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LETTER

Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes

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Abstract

Zero-deforestation commitments seek to decouple agricultural production and forest loss to improve prospects for biodiversity. However, the effectiveness of methods designed to meet these commitments is poorly understood. In a highly fragmented tropical landscape dominated by oil palm, we tested the capacity for the High Carbon Stock (HCS) Approach to prioritize forest remnants that sustain mammal diversity. Patches afforded high priority by HCS protocols (100 ha core area) provided important refuges for IUCN-threatened species and megafauna. However, patch-scale HCS area recommendations conserved only 35% of the mammal community. At least 3,000 ha would be required to retain intact mammal assemblages, with nearly 10 times this area needed if hunting pressure was high. While current HCS protocols will safeguard patches capable of sustaining biodiversity, highly fragmented tropical landscapes typical of zero-deforestation pledges will require thinking beyond the patch toward strategically configured forest remnants at the landscape level and enforcing strict controls on hunting.

KEYWORDS

biodiversity, camera-trapping, habitat fragmentation, High Carbon Stock Approach, land-use planning, occupancy modeling, oil palm, RSPO, Southeast Asia, tropical forest

1 | INTRODUCTION

Tropical forests are important reservoirs for biodiversity, but are compromised by anthropogenic activities (Barlow et al., 2018). Over 200 million ha of tropical forest has been lost since 1950 (Rosa, Smith, Wearn, Purves, & Ewers, 2016), with the remaining 1.1 billion ha comprising 130 million fragments (Taubert et al., 2018). Deforestation and fragmentation erode biodiversity by reducing effective habitat area and quality, and increasing exposure to disturbance

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(Barlow et al., 2016; Pfeifer et al., 2017). To avert biodiversity collapse in tropical regions, deforestation must be curbed.

Agricultural conversion accounts for up to 78% of tropical deforestation, with grave consequences for vertebrates (Curtis, Slay, Harris, Tyukavina, & Hansen, 2018; Deere et al., 2018). Oil palm (*Elaeis guineensis*) is at the forefront of conservation concerns, occupying 18.7 million ha of land with expansion driven by high productivity and accelerating demand (Meijaard et al., 2018). Much of the ecologically suitable land identified to meet future agricultural expansion is in highly biodiverse ecosystems (Pirker, Mosnier, Kraxner, Havlík, & Obersteiner, 2016). We therefore need to capitalize on opportunities to reconcile production and conservation of tropical biodiversity.

Voluntary standards have emerged to help eliminate deforestation from commodity supply-chains through "zero-deforestation" pledges (Lyon & Maxwell, 2008). These pledges are widespread in the oil palm industry, with most leading producers committed to zero deforestation (Meijaard et al., 2018). The High Carbon Stock (HCS) Approach represents the dominant landscape-planning tool to achieve zero-deforestation in the sector and is now embedded in certification standards through the Roundtable for Sustainable Palm Oil (http://highcarbonstock.org/leading-palm-oil-certification-system-adopts-no-deforestation-requirements/). HCS directs agricultural conversion toward degraded land of low carbon and biodiversity value to minimize the environmental footprint of production. Land is stratified into discrete classes based on vegetation density and structure, which serve as proxies for aboveground carbon stocks and support varying levels of biodiversity (Deere et al., 2018). HCS then prioritizes forest remnants for protection or clearance based on ecological criteria (habitat quality, patch size, connectivity). While the protocol seeks to optimize ecological functionality and development outcomes, the influence of these factors on patch biodiversity is yet to be fully evaluated in a HCS context, despite being fundamental to confirming whether methodologies aligned with zero-deforestation commitments are compatible with conservation.

Habitat fragmentation increases human access to forests, yet the combined impacts of fragmentation and secondary disturbances, such as hunting and overexploitation, are rarely considered in policy or research (but see Michalski & Peres, 2007; Peres, 2001). Primarily, this is due to difficulties in detecting and quantifying the spatial signature of human pressure. For instance, hunting can be pervasive in oil palm plantations (Azhar et al., 2013), but remains largely unaccounted for in sustainability commitments. Failure to account for the role of fragmentation in facilitating hunting may introduce systematic bias into assessments of fragmentation impacts, resulting in failure to meet conservation objectives and illustrating the importance of teasing apart multiple drivers of biodiversity loss.

Here, we quantify forest fragmentation impacts on biodiversity to inform the HCS methodology underpinning zero-deforestation commitments. Our study area in Malaysian Borneo has experienced some of the highest tropical deforestation rates globally (Hansen et al., 2013). Malaysia is a major oil palm producer, contributing 34% of the global supply at the expense of 2.1 million ha of forest in Borneo alone (Gaveau et al., 2016). Despite such land-use change, Southeast Asia has been underrepresented in global fragmentation assessments (Deikumah, Mcalpine, & Maron, 2014), limiting the evidence-base supporting regional conservation strategies. We develop a modeling framework to understand the relationship between HCS fragmentation metrics and biodiversity, while accounting for the influence of cumulative disturbance (hunting and forest quality) effects. Our appraisal focuses on tropical forest mammals because they are particularly sensitive to fragmentation and hunting, and prioritized in conservation (Schipper et al., 2008). We ask whether forest patches prioritized under HCS protocols are sufficient to ensure tropical mammal persistence.

