



Quantifying mammal biodiversity co-benefits in certified tropical forests

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ABSTRACT

Aim Financial incentives to manage forests sustainably, such as certification or carbon storage payments, are assumed to have co-benefits for biodiversity conservation. This claim remains little studied for rain forest mammals, which are particularly threatened, but challenging to survey.

Location Sabah, Malaysia, Borneo.

Methods We used photographic data from three commercial forest reserves to show how community occupancy modelling can be used to quantify mammalian diversity conservation co-benefits of forest certification. These reserves had different management histories, and one was certified by the Forest Stewardship Council.

Results Many threatened species occupied larger areas in the certified reserve. Species richness, estimated per 200 × 200-m grid cell throughout all reserves, was higher in the certified site, particularly for threatened species. The certified reserve held the highest aboveground biomass. Within reserves, aboveground biomass was not strongly correlated with patterns of mammal richness (Spearman's rho from 0.03 to 0.32); discrepancies were strongest along reserve borders.

Main conclusions Our approach provides a flexible and standardized tool to assess biodiversity and identify winners of sustainable forestry. Inferring patterns of species richness from camera-trapping carries potential for the objective designation of high conservation value forest. Correlating species richness with aboveground biomass further allows evaluating the biodiversity co-benefits of carbon protection. These advantages make the present approach an ideal tool to overcome the difficulties to rigorously quantify biodiversity co-benefits of forest certification and carbon storage payments.

Keywords

Borneo, carbon payment, community occupancy model, forest stewardship council, REDD+, Southeast Asia, sustainable forestry.

INTRODUCTION

Owing to their exceptional species richness, the destruction of tropical rain forests causes extreme biodiversity losses (e.g. Brook *et al.*, 2003; Gardner *et al.*, 2009). In Southeast Asia, deforestation rates have been higher than in other tropical regions (Miettinen *et al.*, 2011). Protected areas, although a cornerstone of conservation, are not sufficient to halt the loss of biodiversity and need to be combined with sustainable use

of natural resources (Sodhi *et al.*, 2010; Edwards *et al.*, 2014; Struebig *et al.*, 2015). Sustainable use of forests can only be achieved if maintaining forests provides financial benefits to offset the profits offered by plantations (Butler *et al.*, 2009). In this context, two global initiatives have been set up. First, sustainability certification schemes, particularly the Forest Stewardship Council (FSC), allow producers to sell forest products at higher market prices, compensating for the higher costs and reduced timber yields of sustainably

managed forests (Vogt *et al.*, 1999). Sustainability is evaluated against a set of 10 global principles, including the protection of biodiversity and long-term maintenance of ecological value of the forest (FSC, 2014). Second, deforestation and forest degradation are also a major source of anthropogenic carbon emissions (Gullison *et al.*, 2007). The 'reducing emissions from deforestation and degradation' (REDD+) initiative by the United Nations Framework Convention on Climate Change (UNFCCC) grants financial compensation to developing countries for protecting forests as carbon storage. The programme was quickly recognized as an unprecedented opportunity to enhance conservation of forest ecosystems (Strassburg *et al.*, 2010) and has since adopted biodiversity safeguards into its goals (UNFCCC, 2011).

There are concerns about how well certification schemes such as FSC and REDD+ achieve their biodiversity conservation goals in practice (Laurance, 2008). FSC certification requires the use of low-impact forestry practices such as reduced impact logging (RIL), which has been shown to have much reduced negative impacts on biodiversity relative to conventional logging (reviewed in Putz *et al.*, 2008; Wilcove *et al.*, 2013; Bicknell *et al.*, 2014), but nevertheless lead to reduction in diversity (Gibson *et al.*, 2011). The REDD+ principles lack specificity in how biodiversity safeguards are to be achieved (Paoli *et al.*, 2010; Visseren-Hamakers *et al.*, 2012). This issue is compounded by the fact that, while carbon and biodiversity correlate globally (Strassburg *et al.*, 2010; Visseren-Hamakers *et al.*, 2012), they do not necessarily do so on the national or subnational level, where REDD+ projects are planned and implemented (Paoli *et al.*, 2010). This has raised the concern that if biodiversity is not explicitly incorporated into REDD+ planning, the initiative may fail to provide biodiversity co-benefits (Venter *et al.*, 2009a, 2013; Potts *et al.*, 2013). In this context, reliable biodiversity monitoring is urgently required to corroborate the assumed co-benefits and to evaluate impacts of forest management practices on biodiversity (e.g. Gardner *et al.*, 2009; Waldon *et al.*, 2011; Lindenmayer *et al.*, 2012).

It is challenging and costly to monitor biodiversity in tropical forests (Lindenmayer *et al.*, 2000). For that reason, current approaches either focus on single species or use *ad hoc* tools such as opportunistic observations (Sheil, 2001; de Longh & Persoon, 2010). Rain forest mammals pose a particular challenge because of their elusive behaviour and rarity, yet they warrant immediate attention. The larger mammals of Southeast Asia have been identified as one of the groups of highest conservation priority world-wide (Schipper *et al.*, 2008; Hoffmann *et al.*, 2011; Duckworth *et al.*, 2012; Wilcove *et al.*, 2013). Further, mammals are a good umbrella taxon, due to their large area requirements, ecological diversity and variation in sensitivity to human impact (Noss, 1990; Caro, 2003).

