SAFE monitoring programme. These data conform to standardised forest inventory protocols (http://www.rainfor.org), calculating carbon as a function of above-ground biomass (trees >10 cm DBH) using an established pantropical algorithm (Chave *et al.* 2014). Resulting HCS classes were validated using independently derived carbon estimates (Pfeifer *et al.* 2016; see Appendix S2).

Camera-trap sampling of medium-large mammals

We delineated terrestrial mammal diversity as these taxa are consistently prioritised in policy, land-use planning and certification schemes. Remotely-operated digital cameras (HC500 Hyperfire, Reconyx, Wisconsin, U.S.A.) were deployed at 130 locations across the landscape between May and September 2015 (Fig. 1). These locations were separated by a mean distance of 1.4 km and distributed across an elevational gradient (mean=376 m.a.s.l.; range=64-735 m.a.s.l.). Accounting for theft, vandalism and malfunction, data were retrieved from 121 locations. We stratified our sampling according to HCS strata, while capturing the broader heterogeneity of the landscape using reference classes (protected ‘Continuous Logged Forest’ and well-established ‘Oil Palm Plantation’) for comparative purposes. As the extent of Scrub and Open Land was relatively low compared to the other classes, these strata were pooled into a single class, ‘Developed Land’, for biodiversity analyses: Continuous

Logged Forest, *N*=27; Dense Forest, *N*=23; Young Regenerating Forest, *N*=16; Developed Land, *N*=26; and, Oil Palm Plantation, *N*=23.

Due to the number of cameras available, data collection was completed over two rotations, each comprising 65 locations. Single units were deployed for 42 consecutive nights per location, yielding a total survey effort of 4,669 camera nights. Cameras were positioned at a standardised height of 30cm, on low resistance travel routes (e.g. riparian areas, logging roads, skid trails) and off-trail to account for inter- and intra-specific differences in habitat use.

Prior to analyses, all images that could not be identified to species level were discarded (blurred images and photos of non-target species, equating to 17.6% of 142,294 images). Species encounters were considered independent events if they contained different individuals or were separated by a period of >60 minutes. A detection matrix was developed for each species, whereby 42-day sampling periods were divided into six, seven-day temporal replicates. Any camera site active for fewer than seven days was excluded from analysis, leaving 115 analytical units each with 2-6 replicates.

Modelling framework

We employed hierarchical Bayesian multi-species occupancy modelling (Dorazio & Royle 2005) to estimate species diversity from camera data. Hierarchical models permit the separation of ecological and sampling processes that may influence the data (Gelman & Hill 2007). In the context of occupancy, this means that true absences can be differentiated from non-detection by explicitly defining models for occurrence and detection.

Multi-species occupancy models take single-species occupancy detection models as building units (Guillera-Arroita 2016). Following Zipkin *et al.* (2010), we denote the occurrence of species *i* at site *j* by the binary variable $z_{i,j}$ (1=species presence; 0=species not detected). The occurrence state is described as the outcome of a Bernoulli process, $z_{i,j} \sim Bern(\psi_{i,j})$, where $\psi_{i,j}$ denotes the occurrence probability. The true occurrence state is imperfectly observed, so the model includes a second Bernoulli process, $x_{ijk} \sim \mathrm{Bern}(p_{i,j,k}{*}z_{i,j})$, where $x_{i,j,k}$ is the observed detection/non-detection data, *k* is the survey replicate and $p_{i,j,k}$ represents the corresponding detection probability conditional to species presence. The product $p_{i,j,k}{*}z_{i,j}$ reflects that detection at sites where the species is present ($z_{i,j}$=1) happens with detection probability $p_{i,j,k}$, and that detection is not possible at sites where the species is absent ($z_{i,j}$=0). We assume that variation in the abundance of a species across sampling sites does not affect species detection probabilities $p_{i,j,k}$ (Royle & Dorazio 2008).

Occurrence and detection models for individual species were linked via a hierarchical component that modelled regression coefficients as realisations from a common community-level distribution with (hyper)parameters. Under this approach, species are assumed to respond to environmental conditions in a similar, but not identical, manner. Derived species estimates are, therefore, a compromise between individual response and the average response of the community. This results in shrinkage (the borrowing of information by individuals across the community), which has been shown to improve estimation precision, particularly for rare or elusive species that are infrequently detected during surveys (Pacifici *et al.* 2014). We report (hyper)parameters to provide an indication of community-level responses to covariates.

Spatial concordance between HCS classes, carbon and biodiversity

To assess how mammal community representation could vary according to policy relevant carbon variables, we described occupancy and detectability using three models:

Model 1: $\mathrm{logit}(\psi_{i,j}) = \mu_{(i)HCS\ Class(j)}$

$\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Model 2: $\mathrm{logit}(\psi_{i,j}) = \mu_i + \alpha_{1i}CC1000_j + \alpha_{2i}CC1000^2{}_j$

$\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Model 3: $\mathrm{logit}(\psi_{i,j}) = \mu_i + \alpha_{1i}CC25_j + \alpha_{2i}CC25^2{}_j$

$\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Occupancy and detection probabilities were modelled with intercepts on the logit scale specific for each species and HCS class (Model 1). Continuous measures of carbon, including quadratic terms, were incorporated into occurrence models alongside species-specific intercepts to determine the potential for REDD+ to deliver biodiversity co-benefits (Models 2 and 3). These carbon data were from two sources: coarse-grained 1 km resolution global maps ('CC1000'; Avitabile *et al.* 2016), and 25 m resolution maps derived from biomass estimates from the study site linked to Rapideye^{TM} satellite imagery ('CC25'; Pfeifer *et al.* 2016; for a subset of sites not obscured by cloud cover, N=66). HCS-specific intercepts were retained in the detection components of Models 2 and 3 as they broadly describe the influence of habitat type. We chose to model HCS, CC1000 and CC25 separately due to strong evidence of collinearity between these variables ($|r \geq| 0.7$). Continuous carbon and HCS covariates were calculated as average values extracted from a 100 m buffer (ca. 3.1 ha area) around each camera location. Covariates were centred and standardised prior to analysis. We found no evidence of spatial autocorrelation in the detection dataset (Moran's $I=0.08 \leq P \leq 0.92$), indicating that assumptions of independence in occupancy modelling were met (Royle & Dorazio 2008).

The models were fitted to include inference about the number of potential species not observed during sampling (Dorazio & Royle 2005). To achieve this, detection data were augmented with 50 hypothetical species, with all-zero encounter histories, following Royle *et al.* (2007). Predicted species richness was calculated for each camera location allowing for post-hoc comparison between HCS classes.

We compared mammal richness between HCS classes using a Bayesian linear model. We follow a two-stage analytical approach described by Kéry & Royle (2015), whereby estimation uncertainty associated with predicted species richness is propagated by the inclusion of an additional residual component into the model (standard deviation of richness estimates from the hierarchical Bayesian multispecies occupancy models). In principle, parameter estimates could be derived directly from a single model, but this resulted in much lower precision. Since land-use change disproportionately affects species of conservation concern and disturbance-sensitive forest specialists, we report our findings for: (1) all species; (2) threatened species (IUCN red-listed as vulnerable, endangered or critically endangered); (3) non-threatened species (IUCN least concern); (4) disturbance-sensitive species (listed as medium-high sensitivity according to Wilson *et al.* 2010), and; (5) disturbance- tolerant species (low sensitivity; see Appendix S3 for species-specific group assignment).

Biodiversity co-benefits of REDD+

To assess the potential biodiversity co-benefits of REDD+, we extracted predicted species richness values from the hierarchical occurrence model and explored their association with carbon. To determine if these relationships were grain-dependent, we derived carbon data from coarse- (CC1000, 1 km) and fine-grained (CC25, 25m) satellite-derived datasets.

Associations between levels of mammal species richness and carbon at the two different spatial resolutions, and for *a priori* groupings, were assessed via Bayesian two-stage linear models incorporating quadratic terms.

All analyses were conducted in WinBUGS version 1.4.3 through R version 3.3.0 using the package "R2WinBUGS" (Sturtz, Ligges & Gelman 2005); see Appendix S4 for further information on model specification and predictive performance checks.

Results

Camera-trapping yielded 3,237 independent capture events of 28 species, comprising 24 genera distributed across 16 families. In contrast, our models predicted 30.6 species across the landscape (95% Bayesian Credible Interval, BCI=28.0-37.0), suggesting that few mammal species were missed by our sampling. The effect of imperfect detection was more apparent at the camera-trap level, where predicted richness was consistently greater than observed richness (mean=4.35, range=0.02-12.26).

Spatial concordance between biodiversity and HCS classes

Hierarchical Bayesian multi-species models indicated reduced mammalian occupancy in the low carbon strata (Fig 2). Community (hyper)parameters revealed comparable estimates of mean occupancy between Continuous Logged Forest (mean=0.49, BCI=0.32-0.63), Dense Forest (0.36, 0.17-0.60) and Developed Land (0.32, 0.12-0.56). However, community occupancy was low in Young Regenerating Forest (0.23, 0.11-0.45) and Oil Palm plantation (0.05, 0.01-0.31).

Our models demonstrated species-specific associations with HCS classes (Fig. 2). For example, occupancy estimates indicate that *Sus barbatus* Müller (bearded pig) and *Macaca nemestrina* Linnaeus (southern pig-tailed macaque) were common in Continuous Logged Forest (*S. barbatus*: 0.71, 0.53-0.85; *M. nemestrina*: 0.71, 0.53-0.86) and Dense Forest (*S. barbatus*: 0.74, 0.53-0.90; *M. nemestrina*: 0.74, 0.52-0.92), with occupancy of *M. nemestrina* also high in Developed Land (0.71, 0.51-0.87). Conversely, species such as *Tragulus kanchil* Raffles (lesser mouse-deer: 0.20, 0.08-0.40) and *Helarctos malayanus* Raffles (sun bear: 0.21, 0.08-0.44) were rare in Dense Forest. In the Oil Palm plantation five species demonstrated low occupancy, four of which were threatened taxa (Fig. 2e). Species-specific detection summaries for the HCS model are available in Appendix S5.3.

Extremes in predicted species richness were identified between the reference habitat classes (Fig. 3); Continuous Logged Forest was found to have the highest richness (14.12, 13.20-15.07), while Oil Palm plantation supported the most depauperate community (4.54, 3.58-5.52). Estimates of total richness were similar between the Dense Forest (11.38, 10.30-12.51) and Developed Land (10.63, 9.52-11.02), while the number of species found in Young Regenerating Forest was significantly lower (8.15, 7.13-9.27). These patterns were consistent across groupings.

Biodiversity co-benefits of REDD+

The global- versus local-scale carbon values at camera locations were inconsistent. The 1 km resolution global data tended to produce much higher carbon estimates compared to those derived from higher resolution imagery (global mean=152.23 t C ha^{-1}, range=50.39-236.53; local mean=22.95t C ha^{-1}, range= 0.31-94.98). Carbon values from the global- and local-scale maps corresponded broadly with biomass values derived from field inventories (N=164; r_s=0.55 global; r_s=0.51; local-scale). However, local-scale carbon estimates were found to be much more precise (RMSE: local=29.05 t C ha^{-1}; global=130.94 t C ha^{-1}). We found no influence of continuous measures of carbon on mammalian occupancy using either global- or local-scale carbon data (see Appendix S5.4/S5.6). Species-specific detection summaries for the continuous carbon models are available in Appendix S5.5/S5.7.

Grain-dependency between the association of carbon and mammal richness was evident. Using global carbon data no relationship between the two variables was apparent, regardless of the species grouping (Figs. 4a,c,e). However, at the local-scale, positive associations with carbon were identified for threatened and disturbance-sensitive species (Figs. 4d,f). This trend was not consistent across groupings with all species, non-threatened and disturbance-tolerant taxa demonstrating no relationship with carbon (Figs. 4b).

Discussion

The extent to which biodiversity and carbon spatially align is fundamental to our understanding of whether carbon-based policies can deliver positive results for conservation in human-modified tropical landscapes. Among the few studies that assess biodiversity and carbon covariance using primary and/or high-resolution data (Magnago *et al.* 2015; Sollmann *et al.* 2017), ours is the first to verify an association within a tropical landscape mosaic undergoing certification. We show that the strength, nature and extent of biodiversity co-benefits are dependent on how carbon stocks are characterised (i.e. categorical or continuous), the spatial resolution of the carbon data employed, and the species considered.

Contribution of the HCS approach to biodiversity conservation

When evaluating community-level responses to HCS classes, we found comparable levels of mammalian occupancy between Continuous Logged Forest, Developed Land and Dense Forest, while occupancy was reduced in Young Regenerating Forest and Oil Palm. Occupancy can be a viable surrogate for abundance under certain conditions (Efford & Dawson 2012). Our results could therefore suggest the persistence of certain mammal species at lower densities within carbon-poor classes, which confirms previous reports of reduced mammalian abundance in impoverished forest habitats (Bicknell *et al.* 2014).