2 | MATERIALS AND METHODS

2.1 | Study system

Research was conducted at the Stability of Altered Forest Ecosystems (SAFE) project (www.safeproject.net) and adjacent oil palm estates in Sabah, Borneo (4°33′N, 117°16′E). The study area comprises lowland and hill dipterocarp forest, and forest fragments of standardized sizes have been retained within the agricultural matrix for long-term research.

We established 128 randomized sampling locations across the landscape, stratified across continuous forest controls ($N = 60$) and fragmented forest sites ($N = 68$; Figure 1a). Fragments were defined via the HCS protocol (i.e. by core area, determined by applying a negative buffer of 100 m to a forest map; Hansen et al., 2013). Sampled fragments were 1–590 ha in size, broadly capturing the dominant size classes of remnant forest patches across Asia (average = 52 ha; Brinck et al., 2017).

To sample the mammal community, we obtained detection/non-detection data from camera-traps (Reconyx HC500, Wisconsin) between June 2015 and December 2017. We define the community as 38 medium-large species (>1 kg) that can be reliably detected using our methods. Camera-traps were deployed across sampling locations (Figure 1b, mean distance between sites = 1.4 km) using a paired design, whereby coupled units were positioned up to 250 m apart (mean = 207 m). Units were deployed for at

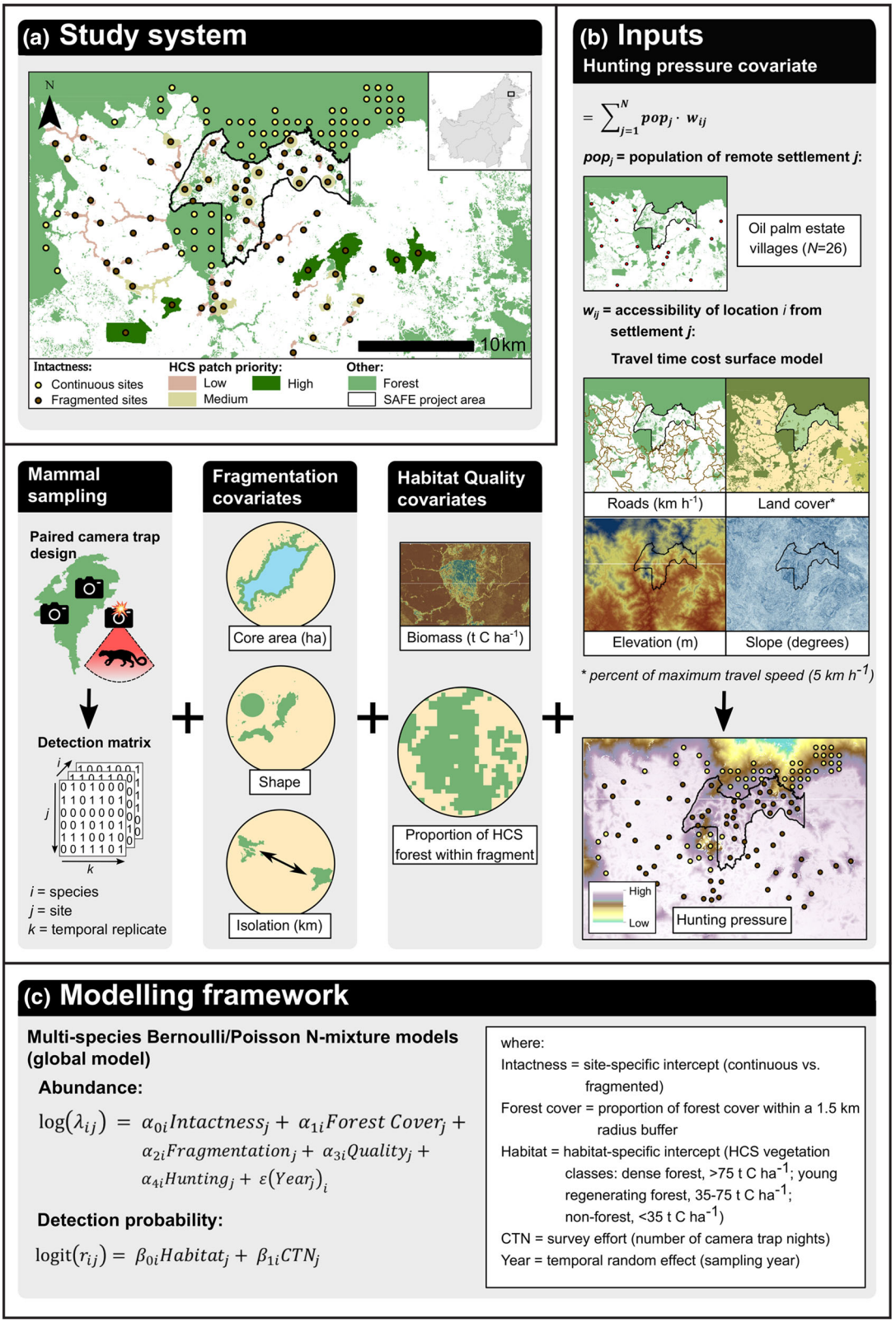


FIGURE 1 Methodological framework to assess the impacts of forest fragmentation and secondary disturbance on tropical mammals, including (a) sampling design across the study region in Sabah, Borneo, including the broader geographic context of Southeast Asia (inset). Camera-trap locations (points) were partitioned across continuous and fragmented forest sites. Sampled forest fragments were color coded to reflect their HCS conservation priority designation; (b) details of mammal sampling, covariates, and processing protocols, and; (c) formal description of our modeling procedure, introducing the global model from which 11 candidate models were formulated to determine the individual and cumulative influence of fragmentation, habitat quality, and hunting metrics on mammal abundance

least 42 consecutive nights, providing a total effort of 10,097 camera-trap nights.