Camera-traps are a prime tool for surveying medium to large forest mammals (e.g. Waldon *et al.*, 2011). Raw camera-trap data, however (e.g. photographic counts and species

counts), are fraught with sampling bias, and adequate survey and analytical protocols are needed to render studies comparable (Sollmann *et al.*, 2013). Species-level detections from camera-traps can be analysed in the framework of occupancy models (MacKenzie *et al.*, 2002, 2006), to provide insight into environmental conditions shaping occurrence of species. Occupancy models have further been combined with the framework of community modelling (Dorazio & Royle, 2005; Dorazio *et al.*, 2006), where data from a group of species are modelled jointly. In addition to species-specific responses to covariates, these models can produce estimates of species richness. Community occupancy modelling has successfully been applied to camera-trapping data (Burton *et al.*, 2011, 2012; Brodie *et al.*, 2014; Tobler *et al.*, 2015; Rich *et al.*, 2016), but its potential for quantifying biodiversity co-benefits has not yet been explored.

Here, we demonstrate how combining camera-trapping data with community occupancy models allows for a quantitative assessment of the mammalian biodiversity co-benefits of certified forests, and an evaluation of the co-occurrence of carbon and mammalian diversity on a fine scale. The approach we present can be adopted and extended to other taxonomic groups to evaluate the effectiveness of forest certification for biodiversity conservation in tropical rain forests world-wide.

METHODS

Study area

We conducted camera-trap surveys in Deramakot Forest Reserve (5°14–28'N, 117°19–36'E), Tangkulap Forest Reserve (5°17–30'N, 117°11–21'E) and Segaliud Lokan Forest Reserve (5°20–27'N, 117°23–39'E). The study sites form a contiguous forest block in the lowlands of central Sabah (Fig. 1a). Deramakot (55,000 ha) was licensed to private logging concessions from the 1950s until 1989, after which management was taken over by the Sabah Forestry Department (SFD) and all logging was ceased. In 1995, the reserve was logged again, using RIL techniques. Approximately 3% of the reserve (1650 ha) is logged each year, and annual harvest volumes since 1995 have been consistently below 15,000 m³, with logging cycles of 40 years (Ong *et al.*, 2013). As a consequence, Deramakot received certification from the FSC in 1997. Tangkulap (27,600 ha) was licensed out to private concessionaires from the 1970s until 2002 and repeatedly logged using conventional selective logging techniques. Logging was ceased in 2001, management was taken over by the SFD, and in June 2011 (after the present study), the reserve also received FSC certification. As a result of the more destructive logging practices, overall forest conditions are poorer compared to Deramakot (Ong *et al.*, 2013). Segaliud Lokan (57,200 ha) was heavily logged until 1982. In 1995, the current management company – KTS Plantation Sdn Bhd – took up logging operations using conventional logging practices, only switching to RIL in 1998. 37,420 ha have been