Occupancy and species richness estimates for the total mammal community highlight comparable levels of biodiversity between the Dense Forest and Developed Land classes, supporting previous studies that demonstrate the conservation value of heavily degraded forest for a range of taxonomic groups (Struebig *et al.* 2013; Edwards *et al.* 2014; Wearn *et al.* 2016). However, we advise caution when interpreting the biodiversity value of Developed

Land, which may not be fully realised for long-lived mammal species until extinction debts, owed to a legacy of disturbance, are repaid (Rosa *et al.* 2016). The biodiversity value of Developed Land that we found is also crucially dependent on the low levels of hunting at our study site. Hunting has been shown to have substantial impacts on mammal communities elsewhere in the region (Harrison *et al.* 2016). Our study adds to the growing body of evidence that shows oil palm plantations to have depauperate mammalian communities, comprised of few generalist species occurring at low densities (Yue *et al.* 2015; Wearn *et al.* 2016). While our data generally conform to the pattern of declining biodiversity relative to structural complexity, Young Regenerating Forest demonstrated comparably lower biodiversity value regardless of the metric examined. Given the difficulties in differentiating between the Young Regenerating Forest and Scrub strata (see Appendix S2), we believe this finding reflects ambiguities in the HCS classification process.

While our analyses demonstrate differences in conservation value between the HCS strata, the ability of land parcels to support biodiversity will also be limited by habitat fragmentation effects. This process is pervasive in human-modified landscapes, and has contributed to species richness declines of up to 75% (Haddad *et al.* 2015). While efforts to account for habitat fragmentation in the HCS prioritisation process are underway, a definitive toolkit is still in development. Therefore, while we have not explicitly accounted for the independent and interactive effects of fragmentation metrics (e.g. patch size, isolation and connectivity) on biodiversity in our analyses, it warrants further consideration as the HCS Approach gains traction across the agricultural sector.

Contribution of REDD+ to biodiversity conservation

Our results indicate that spatial concordance between biodiversity and carbon can be overlooked if the latter is calculated via low-resolution data. Using carbon information from a commonly utilised global dataset, no association with mammal diversity was identified, suggesting that REDD+ initiatives would not provide biodiversity co-benefits in heavily degraded landscapes. However, when high-resolution carbon maps were employed, a positive relationship with species richness was found for threatened and disturbance-sensitive taxa, demonstrating the value of REDD+ to those species most vulnerable to land-use change. When all species were considered these relationships were obscured by non-threatened, generalist species that are resilient to disturbance. Our findings provide further support for biodiversity co-benefits in agricultural land-use mosaics, as previously demonstrated for a range of taxonomic groups (birds and dung beetles: Gilroy *et al.* 2014; amphibians: Basham *et al.* 2016), while highlighting important nuances in the carbon-biodiversity relationship. We advocate the use of fine-grained, field-validated carbon data when determining the extent and nature of biodiversity co-benefits and suggest an emphasis on species of conservation concern.

Our detailed landscape appraisal is the first to identify biodiversity co-benefits for mammals, a taxonomic group that occupies key trophic positions in tropical forest ecosystems and is frequently prioritised by conservation initiatives. Previous studies have proved less convincing. Across a pantropical network of sites, Beaudrot *et al.* (2016) found no association between forest carbon and three measures of mammalian diversity. However, by aggregating fine-scale biomass data at the site level, the authors compromised the resolution of their data, potentially obscuring intra-site relationships that would be more representative of a REDD+ management unit. Similarly, Sollmann *et al.* (2017) found little correspondence between above-ground biomass and mammal occupancy in a certified forest reserve in Malaysian Borneo, despite adopting a comparable methodology to the present study. Contrasting findings may be attributed to spatial variability in hunting pressure.

Implications for HCS implementation

Given that RSPO members have little obligation to protect highly disturbed forest of uncertain conservation value, the HCS Approach is a useful tool to designate high carbon, high biodiversity land in areas that would otherwise be converted to plantation. High Carbon Stock areas can also contribute to national and regional spatial planning initiatives that mitigate the effects of environmental change on tropical biodiversity by promoting connectivity in human-modified landscapes (Struebig *et al.* 2015).

Under current HCS guidelines, 62% (8,150 ha) of the remaining forest in the study system would qualify for protection from agricultural conversion, equating to a net gain of 15.72 t C ha^{-1} (see Appendix S2) at an annual opportunity cost of US$3.7 million (based on Fisher *et al.* 2011). The success of certification depends on financial returns from sustainable production offsetting the economic losses associated with sustainable practices. While the zero deforestation principle of the HCS Approach aligns with consumer goods forum calls to eliminate deforestation from global commodity supply chains, reducing reputational risks, it has been considered economically restrictive for nations with extensive pristine forests (Senior *et al.* 2015), indicating that current guidelines may be too stringent. Strata such as Young Regenerating Forest might, therefore, end up being earmarked for conversion rather than conservation in some circumstances. However, with the conservation value of this stratum likely to increase as forests regenerate, the impact of such a policy change needs to be fully evaluated. Carbon neutral conversion represents an alternative to the current emphasis on zero deforestation. While the specific carbon threshold for delineating forest has proved contentious, Pirker et al. (2016) for example, demonstrated that protecting areas exceeding 100 t C ha^{-1} would safeguard 73% of the climatically suitable area for oil palm expansion. Ultimately, compromise begets progression, and while the industry should still strive for zero deforestation, carbon neutral conversion may be more viable in specific countries and circumstances, if agricultural expansion, economic development and forest conservation are to be reconciled.

Implications for REDD+ implementation

The considerable enthusiasm for biodiversity co-benefits often obscures the fact that REDD+ is fundamentally a carbon-orientated mechanism with limited scope for increasing biodiversity conservation (Venter *et al.* 2013). While we provide further evidence to verify biodiversity co-benefits in human-modified landscapes it is unlikely that REDD+ will be economically viable in carbon-poor environments. Given current economic pressures and weak carbon markets, REDD+ projects currently prioritize carbon gains at low operating costs. Acting optimally for carbon will therefore place increasing agricultural pressure on secondary or degraded forests that are comparatively low in carbon value but retain appreciable levels of biodiversity (Edwards *et al.*2014). Conservationists must ensure that safeguards are in place to support vulnerable species in disturbed habitats that fall beyond the remit of carbon-financing mechanisms.

The viability of REDD+ in human-modified landscapes is further hindered by the profitability of oil palm. Under current voluntary markets avoided deforestation through REDD+ was found to have an opportunity cost of \$3221–8636 ha^{-1} over a 30 year period when compared to potential profits generated from oil palm (Butler, Koh & Ghazoul 2009). For REDD+ to be an economically competitive alternative to oil palm cultivation, climate change policies must legitimise REDD+ carbon credits to facilitate their trade on financially lucrative compliance markets (Butler, Koh & Ghazoul 2009).

Conclusions

Our work highlights the potential for environmental certification and REDD+ financing mechanisms to work in tandem with conservation to mitigate the effects of agricultural expansion on tropical forest carbon stocks and biodiversity. REDD+ is well placed if it prioritises large tracts of contiguous forest, especially if commitments to carbon stock enhancement safeguard degraded forest of biological value. Certification schemes, coupled with land-use planning tools such as HCS, can help secure sizeable forest patches of high conservation value in agricultural estates, and offer a further safeguard to minimise encroachment. Conservationists should capitalise on both types of carbon-based policy to maximise the potential for developed lands to provide ecological stepping stones for threatened wildlife between a network of high-carbon, high-biodiversity areas.

Author Contributions

NJD, MJS and ZGD conceived the ideas and designed the methodology; NJD and ELB collected and processed data, adapting scripts developed by ORW; MP and NJD provided carbon data; NJD and GGA undertook analyses; NJD, MJS and ZGD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

In accordance with NJD's studentship, data collected in fulfilment of this manuscript (forest inventory data and detection histories for 28 mammal species) will be uploaded to the NERC Environmental Information Data Centre.

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Data Sources

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Figures

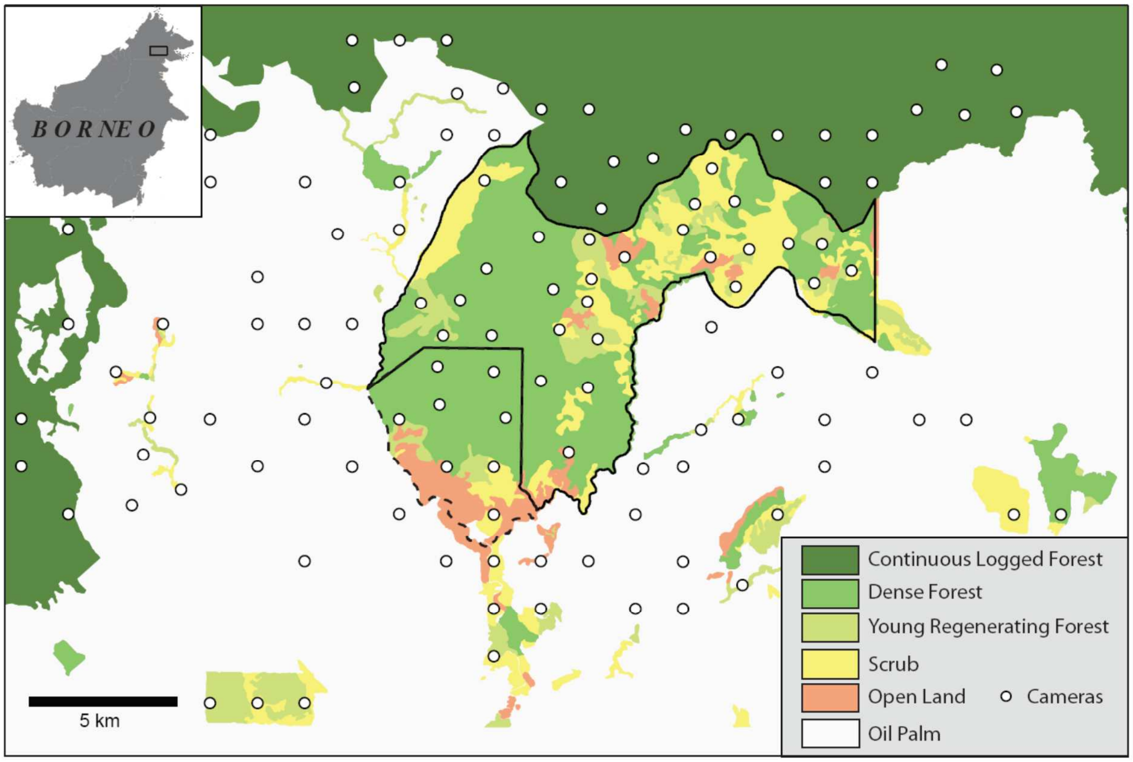


Figure 1: HCS classification of the study landscape in Sabah, Borneo. Forest cover was delineated into four strata on the basis of vegetation density (Dense Forest, Young Regenerating Forest, Scrub, Open Land) and supplemented with two reference classes (Continuous Logged Forest, Oil Palm) to act as forest and agricultural controls. Points indicate camera-trap locations (*N*=115).