2.2 | Determinants of mammal persistence

We compiled spatially explicit, patch-scale fragmentation metrics to capture key criteria from the HCS prioritization decision tree (Rosoman, Sheun, Opal, & Anderson, Trapshah, 2017): core area, shape, and isolation. Following HCS protocols, metrics were quantified for all patches with a threshold carbon value exceeding 35 t C ha^{-1} using LiDAR-derived aboveground carbon maps (Asner et al., 2018). We also derived measures of forest quality and hunting pressure to reflect secondary disturbance impacts. Forest quality was quantified as biomass (t ha^{-1}) and a HCS-specific patch-scale measure of the proportion of dense forest (>75 t C ha^{-1}). We developed a bespoke hunting metric based on modified human population pressure surfaces (Platts 2012), which assumes population pressure at a location increases with population density of remote settlements, weighted by a distance decay function (Figure 1b). The decay function imposes accessibility constraints on the spread of human pressure using a travel time cost surface model (Frakes, Flowe, & Sherrill, 2015). Commonly implicated drivers of hunting pressure (proximity to infrastructure, Benitez-Lopez et al., 2017; and human population density, Harrison et al., 2016) were also examined to gauge the value of our metric. Further details of covariate processing are presented in Supporting Information S1.

2.3 | Modeling framework

We employed hierarchical multi-species Bernoulli/Poisson *N*-mixture models to determine the influence of HCS fragmentation metrics and secondary disturbance impacts on mammal abundance (Royle & Nichols, 2003). Throughout, we interpret abundance as a relative measure and restrict inference to spatial comparisons. Specific model details are presented in Figure 1c and Supporting Information S2.1 and S2.2.

We constructed 11 models to explore the additive effects of predictors on mammal abundance (Table 1). Predictors were calculated as weighted-averages between paired camera-trap units based on the proportion of survey effort each unit contributed to the sampling location. Prior to modeling, scale-optimization methods were used to ascertain the optimal spatial extents for predictors. We ran single covariate hierarchical multi-species models to identify the best fitting buffers for each predictor across a range of radii (50, 100, 250, 500, 1000, 1500, 2500, 5000 m), and calculated WAIC (Watanabe–Akaike Information Criterion; Watanabe, 2010) to select variables at optimal scales and provide quantitative comparisons between candidate models. Models with ΔWAIC <2 were considered to have substantial support,

TABLE 1 Performance of models assessing the impact of alternative forest fragmentation, quality, and hunting metrics on mammal abundance

Model and predictors	WAIC	ΔWAIC	WAIC*w*
1. *Fragmentation* + *Quality*: Core + Shape + Isolation + Biomass + Prop_HCS	**4,196.14**	**0.00**	**0.58**
2. *Fragmentation* + *Hunting* + *Quality*: Core + Shape + Isolation + Hunt_Press + Biomass + Prop_HCS	**4,197.45**	**1.31**	**0.30**
3. *Fragmentation*: Core + Shape + Isolation	4,200.18	4.04	0.08
4. *Fragmentation* + *Hunting*: Core + Shape + Isolation + Hunt_Press	4,202.26	6.12	0.03
5. *Fragmentation* + *Hunting* + *Quality*: Core + Shape + Isolation + Pop_Density + Dist_Roads + Dist_Village + Biomass + Prop_HCS	4,206.00	9.86	0.00
6. *Hunting* + *Quality*: Hunt_Press + Biomass + Prop_HCS	4,208.25	12.11	0.00
7. *Quality*: Biomass + Prop_HCS	4,208.69	12.55	0.00
8. *Fragmentation* + *Hunting*: Core + Shape + Isolation + Pop_Density + Dist_Roads + Dist_Village	4,209.63	13.50	0.00
9. *Hunting*: Hunt_Press	4,210.13	13.99	0.00
10. *Hunting* + *Quality*: Pop_Density + Dist_Roads + Dist_Village + Biomass + Prop_HCS	4,216.10	19.96	0.00
11. *Hunting*: Pop_Density + Dist_Roads + Dist_Village	4,222.68	26.54	0.00

Core: core forest patch area (area within patch after subtracting a 100 m internal buffer; ha); Shape: ratio of patch perimeter and perimeter of an optimally compact patch of comparable area; Isolation: distance (km) to nearest continuous forest (patch > 10,000 ha); Hunt_Press: bespoke hunting pressure metric combining human population density, accessibility (using a travel-time cost surface model), distance from roads and distance to villages; Pop_Density: population density (people km^{-2}); Dist_Roads: distance (km) to the nearest road; Dist_Villages: distance (km) to the nearest village; Biomass: aboveground biomass (t ha^{-1}); Prop_HCS: proportion of High Carbon Stock forest (>35 t C ha^{-1}).