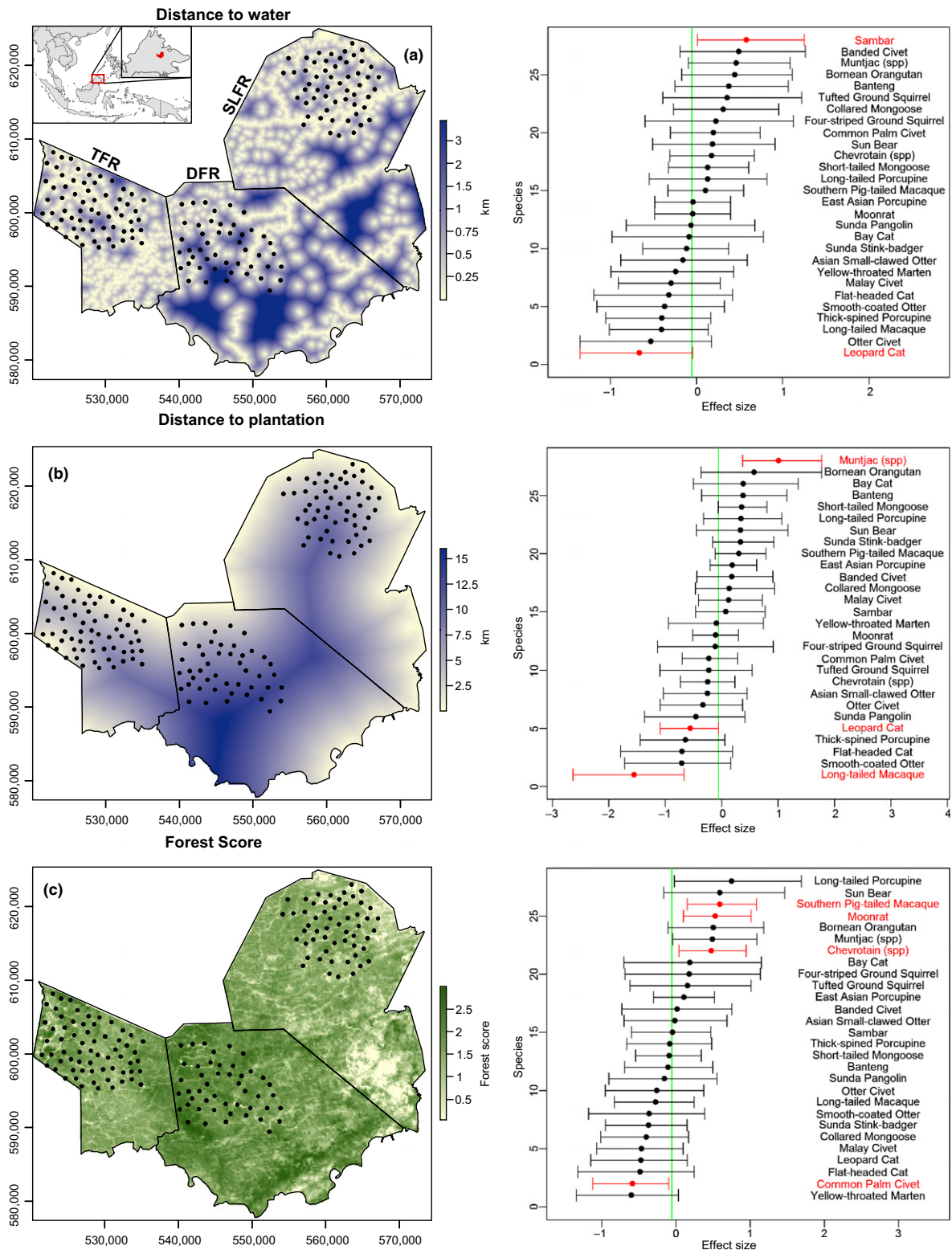


Figure 1 Covariates (left) and respective coefficients (mean and 95% BCI, on the logit scale) on occupancy probability of 28 mammal species (right), as estimated with community occupancy models fit to camera-trapping data from three forest reserves (TFR = Tangkulap Forest Reserve, DFR = Deramakot FR, SLFR = Segaluid Lokan FR) located in Sabah, Malaysian Borneo (inset map). (a) distance to water, (b) distance to plantation and (c) forest score. Dots in covariate maps show camera-trap locations. In coefficient plots, red dots/bars indicate effects strongly different from 0, black vertical line marks no effect, and green vertical line marks community mean effect. [Colour figure can be viewed at wileyonlinelibrary.com]

transformed into tree plantations (mixed and monoculture); natural forest management is practiced in 12,603 ha. Timber production until 2007 averaged an annual extraction volume of 25,000 m³ over an annual logging area of 2,500 ha at 20-year logging cycles. The reserve was certified in 2009 under the Malaysian Timber Certification Scheme (MTCs), which uses weaker criteria than FSC (Visseren-Hamakers & Glasbergen, 2007). Comparing current forest composition (total forest cover and per cent dense forest, see Appendix S1 in Supporting Information) suggests that there is a gradient in forest disturbance from Deramakot (lowest) to Tangkulap to Segaliud Lokan (highest) that is in accordance with the past management histories. Oil palm plantations border the study areas to the north, as well as to the east for Segaliud Lokan. Hunting is forbidden in all three reserves, and in almost 8000 camera-trap nights, we did not photograph a single hunter in the study areas. Although no quantitative information on past hunting pressure is available, villages close to the forest reserves are small, and past hunting would have been for subsistence. Thus, we expect that hunting in the past only had a minor impact on the mammal community that was comparable across the three reserves.

Camera trapping and data preparation

We set up 47, 64 and 55 camera-trap stations in Deramakot, Tangkulap and Segaliud Lokan, respectively (Fig. 1), over a total sampling duration of approximately 4 months. Deramakot was sampled between September 2008 and January 2009, Tangkulap between April and September 2009 and Segaliud Lokan between January and April 2010. Camera stations were spaced approximately 1.4 km apart, in a compromise between logistical feasibility and approximating spatial independence of sampling points (see next paragraph); each station consisted of two passive infrared triggered camera-traps with white flash (models Expert and Capture; Cuddeback, De Pere, Wisconsin) facing each other and operating 24 hours/day (for details, see Mohamed *et al.*, 2013).

We photographed 37 mammal species, of which we included 28 in the analysis. We removed six arboreal species that were only recorded once or twice. Due to the very low number of detections, occupancy models are unable to parse out changes in detection from changes in occupancy, leading to ambivalent inference about occupancy rates of these species (Brodie *et al.*, 2014). Further, occupancy models assume independence of sampling locations (after accounting for correlation due to covariates). This assumption is violated when camera-traps are spaced too closely so that a single individual occurs at several sampling locations. The home range diameters of many of the photographed species exceed the average camera spacing in this study. We removed Sunda clouded leopards (*Neofelis diardi*, G. Cuvier, 1823), bearded pigs (*Sus barbatus*, Müller, 1838) and Bornean elephants (*Elephas maximus*, Linnaeus, 1758) from the data set, because individuals/groups of these species potentially range over entire camera grids (Caldecott *et al.*, 1993; Alfred *et al.*,

2012; Wilting *et al.*, 2012). For the remaining 28 species, we investigated spatial autocorrelation in model residuals using Moran's I (Cliff & Ord, 1981), following Moore & Swihart (2005) (for details, see Appendix S2). We only found evidence of low to moderate spatial autocorrelation in eight of the 28 analysed species. We acknowledge that for these species we may underestimate occupancy. But our analysis is concerned with comparisons of patterns across reserves, not among species, and for a given species, any bias should be similar across reserves.