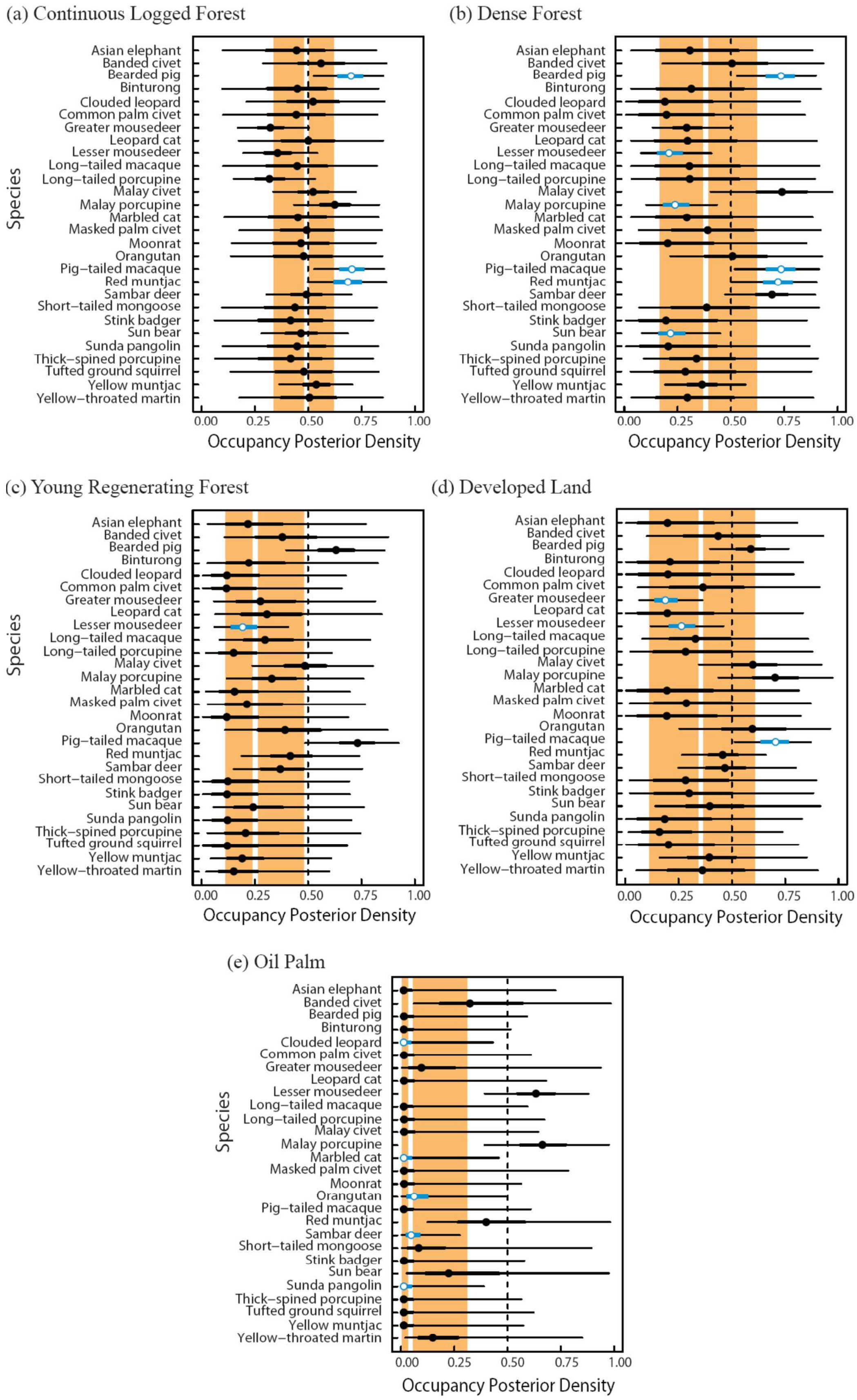

(a) Continuous Logged Forest
(b) Dense Forest
(c) Young Regenerating Forest
(d) Developed Land
(e) Oil Palm
Species
Asian elephant
Banded civet
Bearded pig
Binturong
Clouded leopard
Common palm civet
Greater mousedeer
Leopard cat
Lesser mousedeer
Long−tailed macaque
Long−tailed porcupine
Malay civet
Malay porcupine
Marbled cat
Masked palm civet
Moonrat
Orangutan
Pig−tailed macaque
Red muntjac
Sambar deer
Short−tailed mongoose
Stink badger
Sun bear
Sunda pangolin
Thick−spined porcupine
Tufted ground squirrel
Yellow muntjac
Yellow−throated martin
0.00
0.25
0.50
0.75
1.00
Occupancy Posterior Density

Figure 2: Caterpillar plots of outputs from the hierarchical Bayesian multi-species occupancy model. Graphs show species-specific baseline occupancy estimates (including 95% Bayesian Credible Interval) relative to habitat class (a-e). Mean community (hyper)parameter occupancy values and their associated credible intervals are represented in the shaded (orange) background to each plot. Species exhibiting deviations from a baseline occupancy of 0.5 are shown with shaded (blue) bars.

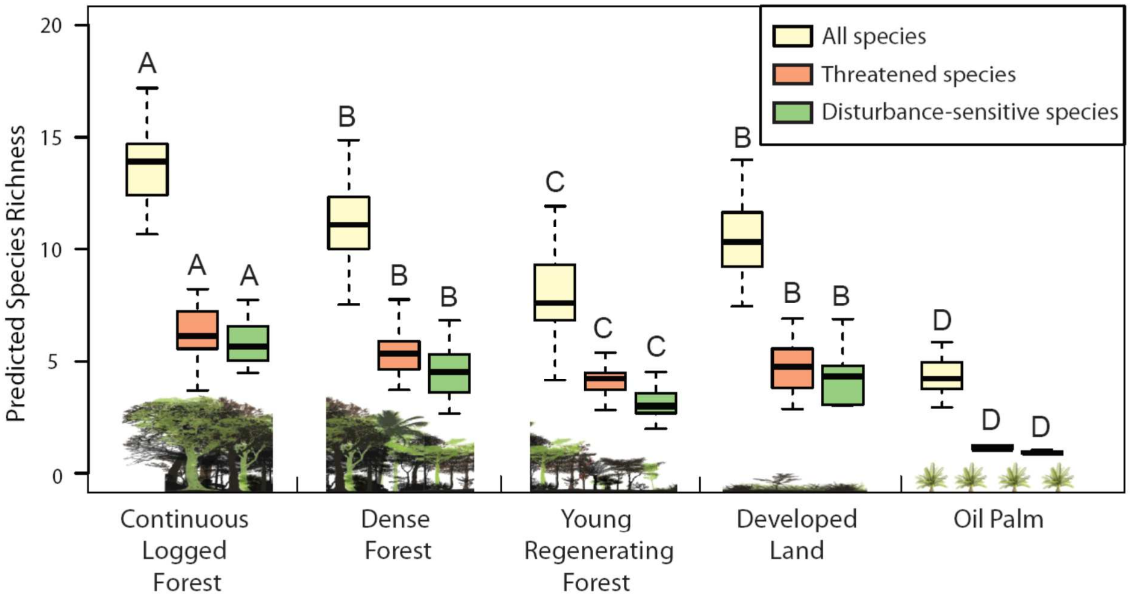


Figure 3: Boxplots demonstrating species richness in relation to habitat class for: (1) all species; (2) threatened species (IUCN red-listed as vulnerable, endangered or critically endangered); (3) disturbance sensitive species. Colour coded capitalised letters indicate significant differences between habitat classes within broader species groupings (different letters suggest significance while identical letters indicate non-significance).

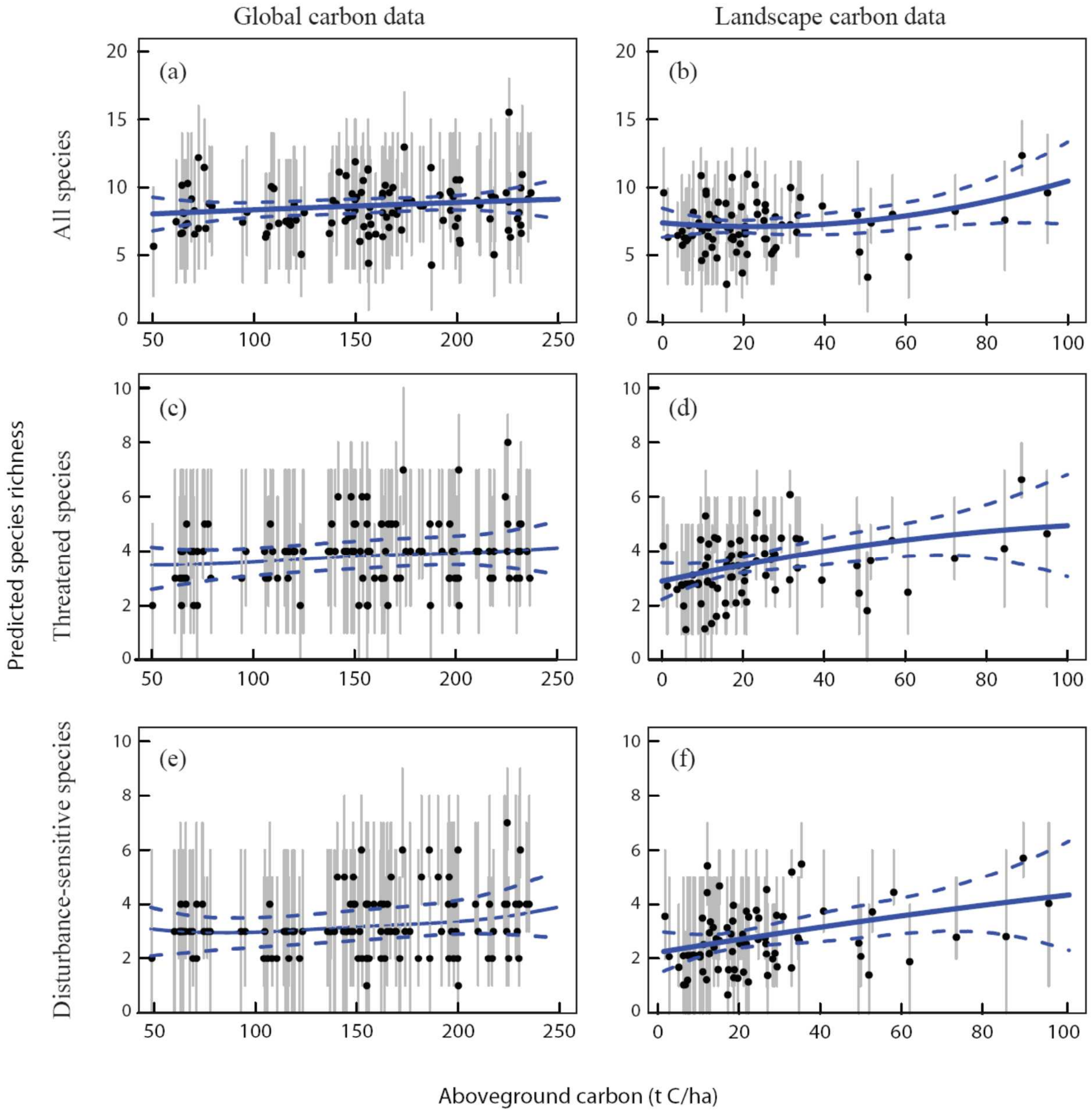
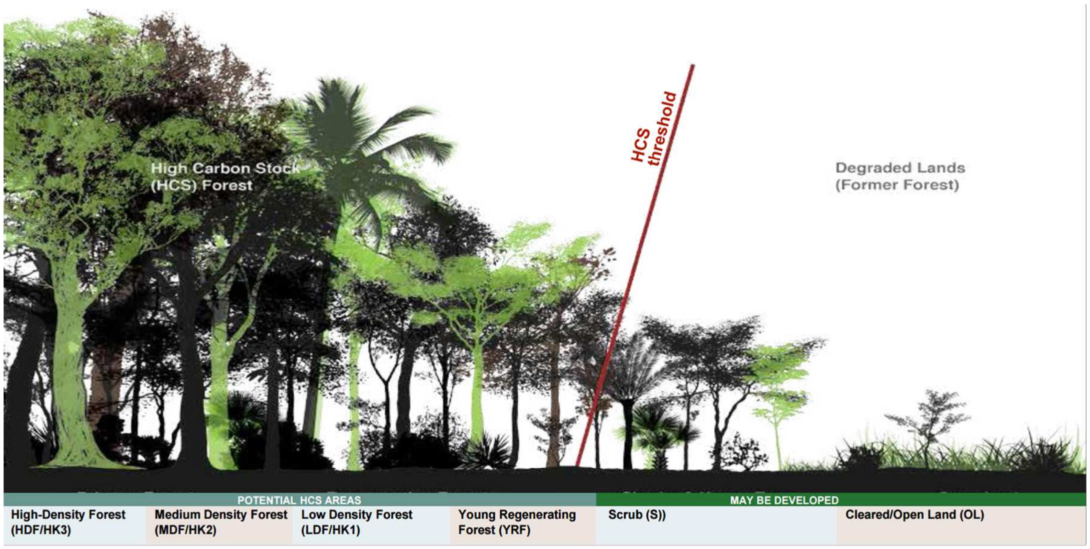


Figure 4: Bayesian linear model outputs demonstrating significant positive relationships between predicted species richness and carbon stock estimates derived from a 25 m resolution local dataset (d: threatened species; f: disturbance-sensitive species). All other associations presented were found to be non-significant. Blue lines indicate predicted mean posterior distribution values, dashed lines refer to predicted 95% Bayesian Credible Intervals and vertical grey lines highlight the error associated with each estimated species richness value.