Models are presented in descending performance order based on Watanabe–Akaike Information criterion (WAIC). ΔWAIC indicates variation in WAIC relative to the top-ranking model; WAIC*w* denotes Akaike weights and further quantifies strength of evidence between competing models. Models were considered to have comparable statistical support if they were within two ΔWAIC (presented in bold). Although not presented, every model contained a forest cover covariate to differentiate fragmentation from habitat loss.

and evidence ratios were calculated to assess the explanatory power of competing models (adapting AIC principles in Burnham, Anderson, & Huyvaert, 2011; see Supporting Information S2.3). Throughout, we only present findings for models deemed to have substantial support, containing predictors derived from optimal scales (Table S1). See Supporting Information S2.4, S3 and Table S2 for further information on model specification and predictive performance checks.

To evaluate HCS patch prioritization protocols, we compared the biodiversity value of forest remnants classified according to core area criteria (low priority: <10 ha; medium priority: 10–100 ha; high priority: >100 ha; Figure 1), where the lowest priority patches are eligible for conversion. To determine trait-mediated responses, we partitioned species according to their IUCN conservation status ("non-threatened": least concern, near-threatened; "threatened": vulnerable, endangered, critically endangered), ecological specialism ("generalist"; "specialist"), body size ("medium": <5 kg; "large": 5–25 kg; "mega": >25 kg), and trophic guild ("carnivore"; "herbivore"; "frugivore"; "insectivore"; "omnivore") (Table S3).

To determine the efficacy of HCS criteria to safeguard mammal communities, we derived species richness estimates from model outputs and explored their association with patch core area, the principal factor governing conservation priority under HCS. Expected species richness was calculated as the sum of species occupancy probabilities (Ψ), derived as a deterministic function of abundance ($\Psi_{ij} = 1 - \exp(-\lambda_{ij})$, under our assumption of a Poisson distribution, i.e. probability of at least one individual using the site). We then used the richness–area relationship to determine the optimal fragment size at which the number of predicted species approached that of an intact mammal community ($N = 38$). Recognizing the potential influences of secondary disturbance on patch suitability, we replicated this process, incorporating measures of hunting pressure and forest quality alongside core area. Throughout these calculations, non-target predictors were fixed at average values. Predictions were extrapolated to provide an indication of the patch-scale core area requirements necessary to maximize mammal representation.

3 | RESULTS

3.1 | Biodiversity value of HCS priority forest remnants

According to results averaged across our highest ranking models (Models 1 and 2; Table 1), high priority patches consistently harbored greater levels of mammal abundance than low and medium priority ones (Figure 2). Specifically, they were important for threatened (compared to medium priority: 37.2% increase, 95% Bayesian credible interval [BCI]: 33.3–37.7%; low priority: 45.1% increase, 37.3–47.7%) and mega-bodied species (medium priority: 40% increase, 37.4–44.9%; low priority: 46.7% increase, 39.9–49.9%). Low and medium priority patches supported comparable mammal abundance across all trait groups and guilds.

3.2 | Model performance

The model incorporating forest fragmentation and quality measures (WAIC = 4,196.14; Table 1) achieved equivalent statistical support to that also including hunting pressure (WAIC = 4,197.45). Evidence ratios suggest that these models were 7.5 and 3.9 times more likely, respectively, than those limited to fragmentation metrics alone. When considered independently, the model containing fragmentation metrics (WAIC = 4,200.18) had greater support than those comprising hunting (WAIC = 4,210.13) or quality metrics (WAIC = 4,208.69) in isolation. The bespoke hunting metric (WAIC = 4,210.13) had greater explanatory power than the disaggregated hunting proxies (WAIC = 4,222.68), and was over 100 times more likely.

3.3 | An evidence base for zero-deforestation support tools

At the community level, forest fragmentation, quality, and hunting influenced mammal abundance (Figure 3). Mean local abundance was positively and strongly associated with patch core area (posterior mean: 0.11, BCI: 0.05–0.21) and the proportion of HCS forest within remnant patches (0.09, 0.02–0.23). Moreover, local abundance was negatively associated with isolation (-0.12, -0.24 to -0.01). Hunting impacts were supported, albeit weakly (-0.16, -0.31 to -0.02), highlighting some sensitivity to anthropogenic pressure. However, some individual species demonstrated a strong negative response to hunting pressure (Figures S2 and S3). Species-specific responses to fragmentation and forest quality metrics are presented in Figures S4–S8.

Only modest gains in mammal diversity were achieved across fragment sizes varying in core area from 0 to 500 ha (Figure 4). At the minimum HCS core area threshold of 10 ha, only 13 (10.7–14.9) of the 38 species (33%, 28.2–39.2%) were estimated to be present (Table 2). At 100 ha, the criterion for high priority patches, no additional species were preserved (predicted richness: 13, 11.2–15.9). Extrapolating this model suggests a core area of 3,199 ha (2,131–5,182 ha) would be needed to conserve diversity equivalent to that of an intact mammal community (Table 2), assuming fragments are of average habitat quality (comprising 60% HCS forest) and free of secondary disturbance impacts. However, core area requirements to retain intact assemblages were reduced to 2,108 ha (1,653–2,749 ha) by increasing forest quality at the patch scale.

