

# Grain-dependent responses of mammalian diversity to land use and the implications for conservation set-aside

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**Abstract.** Diversity responses to land-use change are poorly understood at local scales, hindering our ability to make forecasts and management recommendations at scales which are of practical relevance. A key barrier in this has been the underappreciation of grain-dependent diversity responses and the role that  $\beta$ -diversity (variation in community composition across space) plays in this. Decisions about the most effective spatial arrangement of conservation set-aside, for example high conservation value areas, have also neglected  $\beta$ -diversity, despite its role in determining the complementarity of sites. We examined local-scale mammalian species richness and  $\beta$ -diversity across old-growth forest, logged forest, and oil palm plantations in Borneo, using intensive camera- and live-trapping. For the first time, we were able to investigate diversity responses, as well as  $\beta$ -diversity, at multiple spatial grains, and across the whole terrestrial mammal community (large and small mammals);  $\beta$ -diversity was quantified by comparing observed  $\beta$ -diversity with that obtained under a null model, in order to control for sampling effects, and we refer to this as the  $\beta$ -diversity signal. Community responses to land use were grain dependent, with large mammals showing reduced richness in logged forest compared to old-growth forest at the grain of individual sampling points, but no change at the overall land-use level. Responses varied with species group, however, with small mammals increasing in richness at all grains in logged forest compared to old-growth forest. Both species groups were significantly depauperate in oil palm. Large mammal communities in old-growth forest became more heterogeneous at coarser spatial grains and small mammal communities became more homogeneous, while this pattern was reversed in logged forest. Both groups, however, showed a significant  $\beta$ -diversity signal at the finest grain in logged forest, likely due to logging-induced environmental heterogeneity. The  $\beta$ -diversity signal in oil palm was weak, but heterogeneity at the coarsest spatial grain was still evident, likely due to variation in landscape forest cover. Our findings suggest that the most effective spatial arrangement of set-aside will involve trade-offs between conserving large and small mammals. Greater consideration in the conservation and management of tropical landscapes needs to be given to  $\beta$ -diversity at a range of spatial grains.

**Key words:**  $\beta$ -diversity; Borneo; camera-trapping; environmental heterogeneity; land-use change; mammals; oil palm agriculture; selective logging; spatial grain; species richness.

## INTRODUCTION

It is widely acknowledged that global biodiversity is in decline, primarily due to unprecedented rates of habitat loss and degradation (Hansen et al. 2013). Many attempts have been made to quantify this biodiversity loss due to land-use change at coarse scales and forecast losses into the future (Sodhi et al. 2004, Koh and Ghazoul 2010, Wearn et al. 2012), with the aim of informing policy-making at the highest administrative levels. In reality, biodiversity loss at coarse scales is a summation of the changes occurring at the local scale of landscapes, such as forestry concessions or private

landholdings. Local stakeholders often make management decisions that have substantial impact on the outcomes for biodiversity in these landscapes. At this local scale, however, there is little consensus about the community responses to land use, which hinders our ability to make management recommendations and biodiversity forecasts at scales relevant to local stakeholders.

Much confusion surrounding local-scale biodiversity responses has arisen due to an underappreciation of spatial grain (Sax and Gaines 2003). At the smallest scales (e.g., those of a quadrat or plot), species richness has been shown to be stable (Dornelas et al. 2014) or even increasing in post-disturbance areas (Vellend et al. 2013). On the other hand, a number of other meta-analyses focusing on overtly disturbed areas, and which did not account for spatial grain, have shown the

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contrasting result of declines in species richness (Dunn 2004, Gibson et al. 2011, Burivalova et al. 2014). It is difficult to completely reconcile these two apparently conflicting findings, and make firm conclusions with respect to local-scale biodiversity responses, due to the lumping together of studies using vastly different spatial grains. For example, in a review of past studies, Hill and Hamer (2004) found that the effects of disturbance on Lepidoptera and birds were strongly grain-dependent. Specifically, in response to disturbance, Lepidoptera richness often increased at small scales (<1 ha) and decreased at intermediate scales (1–25 ha), while bird richness also decreased at intermediate scales but then increased at still larger scales (>25 ha). Although consideration of spatial grain has largely been neglected in global meta-analyses, it offers the potential of uniting seemingly contradictory results and allowing better forecasting of biodiversity changes at the local scale. An essential component in this framework will be a better understanding of community variance, or  $\beta$ -diversity, which is an emergent property of a set of communities and is itself generated by processes such as dispersal limitation and habitat filtering. Importantly, the  $\beta$ -diversity present among communities largely determines the relationship between spatial grain and richness (Scheiner 2004). Indeed, changes in  $\beta$ -diversity can potentially explain how, in response to land-use change, species richness might remain constant or even increase at the level of a sampling point, yet decline at the level of a study site.