Community occupancy model

We adopted the hierarchical formulation of occupancy models by Royle & Dorazio (2008). In single-species single-season models (MacKenzie *et al.*, 2002), whether or not a site j is occupied by the species of interest, z_j , is a Bernoulli random variable governed by occupancy probability ψ , which can be modelled as a function of site-specific covariates on the logit scale. Sites are visited on k occasions, and observations, y_{jk} , are treated as a Bernoulli random variable with detection probability being conditional on the latent true occupancy state z_j , either p_{jk} where $z_j = 1$ or 0 where $z_j = 0$. Analogous to ψ , p can be modelled as a logit-linear function of both site and occasion specific covariates.

To extend this to a community occupancy model, the parameters and latent variables of the model described above are further indexed by species, i . The resulting species-specific models are linked by assuming that species-specific parameters come from a common underlying distribution, governed by community (or hyper) parameters. By augmenting the observation data with all-zero observations of hypothetical species, it is possible to estimate the number of species at each sampling site, including those never observed (Dorazio & Royle, 2005; Dorazio *et al.*, 2006). There were only three species of medium to large terrestrial mammals never recorded within the trapping period but known to occur in the area (Mohamed and Wilting, unpublished data), and therefore, we only augmented the observed data set by three.

For this particular application, we modelled occupancy probability as having species-specific random intercept with reserve specific hyperparameters, to allow for different baseline occupancy in the three reserves and among species. We further modelled the effect on occupancy of three habitat covariates (Fig. 1) derived from 5-m resolution RapidEye images as described in Niedballa *et al.* (2015): distance to water, distance to oil palm plantation and forest score. Access to water is a basic requirement of all mammals and often affects their distribution (Rondinini *et al.*, 2011). Distance to plantation quantifies possible edge effects (e.g. Kinnaird *et al.*, 2003; Brodie *et al.*, 2015). Forest score is an index of the degree of forest cover and quality in a 100-m radius surrounding the camera and should positively affect the occurrence of forest species. In exploratory analyses, covariates extracted at the 100-m scale had stronger relationships with mammal occupancy than 250-m and 50-m scale covariates. All

covariates had species-specific random coefficients that, for a given species, were constant across reserves. Note that this formulation assumes that patterns in occupancy are comparable across the reserves even though they were not surveyed simultaneously. Given the relatively stable nature of tropical evergreen rain forest systems close to the equator, this assumption seems reasonable. Detection probability had a species-specific random intercept with reserve specific hyperparameters, to allow for differences in baseline detection among reserves. These differences can arise, for example, from differences in abundance (Royle & Nichols, 2003), or when animals display differences in spatial behaviour (Sollmann *et al.*, 2013); this formulation also accounts for potential seasonal differences in detection introduced by surveying sites at different times. We further modelled the effect of camera placement, either on or off of roads, a factor that has frequently been shown to impact detection (e.g. Harmsen *et al.*, 2010). In addition, we accounted for varying effort due to malfunctioning camera-traps by including the number of days each camera station was functional within a 6-day occasion as a covariate on detection. The formal model description can be found in Appendix S3.

We implemented the model in a Bayesian framework using JAGS (Plummer, 2003); details are given in Appendix S3. The model code (including all prior distributions and hyperparameter specifications) is available in Appendix S4. We report results as posterior mean (in cases of skewed posterior distributions, the mode) and standard deviation, and 95% Bayesian confidence intervals (95BCI, the 2.5% and 97.5% percentiles of the posterior distribution). We consider a coefficient as strong when its 95BCI does not include 0.

Reserve-wide species richness and correlation with plant biomass

To predict species occurrence to unsampled regions in the reserves, we divided all reserves into 200×200 -m grid cells (as an approximation to the 100-m radius circle in the community occupancy model; 13764, 6905 and 14307 cells for Deramakot, Tangkulap and Segaliud Lokan, respectively) and extracted the same covariates as described above for each cell (Fig. 1a–c). Whereas camera stations covered only parts of the three reserves (Fig. 1), covariate values at camera stations were largely representative of values observed across the entire reserves (Table S1-2). Distance to water tended to be lower at camera-trap stations than across the entire study area, but values still ranged from near 0 to >2 km. We assumed that variation was sufficient to apply the estimated relationship of species occurrence with this covariate to the entire study area, where maximum distance to water was almost 4 km (Table S1-2). We then used parameter estimates to predict occupancy probability for each of the observed and estimated species in each grid cell, generated species occurrences and tabulated percentage of cells occupied per species and reserve (percentage of area occupied, PAO), and number of species per cell (all species and species listed on

the IUCN Red List of Threatened Species as Data Deficient, Near Threatened, or higher, henceforth referred to as 'IUCN-listed species' [Table S3-1]). We performed predictions for every 20th posterior sample of the parameters (1,500 samples total for the three Markov chains combined) and report the metrics of interest as the mode over these repeats, with standard deviation and 95% confidence interval (2.5 and 97.5 percentiles). Finally, for each species, we calculated the difference in PAO in Deramakot compared to Tangkulap and Segaliud Lokan, scaled to the average PAO across the three reserves.