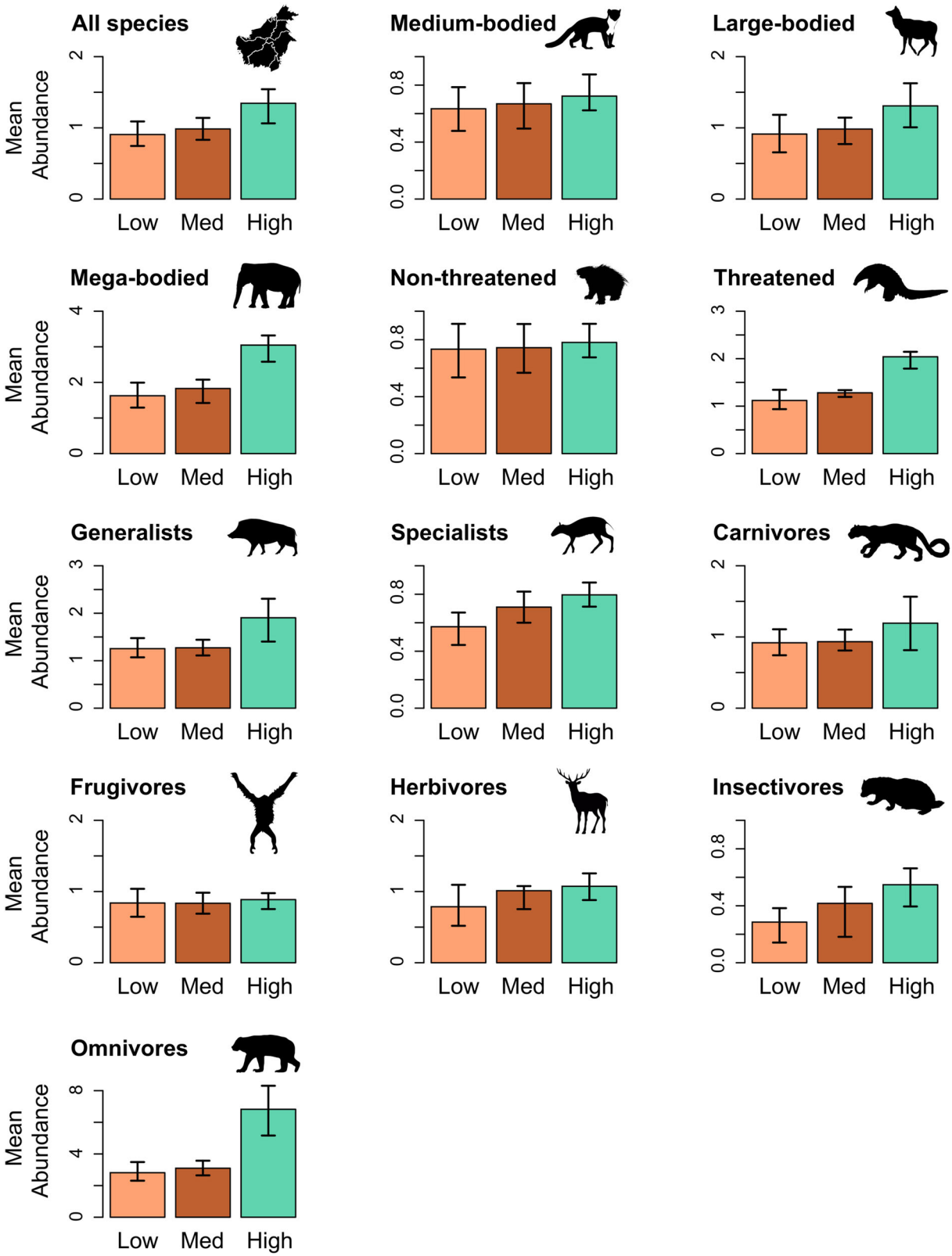


FIGURE 2 Local abundance of mammals (averaged across species) within HCS designated conservation priority forest patches (low priority patch: <10 ha; medium priority patch: 10–100 ha; high priority patch: >100 ha), for all species and partitioned according to body size, threat status, degree of ecological specialism, and trophic guild. Error bars reflect uncertainty and are expressed as 95% Bayesian credible intervals