Supporting Information S1: Definitions of strata delineated by the High Carbon Stock (HCS) Approach (Rosoman *et al.* 2017)



The High Carbon Stock (HCS) methodology seeks to conserve biodiverse and ecologically functional forest networks within agricultural concessions by directing conversion towards heavily degraded land of low carbon value (Greenpeace International, 2013). This is achieved by using high resolution satellite imagery to stratify the landscape into discrete strata according to vegetation density and structure, which are then adopted as proxies for above-ground carbon stocks and assumed to support varying levels of biodiversity. The HCS Approach recognises six distinct vegetation classes (detailed below), each with unique structural characteristics.

Habitat Classes		**Analytical Classification**
	**Continuous Logged Forest** contains similar structural properties to Dense Forest. This class is not considered for development due to its protected status. This class was incorporated as a control against which carbon and biodiversity of other strata could be compared.	Continuous Logged Forest
	**Dense Forest** comprises three classes, high/medium/low density forest, and refers to closed-canopy natural forest characterised by: • >50% canopy cover; • Significant proportion of trees >30cm dbh; • Dominated by climax community trees. Development status: **Conserved**	Dense Forest
	**Young Regenerating Forest** is highly disturbed remnant forest characterised by: • 30-40% canopy cover; • Significant proportion of trees between 10 and 30cm dbh; • Dominated by pioneer tree species.	Young Regenerating Forest

	Development Status: **Conserved**	
	**Scrub** refers to land that has previously been cleared but experienced some regeneration. It is characterised by: • <25% canopy cover; • Dominated by tall grasses and ferns but containing some pioneer species. Development status: **Converted**	Developed Land
	**Open Land** represents a post-clearance habitat dominated by grass or crops with few woody plants. Development status: **Converted**	
	**Oil palm** (*Elaeis guineensis*) represents the final phase of land-use change in the study system when natural forest habitat has been displaced by commodity agriculture. This class was incorporated as a control against which carbon and biodiversity of other strata could be compared.	Oil Palm Plantation

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Supplementary Information S2: Validating the carbon credentials of the High Carbon Stock (HCS) Approach

Rationale

The High Carbon Stock (HCS) land-use planning tool is gaining traction in oil palm certification as companies seek to honour their commitments to sustainable production. However, there is a paucity of information in the scientific literature to validate the accuracy of the HCS stratification process to delineate high carbon conservation priority areas. Here, we provide an assessment of the carbon credentials of the HCS toolkit.

Methods and Materials

HCS classes were delineated across the Stability of Altered Forest Ecosystems (SAFE) Project study site using standardised protocols (HCS Steering Group 2015). These strata were validated using independent high-resolution satellite data of above-ground biomass (RapidEye, 5 m resolution; temporal coverage 2012-2013; Pfeifer *et al.* 2016), across cloud-free areas of the study landscape. Carbon stocks were calculated using a conversion factor of 0.47 (Martin & Thomas 2011), and values were extracted from 200 random points per HCS class (*N*=800) separated by a minimum distance of 50 m. A Bayesian linear model was employed to determine the distribution of carbon values across classes, thus testing the accuracy of the classification process.

Results

Following our land-cover stratification, 62 % of the remaining forest in the study landscape, comprising 6,031 ha of High Carbon Stock forest and 2,120 ha of Young Regenerating Forest, would qualify for conservation under current HCS guidelines (Fig. 1). The classes appropriately reflected modelled carbon content, which was greatest for Dense Forest (45.86t C ha^{-1}, 95% BCI=42.32-49.44) and significantly lower in the other classes (Young Regenerating Forest: 31.30t C ha^{-1}, 27.85-34.80; Scrub: 29.62 t C ha^{-1}, 26.19-33.05; Open Land: 16.09t C ha^{-1}, 12.59-19.62). Pairwise comparisons of carbon content revealed significant differences between all habitat classes with the exception of Young Regenerating Forest and Scrub. On average, land earmarked for conservation contained 41% more carbon than that designated for development (i.e. Scrub and Open Land strata combined) under the HCS Approach, equating to a net value of 15.72 t C ha^{-1} across the landscape.

Discussion

There is a general consensus in the scientific literature that field-derived carbon estimates are laborious, costly and time consuming to implement over large spatial scales (Gibbs *et al.* 2007; Petrokofsky *et al.* 2012). Consequently, there is a need for cost-effective, efficient protocols that can be followed to delineate high carbon stock areas. Our results provide empirical support for the prioritisation of high carbon stock areas for conservation in the humid tropics via the HCS Approach. High Carbon Stock Forest (Dense Forest and Young Regenerating Forest combined) was estimated to store 45.86 t C ha^{-1}, which falls within the range of estimates for highly degraded forest habitat in Borneo (40-100 t C ha-1; Lucey *et al.* 2014), but is considerably lower than pristine lowland tropical forest (477 t C ha-1; Budiharta *et al.* 2014).

Our analyses demonstrate that carbon stocks are similar between land classified as Young Regenerating Forest and Scrub, suggesting that the HCS toolkit cannot reliably distinguish between these strata. This has direct implications for conservation, as Young Regenerating Forest should be retained within the landscape, yet Scrub can be developed. This reflects the concerns of Annisa (2014), who stressed the difficulties associated with partitioning heterogeneous vegetation into categorical carbon classes, as habitat transitions are gradual and not discrete. While the initial version of the HCS toolkit offered a clear carbon threshold value (35 t C ha^{-1}) with which to differentiate between strata suitable for development and conservation, it has been omitted in subsequent revisions, introducing subjectivity and misinterpretation into the classification process. We recommend the adoption of explicit carbon threshold values defining each HCS stratum, to improve calibration and thus classification accuracy. Threshold values would make the HCS methodology more transparent, objective and comparable across concessions. In practice, the thresholds should be regionally-specific, accounting for the recognised geographic variation in standing carbon stock across tropical forests globally (Banin *et al.* 2014; Avitabile *et al.* 2016).

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Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I. *et al.* (2016) Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote Sensing of Environment,* **176,** 84-97.

Supplementary Information S3: Species assignment to grouping categories

Species	**Threat Status**	**Disturbance Response**
Asian Elephant	Threatened	Sensitive
Banded Civet	Threatened	Sensitive
Bearded Pig	Threatened	Tolerant
Binturong	Threatened	Sensitive
Clouded Leopard	Threatened	Sensitive
Common Palm Civet	Non-threatened	Tolerant
Greater Mousedeer	Non-threatened	Sensitive
Leopard Cat	Non-threatened	Tolerant
Lesser Mousedeer	Non-threatened	Sensitive
Long tailed Macaque	Non-threatened	Tolerant
Long tailed Porcupine	Non-threatened	Tolerant
Malay Civet	Non-threatened	Tolerant
Malay Porcupine	Non-threatened	Tolerant
Marbled Cat	Threatened	Sensitive
Masked Palm Civet	Non-threatened	Tolerant
Moonrat	Non-threatened	Sensitive
Orangutan	Threatened	Sensitive
Pig tailed Macaque	Threatened	Tolerant
Red Muntjac	Non-threatened	Tolerant
Sambar Deer	Threatened	Sensitive
Short tailed Mongoose	Non-threatened	Tolerant
Stink Badger	Non-threatened	Tolerant
Sun Bear	Threatened	Sensitive
Sunda Pangolin	Threatened	Tolerant
Thick spined Porcupine	Non-threatened	Tolerant
Tufted Ground Squirrel	Threatened	Sensitive
Yellow Muntjac	Non-threatened	Sensitive
Yellow throated Marten	Non-threatened	Tolerant

Supplementary Information S4: Model Specification and predictive performance checks

All analyses were conducted in WinBUGS version 1.4.3 called through R version 3.3.0 using the package "R2WinBUGS" (Sturtz, Ligges & Gelman 2005). All statistical models were constructed using uninformative priors. Unless stated otherwise, parameter estimates are presented as means alongside 95% Bayesian Credible Intervals (BCIs) and considered statistically significant if their 95% BCIs did not overlap zero. For the hierarchical Bayesian multispecies occupancy model, three parallel chains were run for 75,000 iterations, 25,000 of which were discarded during the burn-in; posterior chains were thinned by 10. For all Bayesian two-stage linear models, three parallel chains were run for 12,000 iterations, following a burn-in of 2,000; posterior chains were thinned by 5. Convergence was assessed using visual inspection of trace plots and the Gelman-Rubin statistic, values ≥ 1.1 indicate failure to converge (Gelman & Hill 2007). Model fit was assessed statistically using a posterior predictive check, which compares model fit for the actual data against a simulated, idealised dataset (Gelman, Meng & Stern 1996). Bayesian *p*-values were extracted as a numerical summary of the posterior predictive distribution, with quantities close to 0.5 indicating adequate model fit. We identified quantitative and visual support for convergence in all models presented, while obtained Bayesian *p*-values did not provide evidence of lack of fit ($0.43 \leq p \leq 0.52$).

Model code

WinBUGS code for hierarchical Bayesian community occupancy model used to assess spatial concordance between biodiversity and HCS classes.

```
model{

#Define prior distributions for community-level model parameters
omega ~ dunif(0,1)

CLF.mean ~ dunif(0,1)
mu.uCLF <- log(CLF.mean) - log(1-CLF.mean)
HCS.mean ~ dunif(0,1)
mu.uHCS <- log(HCS.mean) - log(1-HCS.mean)
YRF.mean ~ dunif(0,1)
mu.uYRF <- log(YRF.mean) - log(1-YRF.mean)
DEV.mean ~ dunif(0,1)
mu.uDEV <- log(DEV.mean) - log(1-DEV.mean)
OP.mean ~ dunif(0,1)
mu.uOP <- log(OP.mean) - log(1-OP.mean)

CLF2.mean ~ dunif(0,1)
mu.vCLF <- log(CLF2.mean) - log(1-CLF2.mean)
HCS2.mean ~ dunif(0,1)
mu.vHCS <- log(HCS2.mean) - log(1-HCS2.mean)
```

```
YRF2.mean ~ dunif(0,1)
mu.vYRF <- log(YRF2.mean) - log(1-YRF2.mean)
DEV2.mean ~ dunif(0,1)
mu.vDEV <- log(DEV2.mean) - log(1-DEV2.mean)
OP2.mean ~ dunif(0,1)
mu.vOP <- log(OP2.mean) - log(1-OP2.mean)

tau.uCLF ~ dgamma(0.1,0.1)
tau.uHCS ~ dgamma(0.1,0.1)
tau.uYRF ~ dgamma(0.1,0.1)
tau.uDEV ~ dgamma(0.1,0.1)
tau.uOP ~ dgamma(0.1,0.1)
tau.vCLF ~ dgamma(0.1,0.1)
tau.vHCS ~ dgamma(0.1,0.1)
tau.vYRF ~ dgamma(0.1,0.1)
tau.vDEV ~ dgamma(0.1,0.1)
tau.vOP ~ dgamma(0.1,0.1)

sigma.uCLF <- 1/sqrt(tau.uCLF)
sigma.uHCS <- 1/sqrt(tau.uHCS)
sigma.uYRF <- 1/sqrt(tau.uYRF)
sigma.uDEV <- 1/sqrt(tau.uDEV)
sigma.uOP <- 1/sqrt(tau.uOP)
sigma.vCLF <- 1/sqrt(tau.vCLF)
sigma.vHCS <- 1/sqrt(tau.vHCS)
```

```
sigma.vYRF <- 1/sqrt(tau.vYRF)
sigma.vDEV <- 1/sqrt(tau.vDEV)
sigma.vOP <- 1/sqrt(tau.vOP)

for (i in 1:(n+nzeroes)) {

#Create priors for species i from the community level prior distributions
w[i] ~ dbern(omega)
u.CLF[i] ~ dnorm(mu.uCLF, tau.uCLF)
u.HCS[i] ~ dnorm(mu.uHCS, tau.uHCS)
u.YRF[i] ~ dnorm(mu.uYRF, tau.uYRF)
u.DEV[i] ~ dnorm(mu.uDEV, tau.uDEV)
u.OP[i] ~ dnorm(mu.uOP, tau.uOP)
v.CLF[i] ~ dnorm(mu.vCLF, tau.vCLF)
v.HCS[i] ~ dnorm(mu.vHCS, tau.vHCS)
v.YRF[i] ~ dnorm(mu.vYRF, tau.vYRF)
v.DEV[i] ~ dnorm(mu.vDEV, tau.vDEV)
v.OP[i] ~ dnorm(mu.vOP, tau.vOP)


#Create a loop to estimate the Z matrix (true occurrence for species i
#at point j).
for (j in 1:J) {
logit(psi[j,i]) <- u.CLF[i]*Ind1[j] + u.HCS[i]*Ind2[j] + u.YRF[i]*Ind3[j] +
u.DEV[i]*Ind4[j] + u.OP[i]*Ind5[j]
```

```
mu.psi[j,i] <- psi[j,i]*w[i]
Z[j,i] ~ dbern(mu.psi[j,i])

#Create a loop to estimate detection for species i at point j during
#sampling period k.
for (k in 1:K[j]) {
logit(p[j,k,i]) <-  v.CLF[i]*Ind1[j] + v.HCS[i]*Ind2[j] + v.YRF[i]*Ind3[j] +
v.DEV[i]*Ind4[j] + v.OP[i]*Ind5[j]

mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
X[j,k,i] ~ dbern(mu.p[j,k,i])

# Create simulated dataset to calculate Bayesian p value
Xnew[j,k,i] ~ dbern(mu.p[j,k,i])
d[j,k,i]<-  abs(X[j,k,i] - mu.p[j,k,i])
dnew[j,k,i]<- abs(Xnew[j,k,i] - mu.p[j,k,i])
d2[j,k,i]<- pow(d[j,k,i],2)
dnew2[j,k,i]<- pow(dnew[j,k,i],2)
}

dsum[j,i]<- sum(d2[j,1:K[j],i])
dnewsum[j,i]<- sum(dnew2[j,1:K[j],i])
}}
```

```
# Calculate discrepency measure, which is then defined as mean(p.fit > p.fitnew) in R
p.fit<-sum(dsum[1:J,1:n])
p.fitnew<-sum(dnewsum[1:J,1:n])
}

#Sum all species observed (n) and unobserved species (n0) to find the
#total estimated richness
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0

#Create a loop to determine point level richness estimates for the
#whole community and for subsets or assemblages of interest.
for(j in 1:J){
Nsite[j]<- inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
Nleast[j]<- inprod(Z[j,1:n],least.concern[1:n])
Nthreat[j]<- inprod(Z[j,1:n],threatened[1:n])
Ntolerant[j]<- inprod(Z[j,1:n],tolerant[1:n])
Nsensitive[j]<- inprod(Z[j,1:n],sensitive[1:n])
}
}
```