To evaluate whether species richness correlates with carbon stock, we constructed aboveground biomass (AGB) maps for our study areas, using the National Dataset of Aboveground Live Woody Biomass density at spatial resolution of 500 m, derived from field/LiDAR(GLAS)/MODIS data collected between 2006 and 2008 (Baccini *et al.*, 2012). Landsat-based ground-truthed biomass reference data are available for Tangkulap and Deramakot (Langner *et al.*, 2012), and we used these to confirm the accuracy of the larger data set in our study areas (Appendix S5). The species richness predictions were resampled to the 500-m resolution of the AGB data. We centred and scaled both AGB and species richness data so that both data sets had a mean of 0 and a standard deviation of 1. We then subtracted the converted AGB values from converted richness values and plotted the resulting contrast scores for visual evaluation. We further present Spearman correlation coefficients between AGB and richness for each forest reserve and for all reserves combined.

RESULTS

Of the 28 mammal species in the analysis, we observed 27 in DFR and 25 in Tangkulap and Segaliud Lokan during a total of 2940 detections (Table S3-1). Pictures of muntjacs and chevrotains often could not be identified to the species level, and we therefore used the genus as analytical units. Identifiable records indicate that *Muntiacus* spp. consists mainly ($>90\%$) of Bornean Yellow (*M. atherodes*, Groves & Grubb, 1982) and potentially Southern Red Muntjac (*M. muntjak*, Zimmermann, 1780), and *Tragulus* spp. consists of Greater (*T. napu*, F. Cuvier, 1822) ($>60\%$) and Lesser Chevrotain (*T. kanchil*, Raffles, 1821).

All 31 species known from the study area were estimated to occur in the study sites (95 BCI 29–31 species). Associations with distance to water, distance to plantation and forest score varied among species in direction and strength (Fig. 1a–c). Occupancy probability was strongly associated with distance to water for three species (one positive, two negative, Fig. 1a). Two species showed a strong association with distance to plantation (one positive, one negative, Fig. 1b). Four species had strong associations with forest score (three positive, one negative, Fig. 1c). Detailed results can be found in Appendix S3.

Deramakot showed higher species richness per 200×200 -m cell than the other reserves, followed by Tangkulap, then

Segaliud Lokan (Fig. 2a). The pattern was similar when considering IUCN-listed species only (Fig. 2b). The percentage of area occupied (PAO) by the 28 observed species differed among reserves. Overall, 15 species had larger PAOs in Deramakot than in both other reserves, and five additional species had larger PAOs in Deramakot than one of the other reserves (Fig. 3). Predictions of PAOs can be found in Appendix S6.

AGB was highest in Deramakot, followed by Tangkulap, then Segaliud Lokan (Fig. 2c, Table S5-1). Overall correlation between AGB and richness was 0.55 (Spearman's rho; P -value < 0.01); by reserve, correlation was 0.17 for Deramakot ($P < 0.01$), 0.03 for Tangkulap ($P = 0.23$) and 0.32 for

Segaliud Lokan ($P < 0.01$). Areas high in AGB coincided largely with patterns in species richness (86–91% of all 500-m pixels had contrast values between 1.5 and -1.5 , Table S5-2), but there were notable exceptions: AGB was higher than species richness along the northern/north-western border of the study areas, and species richness was higher than AGB in southern parts of Deramakot, south-central parts of Segaliud Lokan and the centre of Tangkulap (Fig. 2d).

DISCUSSION

Forest certification schemes and carbon storage payments contribute to protecting tropical forests (Venter *et al.*, 2009b;