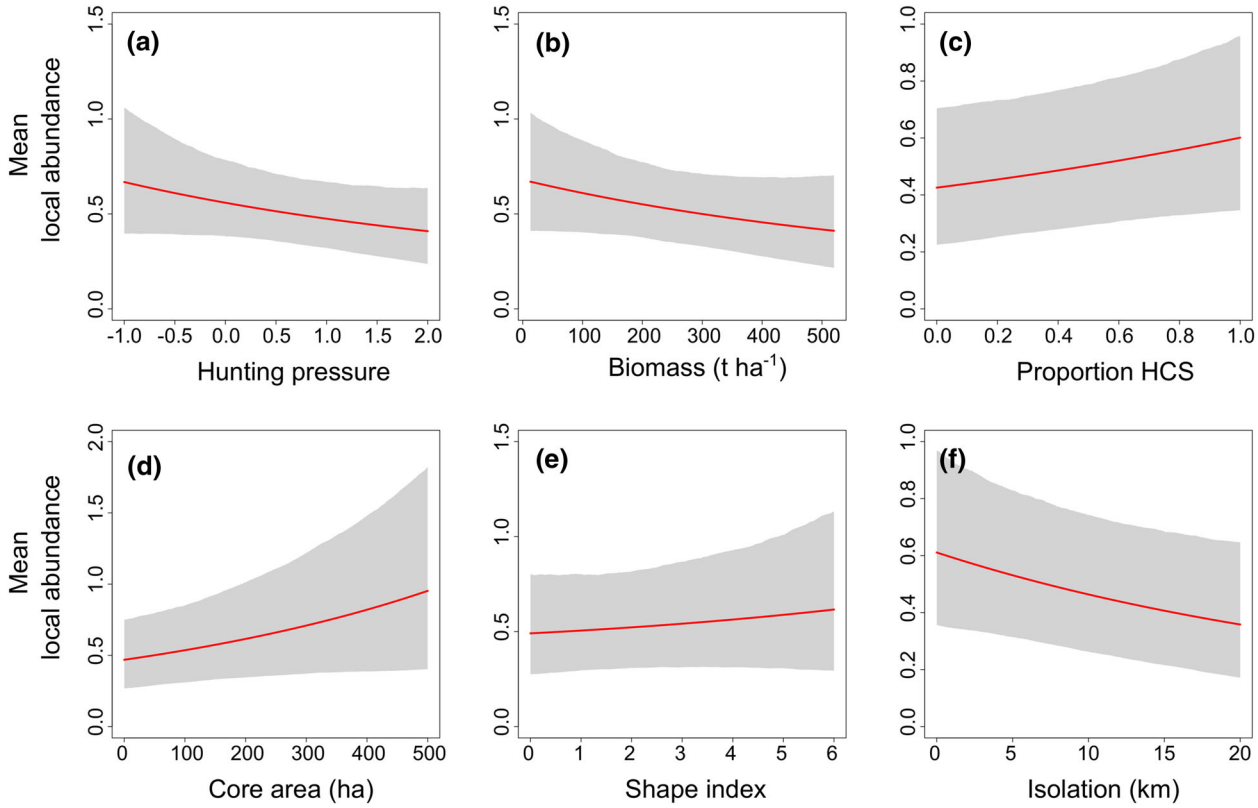


FIGURE 3 Local mammal abundance (averaged across species) relative to (a) hunting; forest quality (b: biomass; c: proportion HCS), and; forest fragmentation (d: core area; e: shape; f: isolation). Predicted mean posterior distribution values are presented in red, while 95% Bayesian credible intervals are shaded gray

Under a range of patch size configurations, hunting pressure limited the potential conservation gains of increasing patch core area (Figure 4). We predict that in forest fragments experiencing hunting, at least 27,498 ha of core area (17,870–85,797 ha) would be required to achieve the full complement of mammal species. However, the deleterious impacts of hunting can be offset considerably by habitat quality, reducing the area required to conserve intact communities to 4,531 ha (2,536–6,082 ha).

4 | DISCUSSION

4.1 | Biodiversity in HCS-delineated forest remnants

HCS is the principle methodology to support zero-deforestation commitments for oil palm companies. Therefore, the extent to which zero-deforestation pledges contribute to conservation is dependent on the capacity of HCS-prioritized forest remnants to sustain biodiversity. We found that high priority patches contained significantly higher concentrations of mega-bodied and threatened species compared to low/medium priority ones. Such species tend to have traits that make them sensitive to habitat fragmentation (Keinath et al., 2017) and, within current HCS guidelines, the high priority designation affords them greater refuge.

Low and medium priority patches supported comparably lower mammal abundance across all species and guilds. Under HCS, these patches can be converted to oil palm if they are shown to have negligible biodiversity value. These results indicate that directing conversion toward smaller fragments could minimize biodiversity impacts in agricultural concessions if larger patches are conserved. However, meeting area-requirements for many species will be difficult to achieve in most conversion settings because the majority of patches (91%) are low and medium priority (i.e., 10–100 ha) in our study landscape and elsewhere in the tropics.

Patch-scale fragmentation metrics were the strongest determinants of mammal abundance. At the community level, mammals were more abundant in forest remnants comprising a large core area and close to continuous logged forest. Larger fragments harbor greater capacity to sustain wildlife populations and are more robust to edge effects (Laurance, 2008). In a pan-tropical assessment, mammal abundance declined by 57% toward forest edges (Pfeifer et al., 2017). Less isolated fragments experience higher colonization rates, with immigration providing a demographic safeguard from local extinction.