Patterns in  $\beta$ -diversity are important in systematic conservation planning, as they determine the complementarity of communities across sites (Ferrier 2002). This also applies, at smaller scales, to decisions about how to allocate conservation set-aside. Major certification schemes, including those of the Forest Stewardship Council (FSC), Round-table on Responsible Soy (RTRS) and Round-table on Sustainable Palm Oil (RSPO), require concession holders to identify and set-aside forest patches with High Conservation Value (HCV), but do so without explicit consideration of local-scale  $\beta$ -diversity. Beta diversity is a crucial determinant of the conservation values, such as the number of species, ultimately conserved within a concession's set-aside patches, and should play an important role in management decisions about the spatial distribution of patches and how large each patch should be (Nekola and White 2002). This is relevant in the context of the expansion of both cropland and tree plantations into forested landscapes, which is ongoing at a rapid rate (Wilcove et al. 2013), and of the increasing uptake of sustainability principles by logging companies, as required under certification schemes such as the FSC, but also more broadly under the banner of retention forestry (Lindenmayer et al. 2012).

Selective logging is the main driver of tropical forest degradation worldwide (Asner et al. 2009) and, by modifying the structure (Cannon et al. 1994), resources (Johns 1988), and microclimate (Hardwick et al. 2015) of forests

through space, may act as a strong environmental filter on the occurrence patterns of species post-logging. Only a handful of studies have investigated  $\beta$ -diversity in logged forests, mostly focusing on arthropods, but these support the notion that environmental heterogeneity in logged forests increases  $\beta$ -diversity (Hill and Hamer 2004, Berry et al. 2008, Woodcock et al. 2011, but see Kitching et al. 2013). Plantation habitats, by contrast, may be more homogeneous in space than natural forest, not only in terms of floral species composition, but also in terms of structure, resources, and microclimate (Scales and Marsden 2008). This may be true of oil palm (*Elaeis guineensis*) plantations (Luskin and Potts 2011), which are expanding across the tropics at a rapid rate, particularly in Southeast Asia (Wilcove et al. 2013).

Across taxa,  $\beta$ -diversity may vary depending on dispersal capacity, as well as the typical home-range sizes of individuals: all else being equal, poor dispersers with small home ranges will both be more dispersal-limited and less able to buffer spatial variation in habitat quality, leading to higher  $\beta$ -diversity. Soininen et al. (2007) found evidence across past studies that larger-bodied organisms, which have higher dispersal capacity and larger home ranges, generally exhibited lower levels of  $\beta$ -diversity. Despite the expected differences among taxa, few studies have explored this at the local scale using data collected simultaneously on multiple species groups at the same spatial locations (but see: Kessler et al. 2009, Gossner et al. 2013).

The primary aim of our study was to quantify the species richness and  $\beta$ -diversity of mammal communities across a land-use gradient and investigate whether diversity responses to land-use were dependent on spatial grain. In doing so, we used robust estimators and comparisons with null models to control for the specific properties of our sampling design. As a secondary aim, we also investigated differences in richness and  $\beta$ -diversity among large and small mammals across a range of spatial grains. We chose mammals as our focus due to the fact that they are a high-profile group that are often the targets of policy and land-use decisions, and are often given strong weighting in conservation planning, especially the HCV assessment process.

We made three specific hypotheses with regard to  $\beta$ -diversity. We hypothesized that logged forest areas would be more environmentally heterogeneous than old-growth forest, therefore giving rise to higher levels of  $\beta$ -diversity ( $H_1$ ), while oil palm would be environmentally homogeneous, giving rise to lower levels of  $\beta$ -diversity ( $H_2$ ). We also hypothesized that small mammals (<1 kg) would be more dispersal-limited than large mammals, owing to their smaller body size, and less able to buffer fine-grained variation in habitat quality ( $H_3$ ). We therefore expected small mammals to exhibit greater levels of  $\beta$ -diversity than large mammals. To address these hypotheses, we gathered one of the most comprehensive data sets on local-scale mammal occurrence from the tropics that we are aware of, using multiple

sampling methods to incorporate nearly the entire non-volant community, from the smallest murid rodents (~0.03 kg) up to the Asian elephant *Elephas maximus* (~2700 kg). Our findings with respect to the importance of spatial grain and  $\beta$ -diversity have important implications for the conservation and management of biodiversity in these systems and, in particular, with regard to optimal designs for conservation set-aside.