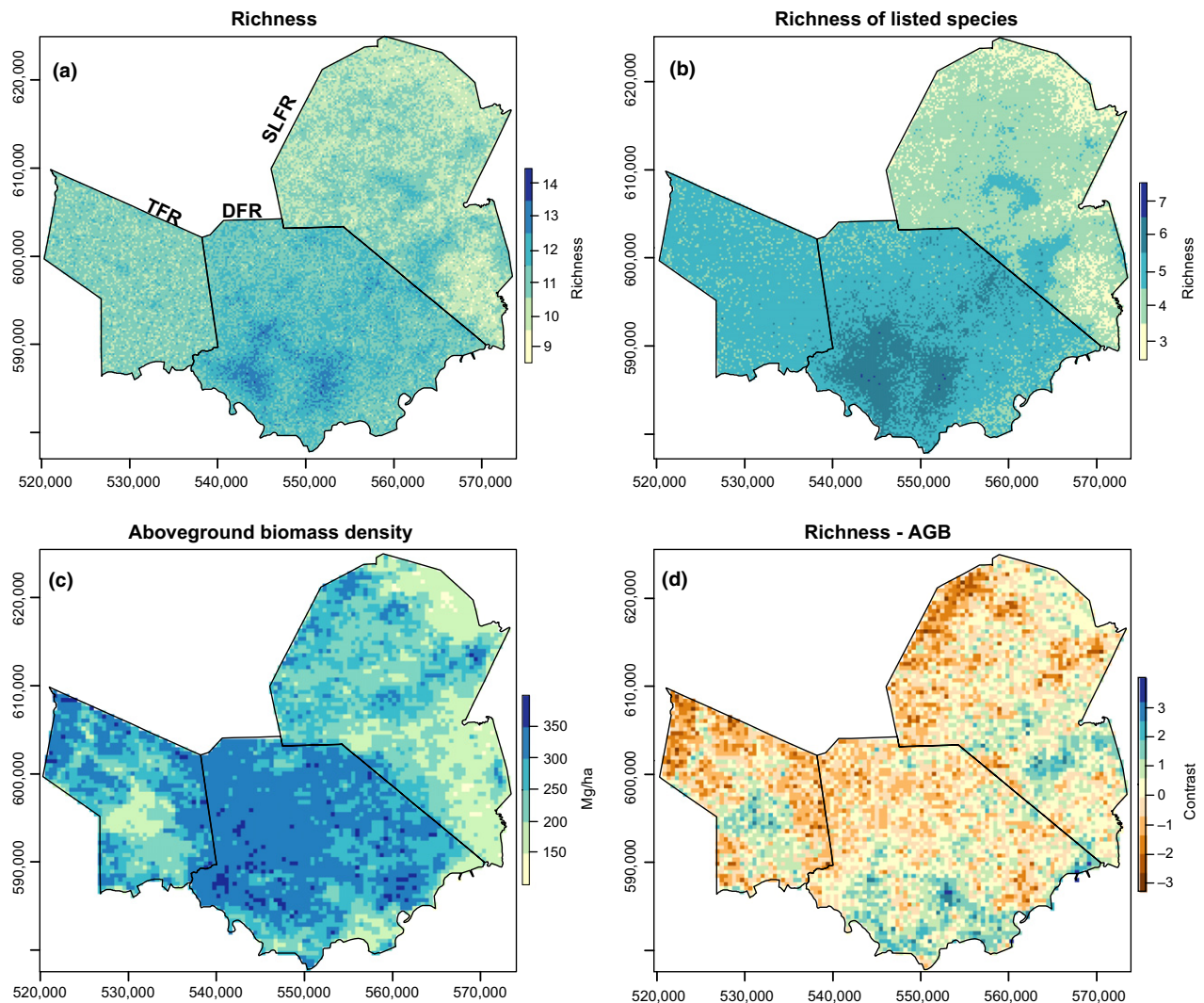


Figure 2 Predicted mammal species richness for Deramakot Forest Reserve (DFR), Tangkulap Forest Reserve (TFR) and Segaliud Lokan Forest Reserve (SLFR), from community occupancy model fit to camera-trapping data of 28 mammal species from the same reserves; (a) richness for all 31 species estimated to occur in the area; (b) for 15 species with IUCN Red List status of Near Threatened or higher. Legend for a and b shows number of species per 200×200 -m cell. (c) Aboveground biomass (AGB) density (Baccini *et al.*, 2012) and (d) difference between scaled species richness and scaled AGB (labelled 'contrast'; scores are close to 0 if both AGB and richness are at similar levels; positive when richness is higher than AGB [e.g. richness is high and AGB is average or low]; and negative when this situation is reversed); c and d at 500×500 m resolution. [Colour figure can be viewed at wileyonlinelibrary.com]