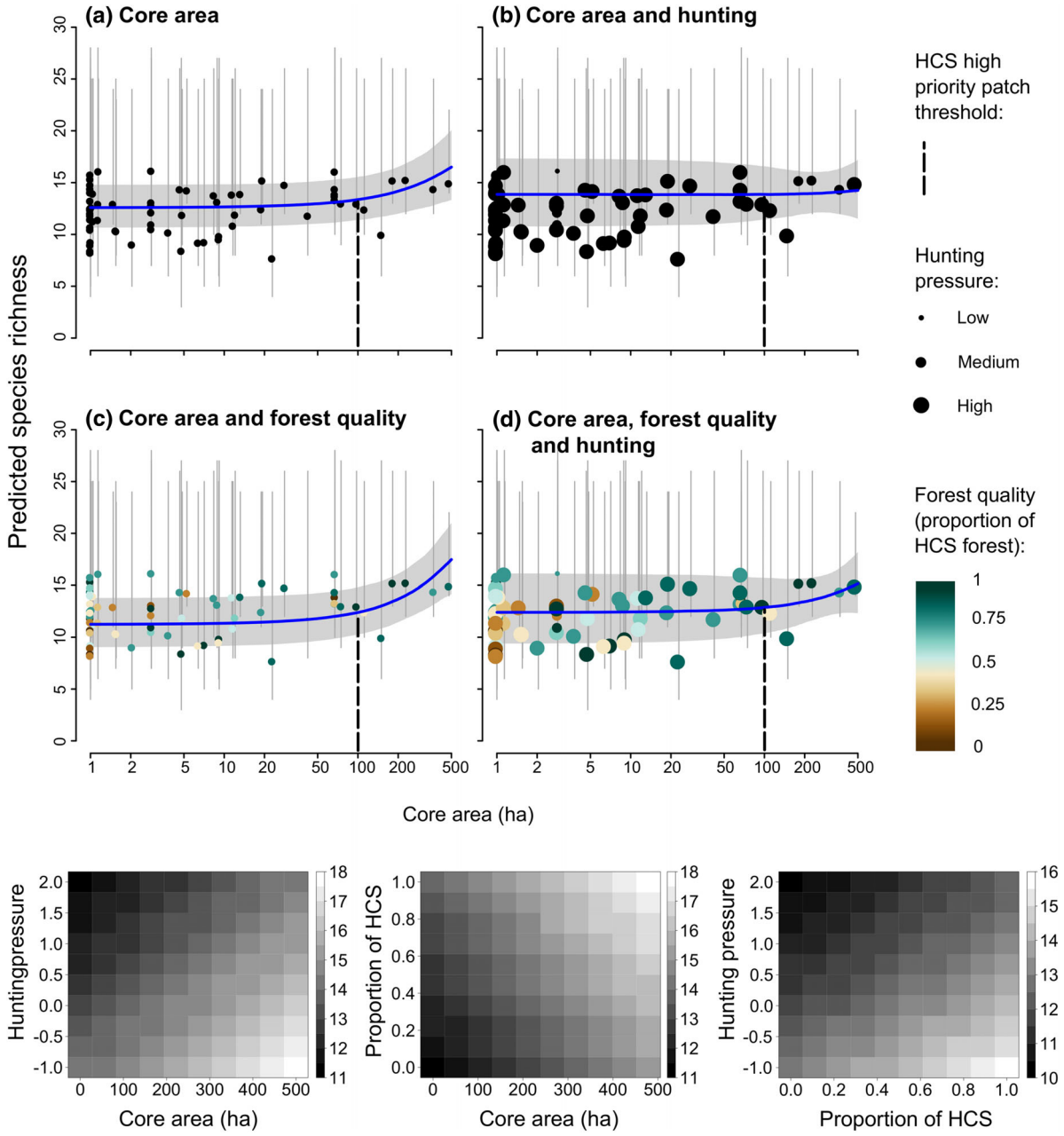


FIGURE 4 Total estimated species richness at sampled forest fragments based on (a) core area; (b) additive effects of core area and hunting pressure; (c) core area and habitat quality, and; (d) core area, hunting pressure, and habitat quality. Black points represent site-specific species richness values (derived as the sum of conditional occupancy) and their associated error (95% Bayesian credible intervals [BCI]; vertical gray lines). Color graded points denote habitat quality expressed as the proportion of HCS forest contained within the fragment. Hunting pressure is expressed through point size, with larger points indicating increasing hunting pressure. Solid blue lines indicate predicted mean posterior distribution values for species richness, while gray shaded areas represent 95% BCIs. The HCS high priority patch threshold is presented as a dashed black line. All horizontal axes on scatterplots are visualized on the logarithmic scale. Level plots (e–g) demonstrate pairwise responses between core area, hunting pressure, and forest quality. All predictions were based on parameters extracted from models with substantial support, with non-target predictors fixed at average values

Hunting can potentially amplify fragmentation impacts on mammals. Indeed, models incorporating the hunting metric had considerably more support than those containing fragmentation metrics alone. Mammals generally declined in areas of high hunting pressure, characterized by high human density and ease of access, which are both considered key determinants of hunting across the tropics (Benitez-Lopez et al., 2017; Harrison et al., 2016). Given the scale of road development associated with commodity agriculture, even forest fragments remote from settlements are vulnerable

TABLE 2 Estimated number of mammal species that can be conserved for a given forest patch core area (ha) in oil palm

Core area (ha)	Species richness	BCI
10	12.7	10.7–14.9
Minimum HCS patch threshold criteria	(33.3)	(28.2–39.2)
100	13.4	11.2–15.9
Current HCS High Priority Patch threshold	(35.2)	(29.4–41.8)
200	14.2	11.7–17
Recommended by (Lucey et al., 2017)	(37.3)	(30.8–44.7)
500	16.6	13.3–20.2
	(43.6)	(35–53.3)
1000	20.5	15.9–25.7
	(54.0)	(41.9–67.6)
1500	24.5	18.6–31.1
	(64.5)	(48.9–81.9)
2000	28.5	21.2–36.6
	(74.9)	(55.8–96.2)
2500	32.4	23.8–42.0
	(85.4)	(62.8–100.0)
3200	38.0	27.5–49.6
Required to achieve species richness equivalent to an intact mammal community	(100.0)	(72.5–100.0)

Species richness was derived as the sum of species occupancy probabilities (derived from abundance estimates). Uncertainty is expressed using 95% Bayesian credible intervals (BCI). We report the proportion of an intact mammal community ($N = 38$) represented by these richness values in parentheses.

to anthropogenic encroachment. We found little evidence of scale-dependent effects of patch size on hunting pressure, specifically in relation to HCS priority designation (average hunting pressure: low priority = 1.12; medium priority = 1.10; high priority = 0.96) and core area ($r = 0.11$). This suggests that any interaction between fragment area and anthropogenic pressure may break down when accessibility is high.