WinBUGS code for hierarchical Bayesian community occupancy model used to assess the potential for biodiversity cobenefits under REDD+.

```
model{
  #Define prior distributions for community-level model parameters
   omega ~ dunif(0,1)


   psi.mean ~ dunif(0,1)
   a <- log(psi.mean) - log(1-psi.mean)
   mu.alpha1 ~ dnorm(0,0.001)
   mu.alpha2 ~ dnorm(0,0.001)
   tau1 ~ dgamma(0.1,0.1)
   tau.alpha1 ~ dgamma(0.1,0.1)
   tau.alpha2 ~ dgamma(0.1,0.1)


   CLF2.mean ~ dunif(0,1)
   mu.vCLF <- log(CLF2.mean) - log(1-CLF2.mean)
   HCS2.mean ~ dunif(0,1)
   mu.vHCS <- log(HCS2.mean) - log(1-HCS2.mean)
   YRF2.mean ~ dunif(0,1)
   mu.vYRF <- log(YRF2.mean) - log(1-YRF2.mean)
   DEV2.mean ~ dunif(0,1)
   mu.vDEV <- log(DEV2.mean) - log(1-DEV2.mean)
   OP2.mean ~ dunif(0,1)
   mu.vOP <- log(OP2.mean) - log(1-OP2.mean)
```

```
tau.uCLF ~ dgamma(0.1,0.1)
tau.uHCS ~ dgamma(0.1,0.1)
tau.uYRF ~ dgamma(0.1,0.1)
tau.uDEV ~ dgamma(0.1,0.1)
tau.uOP ~ dgamma(0.1,0.1)
tau.vCLF ~ dgamma(0.1,0.1)
tau.vHCS ~ dgamma(0.1,0.1)
tau.vYRF ~ dgamma(0.1,0.1)
tau.vDEV ~ dgamma(0.1,0.1)
tau.vOP ~ dgamma(0.1,0.1)

sigma.tau1 <- 1/sqrt(tau1)
sigma.alpha1 <- 1/sqrt(tau.alpha1)
sigma.alpha2 <- 1/sqrt(tau.alpha2)
sigma.vCLF <- 1/sqrt(tau.vCLF)
sigma.vHCS <- 1/sqrt(tau.vHCS)
sigma.vYRF <- 1/sqrt(tau.vYRF)
sigma.vDEV <- 1/sqrt(tau.vDEV)
sigma.vOP <- 1/sqrt(tau.vOP)

for (i in 1:(n+nzeroes)) {

#Create priors for species i from the community level prior distributions
```

```
w[i] ~ dbern(omega)

u[i] ~ dnorm(a, tau1)
alpha1[i] ~ dnorm(mu.alpha1, tau.alpha1)
alpha2[i] ~ dnorm(mu.alpha2, tau.alpha2)

v.CLF[i] ~ dnorm(mu.vCLF, tau.vCLF)
v.HCS[i] ~ dnorm(mu.vHCS, tau.vHCS)
v.YRF[i] ~ dnorm(mu.vYRF, tau.vYRF)
v.DEV[i] ~ dnorm(mu.vDEV, tau.vDEV)
v.OP[i] ~ dnorm(mu.vOP, tau.vOP)

#Create a loop to estimate the Z matrix (true occurrence for species i
#at point j.
for (j in 1:J) {
logit(psi[j,i]) <- u[i] + alpha1[i]*carbon1[j] + alpha2[i]*carbon2[j]

mu.psi[j,i] <- psi[j,i]*w[i]
Z[j,i] ~ dbern(mu.psi[j,i])

#Create a loop to estimate detection for species i at point j during
#sampling period k.
for (k in 1:K[j]) {
logit(p[j,k,i]) <-  v.CLF[i]*Ind1[j] + v.HCS[i]*Ind2[j] + v.YRF[i]*Ind3[j] +
v.DEV[i]*Ind4[j] + v.OP[i]*Ind5[j]
```

```
mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
X[j,k,i] ~ dbern(mu.p[j,k,i])

# Create simulated dataset to calculate Bayesian p value
Xnew[j,k,i] ~ dbern(mu.p[j,k,i])
d[j,k,i]<-  abs(X[j,k,i] - mu.p[j,k,i])
dnew[j,k,i]<- abs(Xnew[j,k,i] - mu.p[j,k,i])
d2[j,k,i]<- pow(d[j,k,i],2)
dnew2[j,k,i]<- pow(dnew[j,k,i],2)
}

dsum[j,i]<- sum(d2[j,1:K[j],i])
dnewsum[j,i]<- sum(dnew2[j,1:K[j],i])
}}

# Calculate discrepency measure, which is then defined as mean(p.fit > p.fitnew)
p.fit<-sum(dsum[1:J,1:n])
p.fitnew<-sum(dnewsum[1:J,1:n])
}

#Sum all species observed (n) and unobserved species (n0) to find the
#total estimated richness
n0 <- sum(w[(n+1):(n+nzeroes)])
N <- n + n0
```

```
#Create a loop to determine point level richness estimates for the
#whole community and for subsets or assemblages of interest.
for(j in 1:J){
Nsite[j]<- inprod(Z[j,1:(n+nzeroes)],w[1:(n+nzeroes)])
Nleast[j]<- inprod(Z[j,1:n],least.concern[1:n])
Nthreat[j]<- inprod(Z[j,1:n],threatened[1:n])
Ntolerant[j]<- inprod(Z[j,1:n],tolerant[1:n])
Nsensitive[j]<- inprod(Z[j,1:n],sensitive[1:n])
}

#Finish writing the text file into a document we call covarmodel.txt
}
```

References

Gelman, A. & Hill, J. (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge.

Gelman, A., Meng, X.-L. & Stern, H. (1996) Posterior predictive assessment of model fitness via realized discrepancies. *Statistica sinica***,** 733-760.

Sturtz, S., Ligges, U. & Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical software,* **12,** 1-16.

Supporting Information S5: Model description and parameter estimates for hierarchical Bayesian multispecies occupancy models

Table S5.1: Model description, where μ and υ refer to the intercept terms for the occupancy and detection probability models respectively, $\alpha 1$ and $\alpha 2$ represent parameters describing carbon standard and quadratic covariates at 5m- ('CC5') and 1km resolution ('CC1000') and 'HCS class' refers to coarse delineations of carbon designated by the High Carbon Stock (HCS) Approach.

Model 1:	$\mathrm{logit}(\psi_{i,j}) = \mu_{(i)HCS\ Class(j)}$ $\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$
Model 2:	$\mathrm{logit}(\psi_{i,j}) = \mu_{(i,j)} + \alpha 1_i CC1000_j + \alpha 2_i CC1000^2_j$ $\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$
Model 3:	$\mathrm{logit}(\psi_{i,j}) = \mu_{(i,j)} + \alpha 1_i CC5_j + \alpha 2_i CC5^2_j$ $\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)HCS\ Class(j)}$

Table S5.2: Model 1: Species-specific posterior summaries for occupancy as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP). We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).

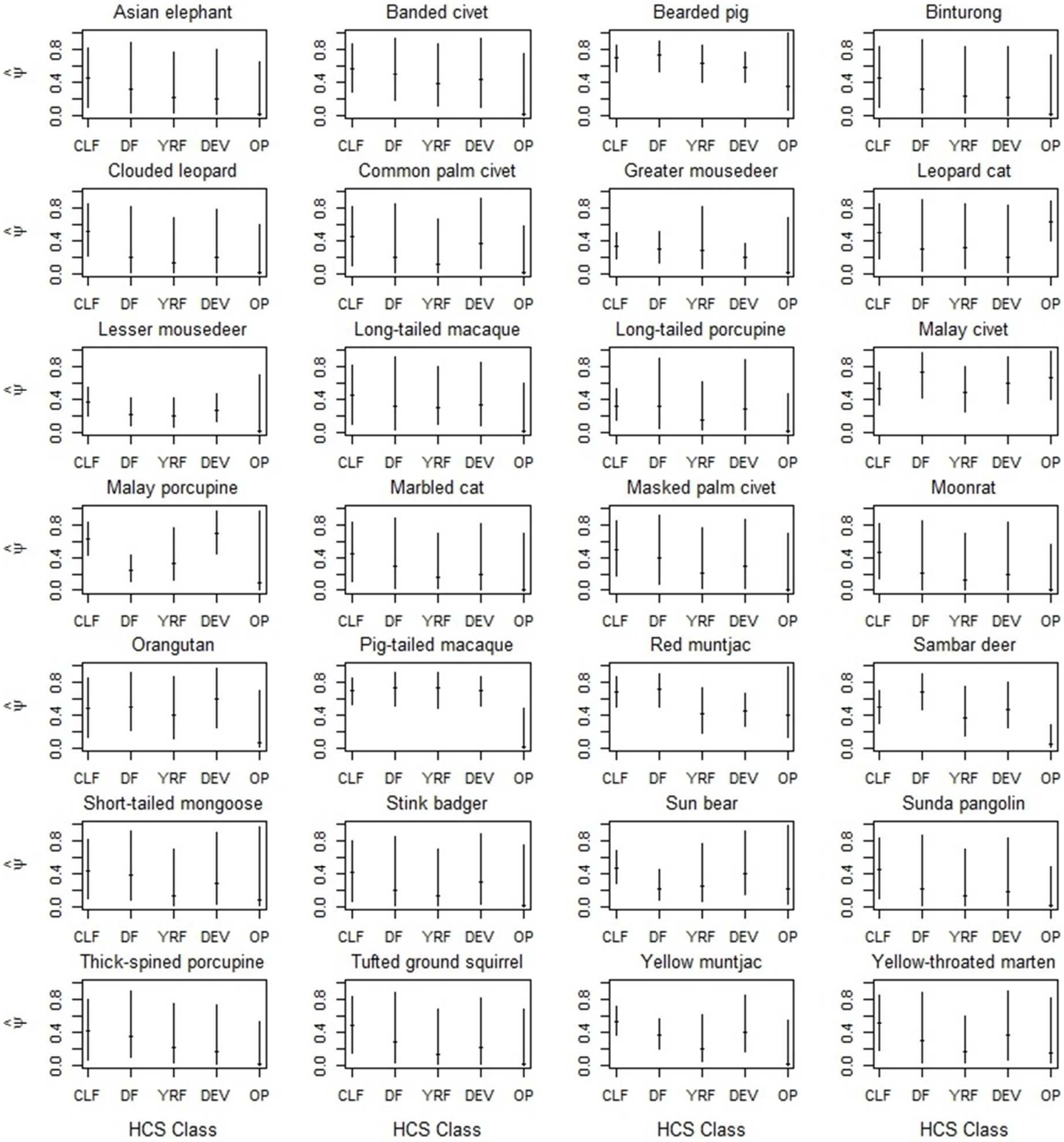


Table S5.3: Model 1: Species-specific posterior summaries of detection probability as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP). We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).