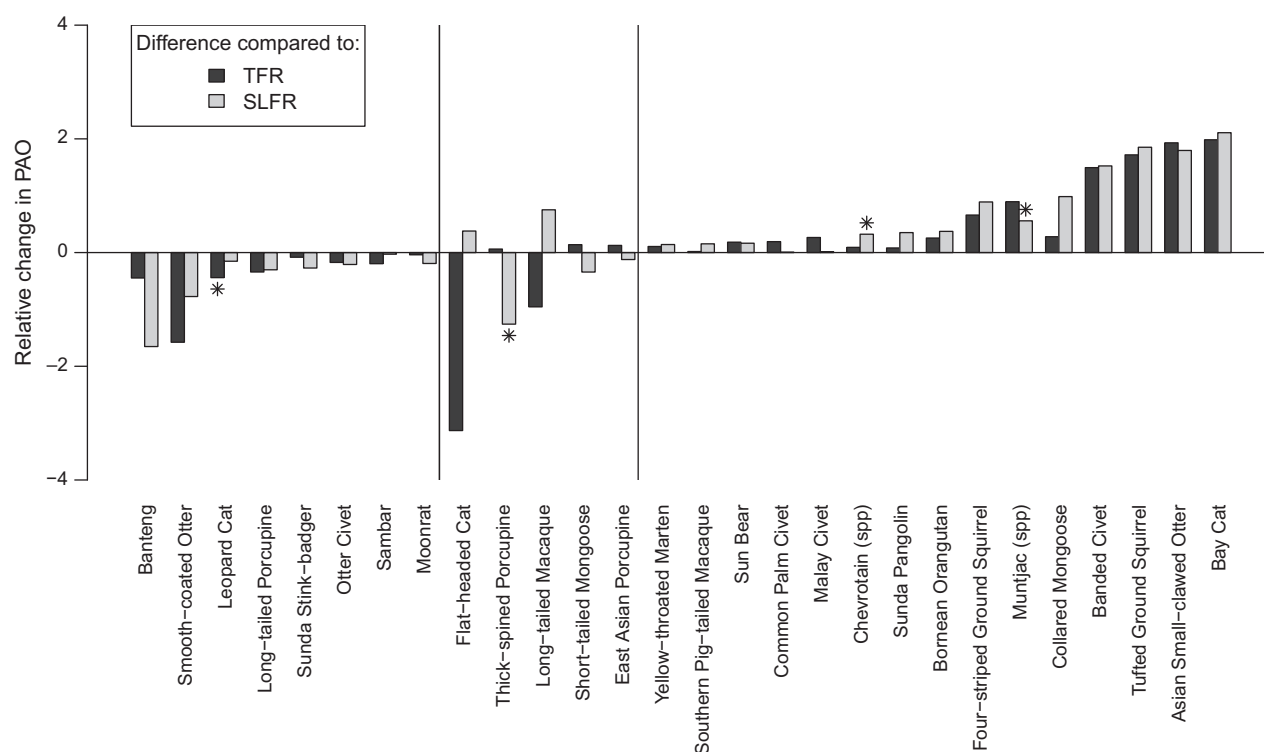


Figure 3 Difference in percentage of area occupied (PAO) between Deramakot Forest Reserve compared to Tangkulap Forest Reserve (TFR) and Segaliud Lokan Forest Reserve (SLFR), scaled to average PAO across reserves, for 28 Bornean mammal species, from a community occupancy model fit to camera-trapping data of 28 mammal species from the same reserves (left: PAO smaller in DFR; middle: PAO bigger in DFR compared to one other site; right: PAO bigger in DFR). Asterisks indicate a strong difference in PAO.

Strassburg *et al.*, 2010, 2012; Gibson *et al.*, 2011; Bicknell *et al.*, 2014), but their co-benefits for biodiversity conservation are challenging to quantify (Lindenmayer *et al.*, 2000). In the present study, we address this problem using camera trapping in combination with community occupancy modelling. Because our study includes only one certified site, we cannot make general statements about the benefits of FSC certification for the medium to large terrestrial mammal community. However, our case study does demonstrate that our approach presents a powerful tool for the evaluation of these benefits. The approach allows us to investigate spatial patterns of species richness and evaluate these patterns against forest management strategies or carbon stocks. At the same time, these models account for our imperfect ability to detect species, as well as for variation of detection probability across space, time and species. In modelling this variation, ecological parameters become comparable across time and space – a key requirement for a monitoring tool (e.g. Waldon *et al.*, 2011).

Although estimates of overall species numbers were similar across reserves, the more sustainable forest management practices in the FSC-certified Deramakot appeared to benefit the mammal community on two levels: it harboured higher levels of species richness for IUCN-listed species; and half of all species occupied consistently larger areas in Deramakot. These ‘winners’ of sustainable forestry included eight of the

15 IUCN-listed species, including the Endangered Bornean Orangutan (*Pongo pygmaeus*, Linnaeus, 1760) and the Critically Endangered Sunda Pangolin (*Manis javanica*, Desmarest, 1822, Fig. 3). In contrast, four of eight species occupying larger areas in both more intensely logged reserves were least concern, indicating higher tolerance to logging activities, or possibly even a benefit from the opening of the forest (e.g. Mohamed *et al.*, 2013). Our analysis also suggested that two endangered species were ‘losers’ of sustainable forestry, the Otter Civet (*Cynogale bennettii*, Gray, 1837) and Banteng (*Bos javanicus*, d’Alton, 1823). As a grazer, the Banteng is associated with open habitats (Wharton, 1968) and the semi-aquatic otter civet is associated with wetlands (Veron *et al.*, 2006). In our analysis, both habitats are confounded with disturbed areas, because we consider forest as high quality habitat.

Brodie *et al.* (2014) suggest that mammalian richness recovered from logging impacts within a decade. Tangkulap had not been logged for 8 years before our survey and is located next to Deramakot, enhancing the chances of locally extinct species to recolonize from the less disturbed reserve. Nevertheless, we found that it harboured lower cell-level species richness than Deramakot and lacked the richness ‘hot-spots’ (dark blue regions in Fig. 2a) observed in the other reserves. Tangkulap received FSC certification in 2011. Assuming that mammalian richness did not change

significantly in the two years after the present study, this would indicate that certification status alone is not a sufficient indicator of the biodiversity value of a forest. Systematic evaluation of the contribution that FSC-certified forests to biodiversity conservation can help determine whether restoration actions rather than mere safeguards of the status quo are needed in order to meet the biodiversity related FSC principles and criteria (FSC, 2014).