The relatively weak mammal community response to hunting pressure obscured steep declines in ungulates (Figures S2 and S3), which comprise >70% of hunted species consumed in Sabah (Bennett, Nyaoi, & Sompud, 2000) and the dominant taxa in forest fragments. Hunting in much of tropical Asia is opportunistic (Harrison et al., 2016), so the most affected species tend to be those with the highest abundance. Previous work found that plantation workers and poachers from neighboring settlements hunt in oil palm estates (Azhar et al., 2013). It is possible that our metric underestimated hunting pressure since it was restricted to the impacts of plantation workers, but this is unlikely as other settlement types are situated a considerable distance away. Due to the high level of immigrant workers employed on plantations, it is difficult to generalize hunting behavior, as it tends to be culturally specific (Luskin, Christina, Kelley, & Potts, 2014). Nonetheless, our findings indicate that in landscapes devoid of detailed socio-demographic/economic data, effective spatially explicit proxies for hunting pressure can be developed using freely available remote-sensing data at scales appropriate to conservation management.

Habitat quality, measured as the proportion of HCS-delineated forest within a patch, was positively associated with abundance. An increasing proportion of HCS forest within remnant patches likely corresponds to greater structural complexity, which has been identified as a key determinant of animal abundance (Davies & Asner, 2014). Moreover, structurally complex environments could potentially hinder human hunting practices, particularly where dense understory vegetation precludes access. Maintaining and restoring patch quality, as well as quantity, should therefore be central to forest management in production landscapes.

4.2 | Policy recommendations

A key obstacle to effective policy in production landscapes is a limited understanding of the optimal patch sizes needed to sustain biodiversity. This is particularly relevant to HCS, which specifies core area as the principle criterion underpinning prioritization. Our results indicate that by conserving any forest fragment with a core area >100 ha, the current HCS high priority patch threshold is effective at safeguarding ~35% of mammal species that would be present in contiguous forest. This is far lower than the 70% representation reported previously in the oil palm fragmentation literature (Lucey et al., 2017). Indeed, patches would need to be far larger (1,500 ha) to represent this proportion of the mammal community. Where available, patches approaching this size class should be retained as a conservation priority to meet biodiversity conservation objectives in production landscapes. However, with the average patch size in sustainably managed plantations falling well below this threshold (120 ha; Scriven et al., 2019), it is clear that collective conservation management of multiple fragments is more realistic than patch-based approaches in real world applications. Consequently, we advocate a shift to cumulative patch management, placing greater emphasis on total forest cover and patch configuration. For example, depending on forest quality, 2,000–3,000 ha core area would be required to retain species richness equivalent to that of an intact mammal community in our study landscape. Given the high opportunity costs of forgoing development, it is unlikely that these area requirements can be met at the patch–scale. To this end, riparian remnants and small fragments, regardless of HCS designation, should also be viewed

as integral components of the landscape to enhance connectivity between high priority patches and contiguous forest areas.

We demonstrated that hunting pressure suppresses area-mediated gains in species numbers, increasing the area required to maintain species richness equivalent to an intact mammal community by an order of magnitude. Hunting is often highly restricted on plantations and illegal for some species, but previous work indicates that restricted admission and plantation patrols are often insufficient deterrents (Azhar et al., 2013). Similarly, research from nearby Sumatra indicates that species-focused awareness raising activities may also be ineffectual, so anti-hunting campaigns should lever personal values to incentivize behavioral change (St. John et al., 2018). The impacts of hunting pressure can be alleviated to some degree by the maintenance and restoration of forest quality within fragments, which reduces the area required to support intact mammal communities to around 50% higher than an otherwise equivalent fragment free from hunting pressures.

4.3 | Conclusions

As zero-deforestation commitments gain traction, it is imperative to qualify their biodiversity credentials. This is especially true for oil palm as production has doubled every decade since 1970, often at the expense of highly biodiverse ecosystems (Austin et al., 2017). HCS is formally integrated into oil palm certification standards, influencing the landscape management of 10 million ha to date (G. Rosoman, pers. comm.). In summary, our findings show that cumulative patch management is needed if production and biodiversity conservation are to be reconciled. Prioritization protocols such as HCS should recognise the ecological role of small patches beyond their immediate biodiversity value (Struebig et al., 2011; Wintle et al., 2019), and provide clearer guidelines on riparian remnants, which tend to have low core area (Luke et al., 2018), since these features could be vital for connecting patches. Nonetheless, the extent to which these efforts are successful will depend on how secondary disturbances are managed. Clearly, if population sinks in HCS-designated forest remnants are to be avoided, minimizing hunting pressure and maximizing habitat quality is crucial. HCS applications must be augmented with stringent management actions, sufficiently enforced regulations, and anti-hunting campaigns that safeguard forest integrity as well as cover.

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