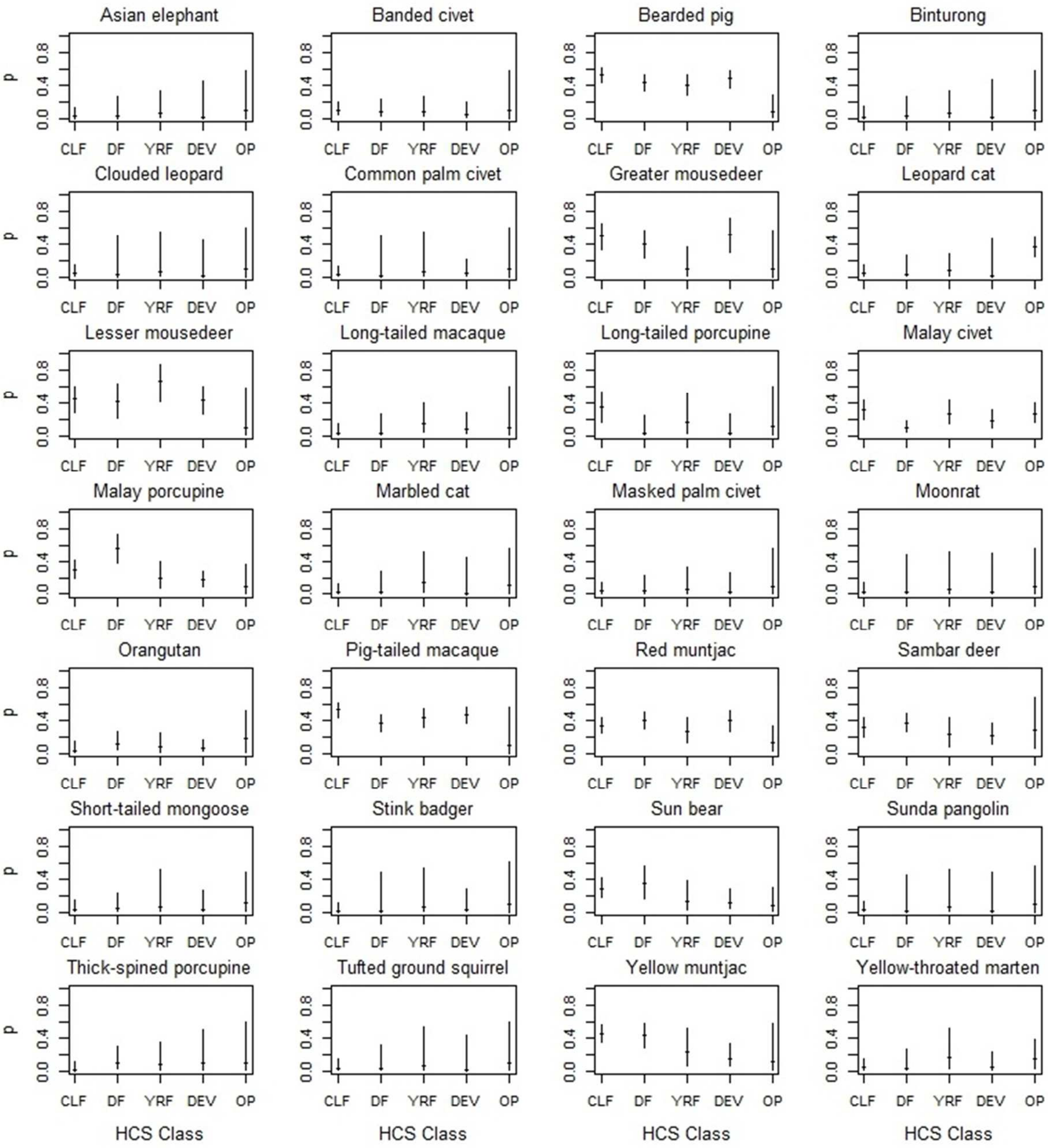


Table S5.4: Model 2: Species-specific posterior summaries of occupancy as a function of continuous carbon derived from a 1 km resolution dataset (Avitabile *et al.* 2016). We present predicted mean posterior distribution values (blue line) and 95% Bayesian credible intervals (blue shaded region).

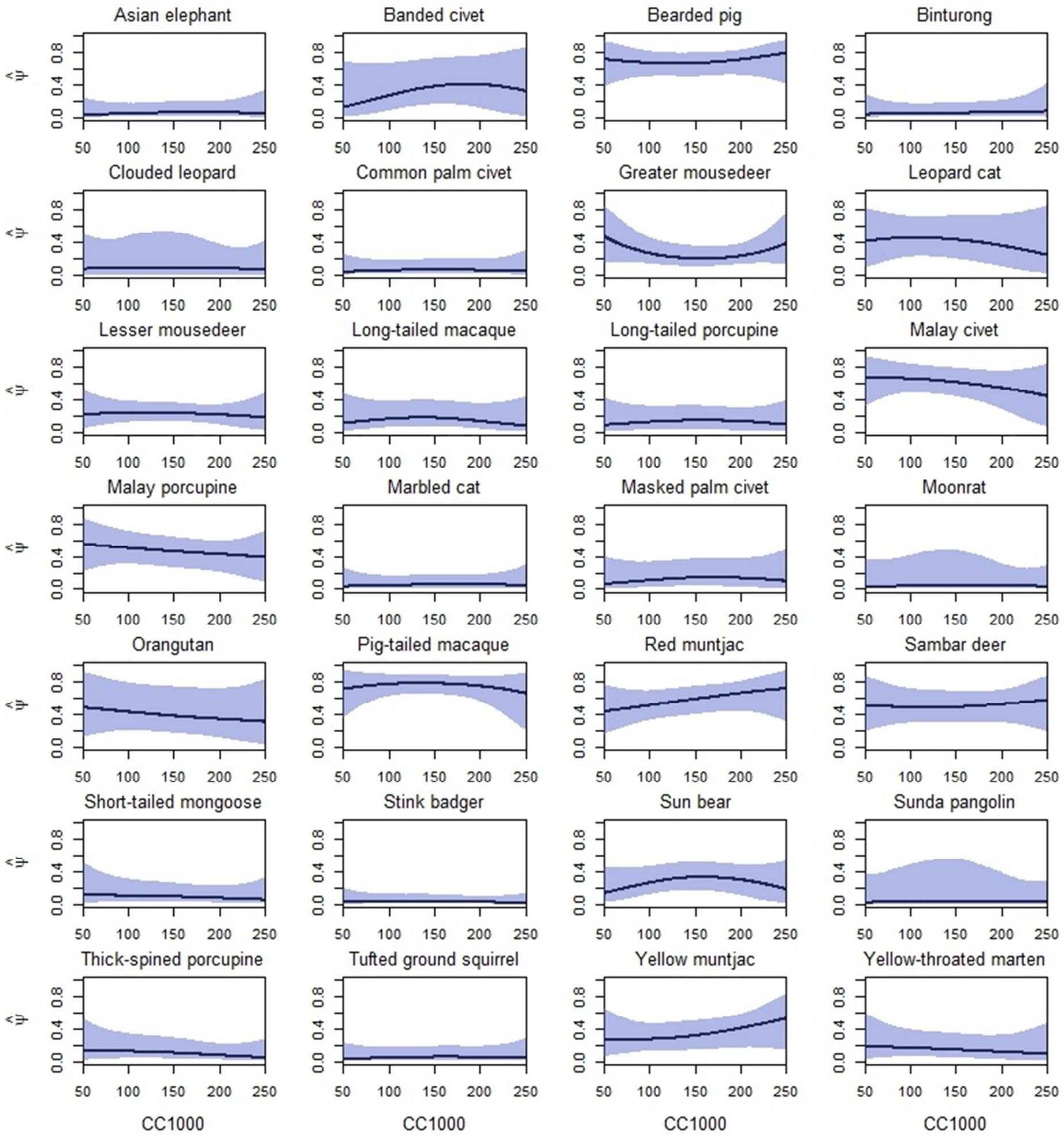


Table S5.5: Model 2: Species-specific posterior summaries of detection probability as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP), broadly representing the influence of habitat type. We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).

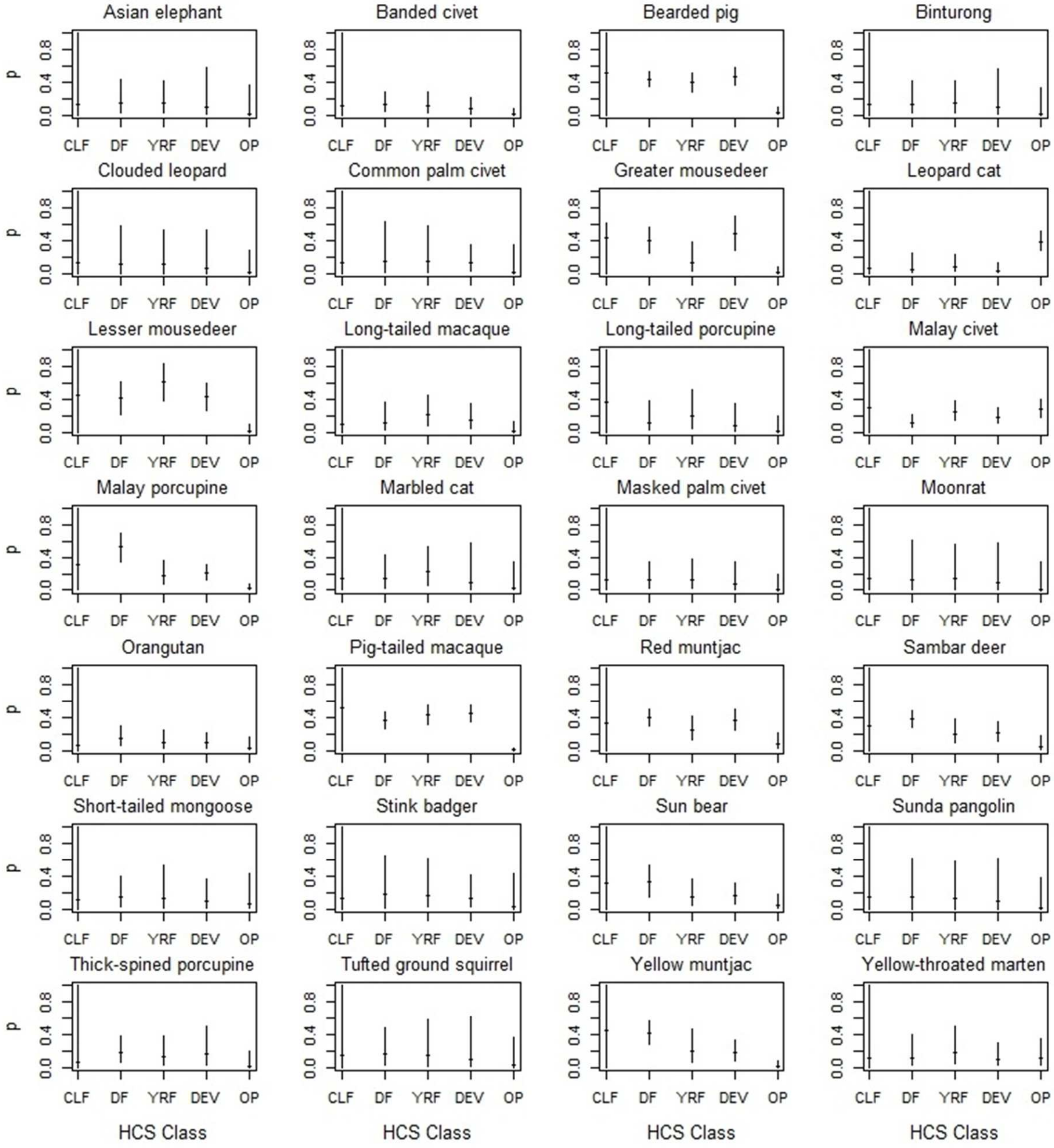


Table S5.6: Model 3: Species-specific posterior summaries of occupancy as a function of continuous carbon derived from a 25 m resolution dataset (Pfeifer *et al.* 2016). We present predicted mean posterior distribution values (blue line) and 95% Bayesian credible intervals (blue shaded region).