Besides habitat degradation and loss, hunting is a widespread threat to mammals throughout Southeast Asia (Corlett, 2007; Wilkie *et al.*, 2011), and the effects of hunting on occurrence of Bornean mammals have been identified as more severe than those of logging (Brodie *et al.*, 2014). Hunting pressure is much harder to quantify than structural habitat disturbances, and its intensity does not necessarily correlate with structural integrity of a forest (Peres *et al.*, 2006). Consequently, there are concerns that unless forest certification schemes directly address these threats, they may end up protecting structurally intact but 'empty' forests (Visseren-Hamakers *et al.*, 2012). Such 'empty' forests are a widespread phenomenon in Indochina, even in fully protected areas (Corlett, 2007). Although virtually absent from our study sites, there is likely some level of hunting, mainly along the reserve borders with oil palm plantations, which serve as an access point for hunters and stray dogs. Activity of domestic carnivores can reduce occupancy and impact activity patterns of native mammals (Gerber *et al.*, 2012; Farris *et al.*, 2015). This may contribute to the apparent pattern of decreasing IUCN-listed species richness near the northern/north-western limit of the forest reserves (Fig. 2b).

REDD+ payments are an opportunity to achieve biodiversity conservation under the umbrella of reducing carbon emissions (Strassburg *et al.*, 2010, 2012), but carbon stocks are not necessarily good predictors of biodiversity (Beaudrot *et al.*, 2016). Studies in Indonesia suggest that cost-effective allocation of REDD+ funds would provide protection for a large number of threatened mammal species (Venter *et al.*, 2009b), but also carry the risk of putting increased pressure on low-carbon, high diversity ecosystems (Paoli *et al.*, 2010). In our study, on a reserve scale, Deramakot had the highest amount of AGB (Table S5-1), while also being the most favourable site for mammals. On a smaller (within-reserve) scale, however, high AGB was not a consistent indicator of high species richness. Carbon and biodiversity are fundamentally different entities (Potts *et al.*, 2013), and whereas AGB is stationary, mammals are highly mobile and can readily adjust their distributions to real or perceived anthropogenic pressures from outside the reserve. Successful biodiversity conservation under REDD+ requires careful evaluation of the spatial distribution of carbon and biodiversity at multiple scales. The approach presented here provides a valuable tool to address these questions on a local and regional scale.

The combination of camera-trapping data with community occupancy models also has potential for the designation of high conservation value (HCV) forests. These forests are an integral part of FSC certification, require particularly

precautious forest management and are designated based on 'critical values', including the presence of globally, regionally or nationally significant concentrations of endemic or endangered species (FSC, 2009). Nevertheless, the scientific underpinning for the designation of HCV and objective criteria to evaluate their effectiveness is lacking (Edwards & Laurance, 2012; Senior *et al.*, 2014). In estimating the spatial distribution of species richness, the present approach provides an intuitive measure of 'concentrations of species in space', allowing the objective assessment of this designated critical value. A HCV forest patch may not be an appropriate spatial conservation unit in itself for wide-ranging species like mammals, but these patches have to be considered in the context of the entire (ideally sustainably) managed forest reserve. Here, a patch that is suitable for more species should contribute more to the overall conservation potential of the reserve than a patch that is used only by few species.

Camera-trapping surveys and occupancy modelling are no panacea: sampling effort is considerable, and in spite of a fairly large spatial coverage, parameter estimates of the present study could likely be improved with additional sampling stations. As mentioned, we had to remove some arboreal and wide-ranging species from the analysis. Further, community occupancy models can be sensitive to choice of the community (Pacifi *et al.*, 2014). Grouping all species may have caused us to miss some effects that are only present in certain subcommunities, but provides the best predictive performance of species richness, a key aspect of the present analysis. Finally, occurrence of a species does not necessarily reflect its abundance, which is a more informative measure of species status (MacKenzie & Nichols, 2004). Nevertheless, robust estimates of occurrence and species richness provide objective and ecologically meaningful measures to quantify co-benefits of certified forests. Occupancy modelling is equally suitable for other taxa, such as birds (White *et al.*, 2013) or amphibians (Bailey *et al.*, 2004), and for other survey techniques, such as direct encounters or novel invertebrate-derived DNA (iDNA) sampling (Calvignac-Spencer *et al.*, 2013; Ficetola *et al.*, 2014; Schnell *et al.*, 2015). Thus, community occupancy models provide a broadly applicable framework for comprehensive biodiversity monitoring. As such, it is an ideal tool in the context of forest certification schemes and carbon stock enhancement programmes, where standardized protocols to assess biodiversity co-benefits are urgently needed (Waldon *et al.*, 2011; Gardner *et al.*, 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Habitat composition in study sites.

Appendix S2 Analysis of spatial autocorrelation in model residuals.

Appendix S3 Data summary, formal model description and parameter estimates of the community occupancy model for Bornean mammals.

Appendix S4 JAGS model code for community occupancy model.

Appendix S5 Validation of the national aboveground biomass data set and contrast of aboveground biomass with mammal species richness.

Appendix S6 Community occupancy model predictions.

BIOSKETCH

Our group (Junior Research Group: Biodiversity and Biogeography of Southeast Asia, <http://www.izw-berlin.de/about-us-729.html>) is interested in developing standardized biodiversity survey and monitoring approaches for the threatened medium to larger sized mammal communities of Southeast Asia. We combine field surveys with state-of-the-art analytical techniques that take into account the imperfect ability to detect these elusive species. We mainly focus on camera-trapping projects, but we are also developing modern environmental and invertebrate-derived DNA techniques.

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