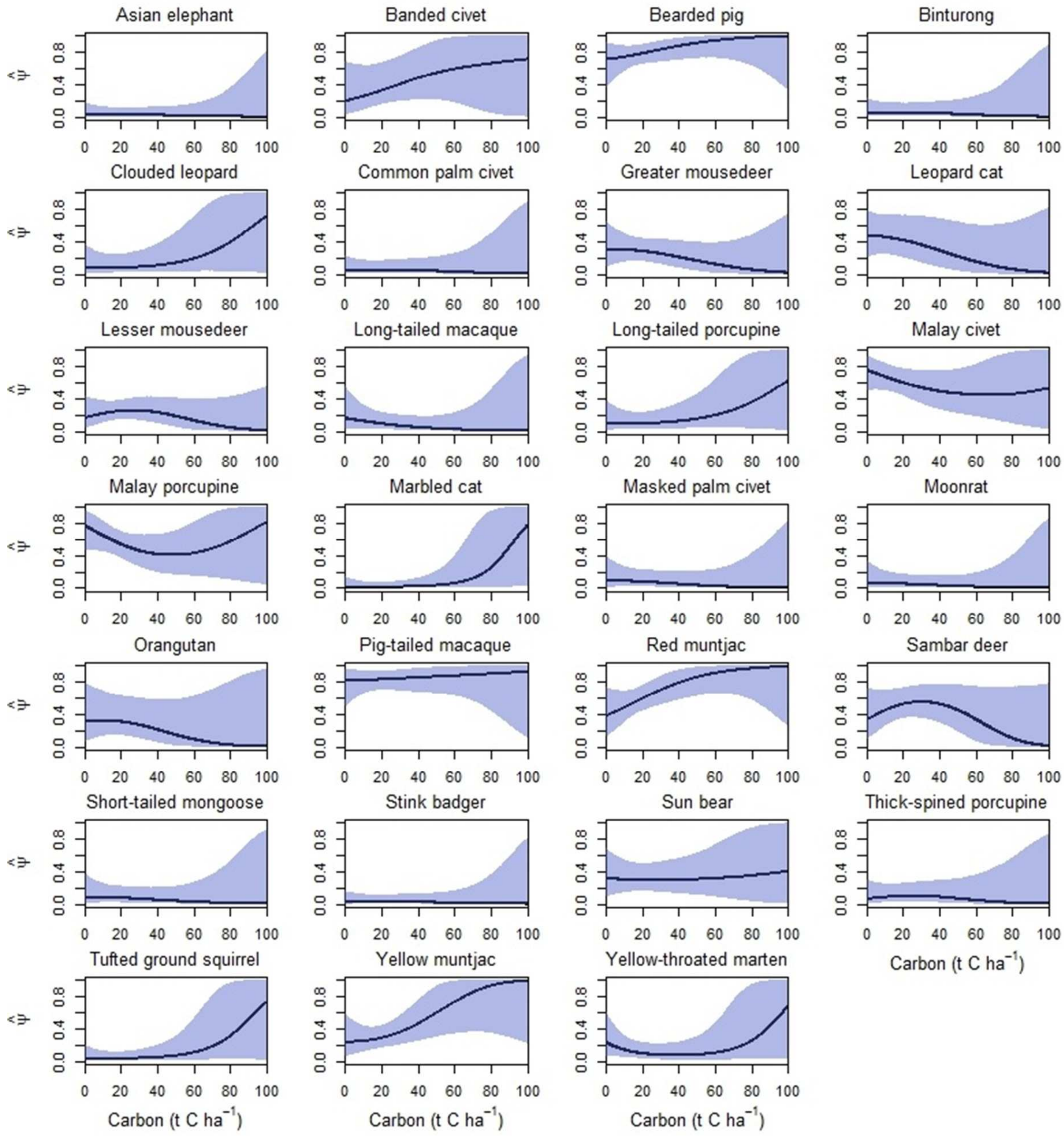
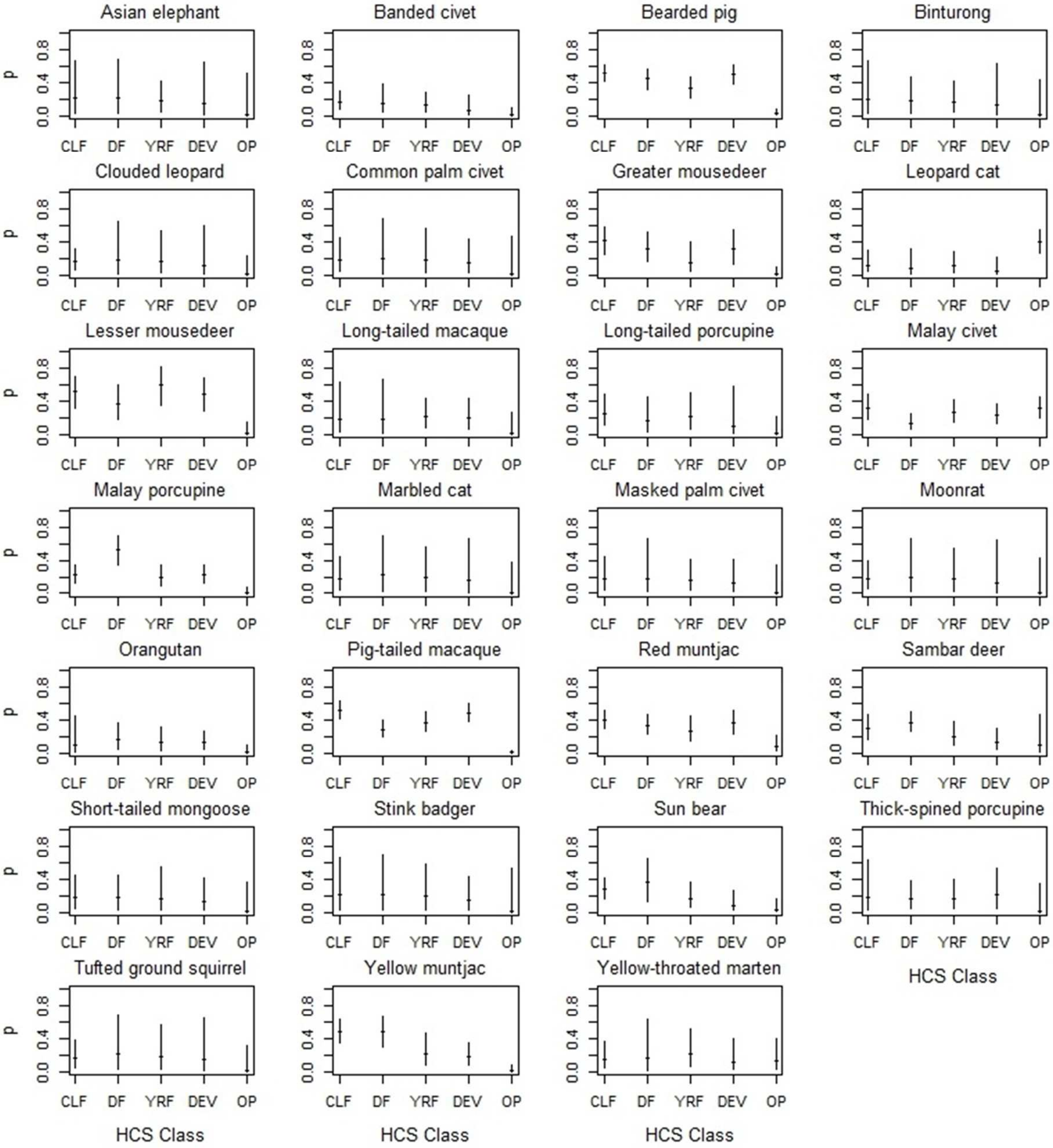


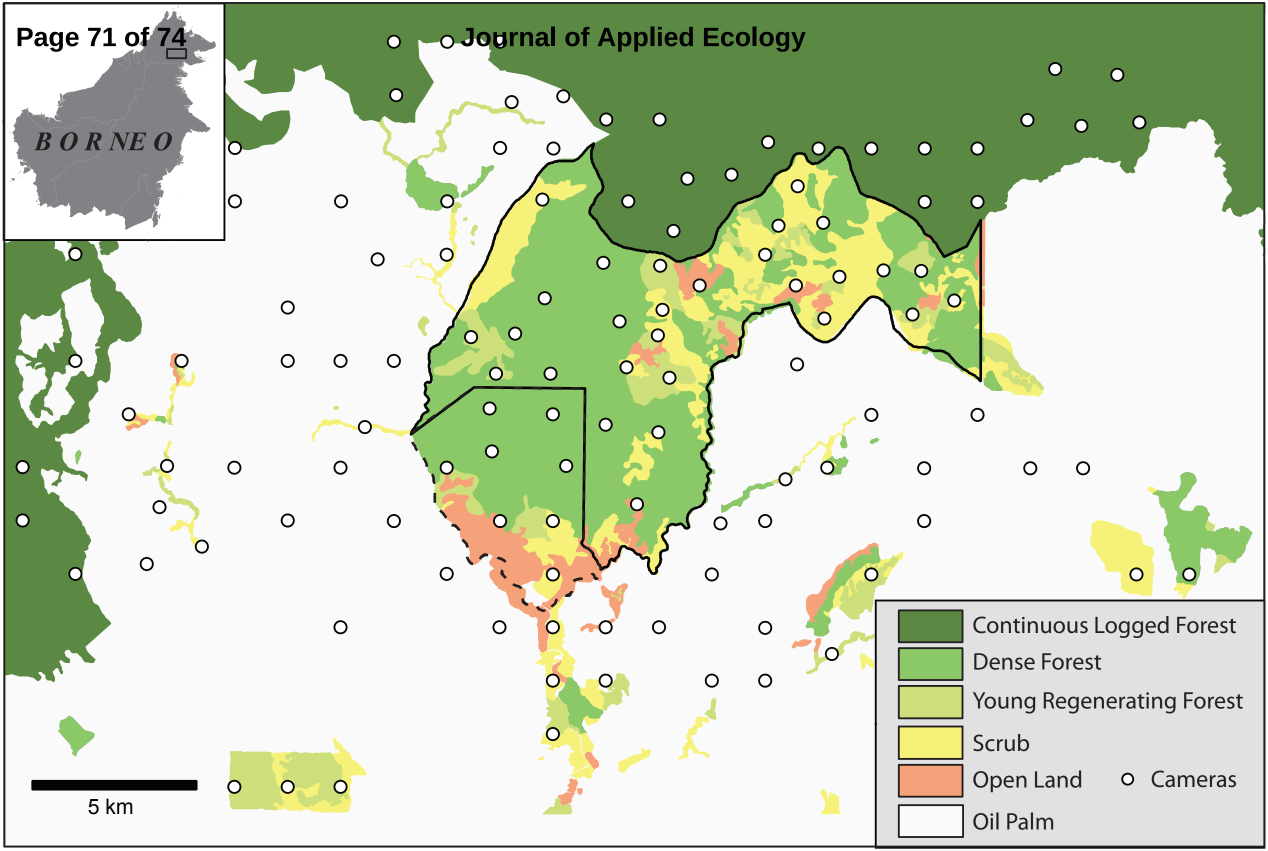
Table S5.7: Model 3: Species-specific posterior summaries of detection probability as a function of HCS class (Continuous Logged Forest: CLF; Dense Forest: DF; Young Regenerating Forest: YRF; Developed Land: DEV; Oil Palm: OP), broadly representing the influence of habitat type. We visualise mean predicted posterior distribution values (horizontal lines), accompanied by 95% Bayesian Credible Intervals (vertical lines).



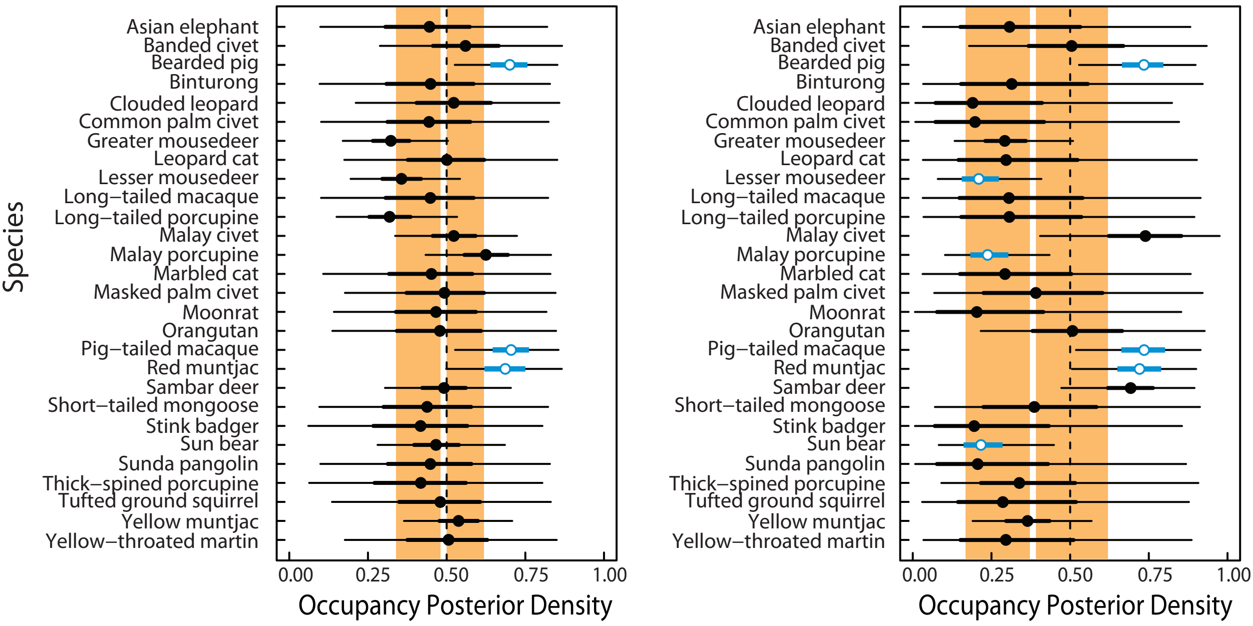
References

Avitabile, V., Herold, M., Heuvelink, G.B.M., Lewis, S.L., Phillips, O.L., Asner, G.P. *et al.* (2016) An integrated pan-tropical biomass map using multiple reference datasets. *Global Change Biology,* **22,** 1406-1420.

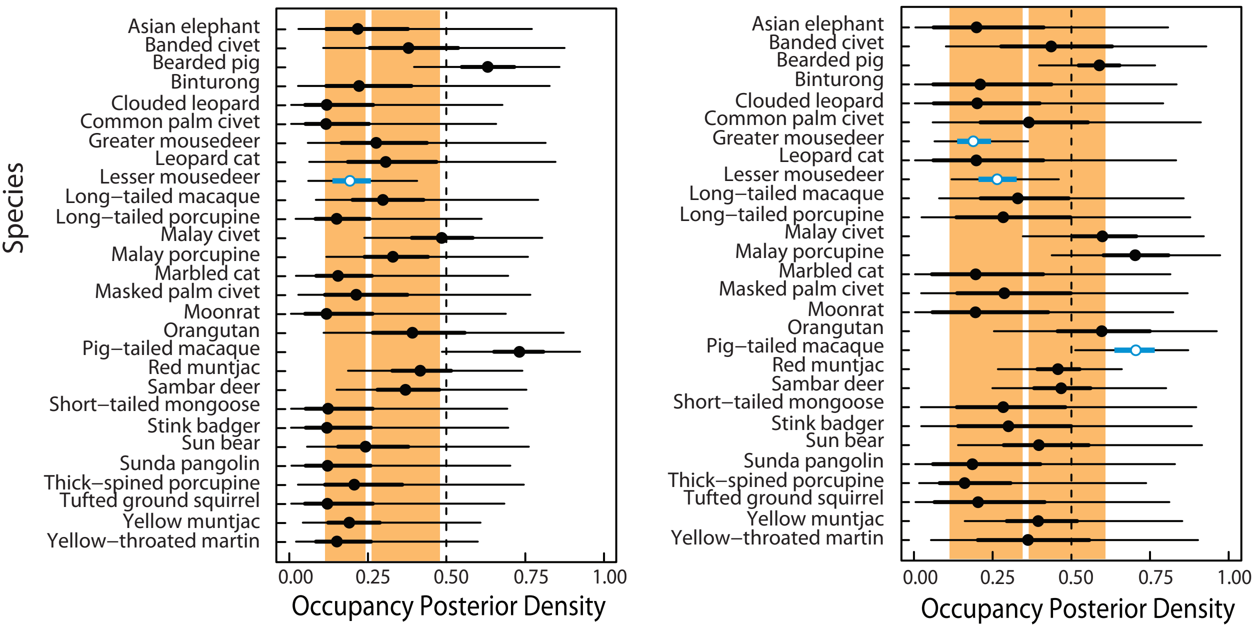
Pfeifer, M., Kor, L., Nilus, R., Turner, E., Cusack, J., Lysenko, I. *et al.* (2016) Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote Sensing of Environment,* **176,** 84-97.


BORNEO
Continuous Logged Forest
Dense Forest
Young Regenerating Forest
Scrub
Open Land
Cameras
Oil Palm
5 km

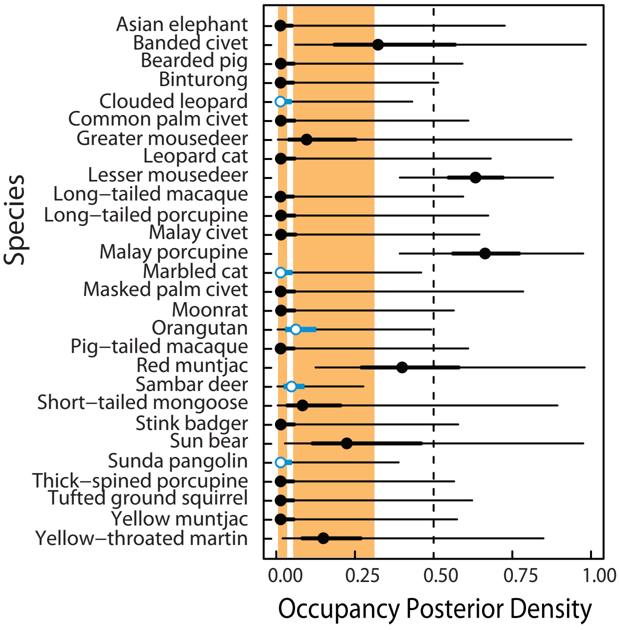
(a) Continuous Logged Forest (b) Dense Forest

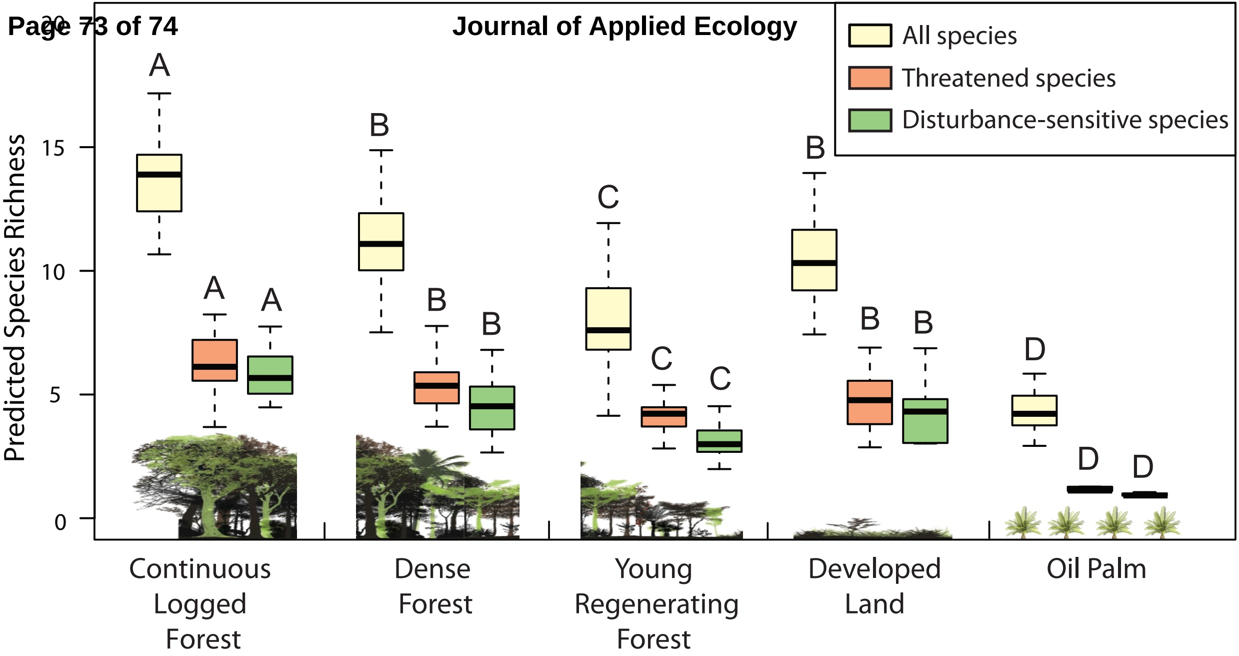


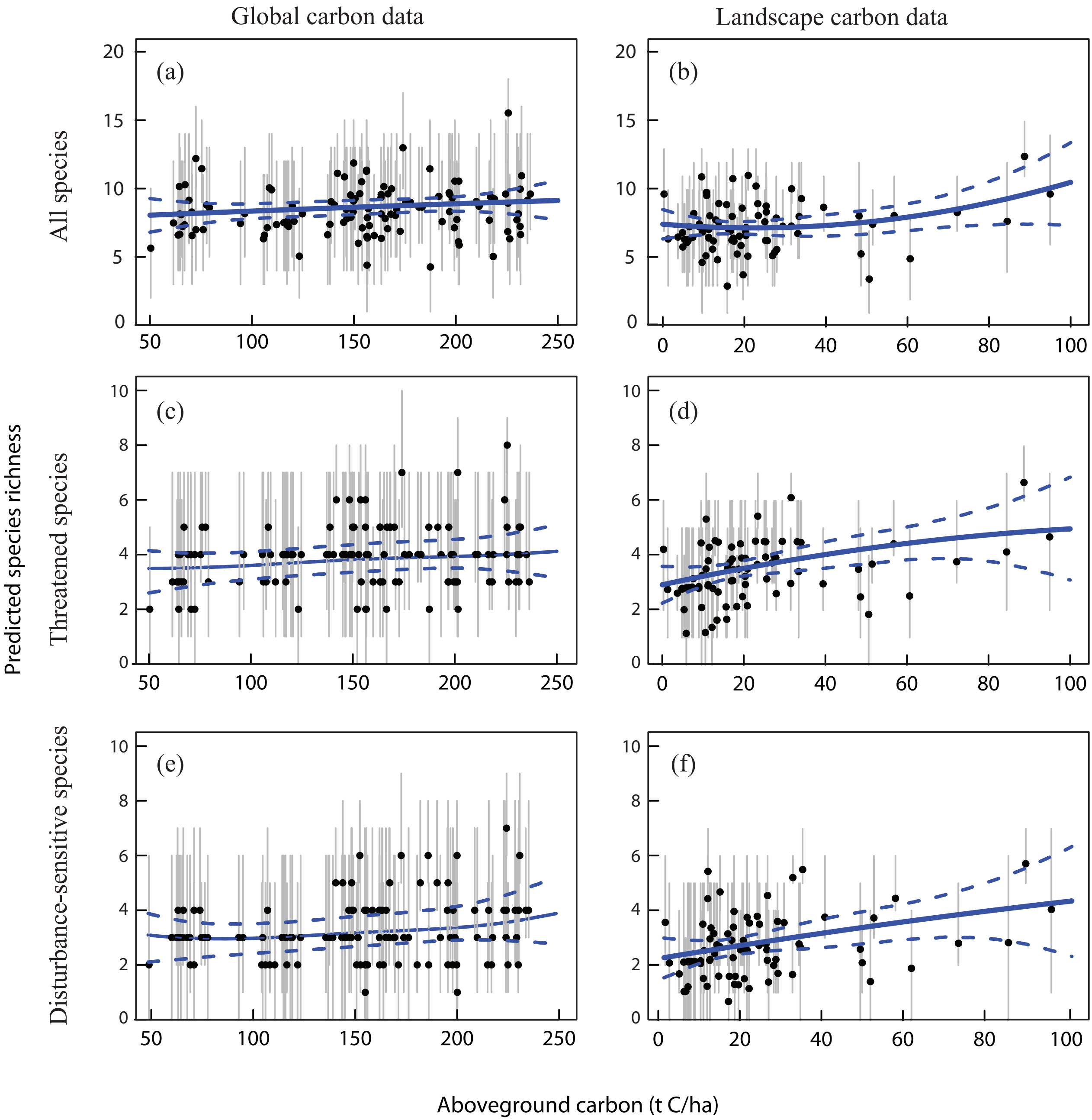
(c) Young Regenerating Forest (d) Developed Land



(e) Oil Palm




Predicted Species Richness
0
5
10
15
20
All species
Threatened species
Disturbance-sensitive species
A
A
A
B
B
B
C
C
C
B
B
B
D
D
D
Continuous Logged Forest
Dense Forest
Young Regenerating Forest
Developed Land
Oil Palm


Global carbon data
Landscape carbon data
Predicted species richness
All species
Threatened species
Disturbance-sensitive species
(a)
(b)
(c)
(d)
(e)
(f)
0
5
10
15
20
0
2
4
6
8
10
50
100
150
200
250
0
20
40
60
80
100
Aboveground carbon (t C/ha)