## METHODS

### *Study sites and sampling design*

We sampled mammals in three different land uses, taking advantage of the experimental design of the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysian Borneo (Ewers et al. 2011). This consists of old-growth forest within the Maliau Basin Conservation Area, repeatedly logged forest within the Kalabakan Forest Reserve, and two adjacent oil palm plantations straddling the Kalabakan Forest Reserve boundary (Appendix S1).

We used a hierarchical nested sampling design in order to explore  $\beta$ -diversity at three different spatial grains (Fig. 1). We based this on the fractal sampling design of the SAFE Project (Ewers et al. 2011), which is an

especially efficient design for quantifying  $\beta$ -diversity (Marsh and Ewers 2012). At the lowest level in the hierarchy were individual sampling points. These were clustered into rectangular sampling grids, which we call here plots, of 48 ( $4 \times 12$ ) points separated by 23 m (covering an area of 1.75 ha). In turn, three to six plots were clustered together into blocks (covering an average minimum convex polygon of 25 ha; range: 24.1–25.4), and there were three to four blocks per land use (Fig. 1). These were arranged differently in the logged forest compared to the other two land uses (Fig. 1), in order to overlay the locations of future experimental fragments (Ewers et al. 2011), but separation distances between plots (170–290 m) and between blocks (0.6–3 km) were similar across the land uses. The spatial arrangement of sampling points at the SAFE Project has been deliberately designed to minimize confounding factors across the land-use gradient, including latitude, slope, and elevation (Ewers et al. 2011), and this applied equally to our sampling design for mammals.

### *Mammal sampling*

Small mammal trapping was conducted at the level of the plot, with a session consisting of 7 consecutive days. Two locally made steel-mesh traps (18 cm wide,

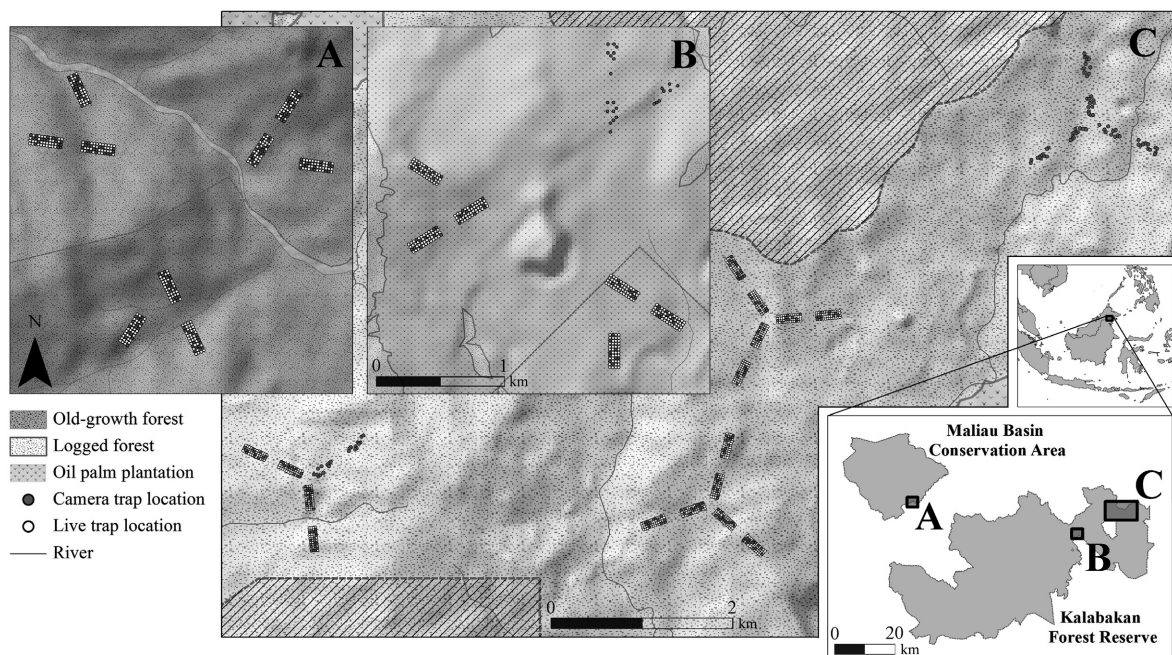


FIG. 1. Sampling design across (A) old-growth forest, (B) oil palm, and (C) logged forest used in this study, illustrating the three spatial grains within each land use: individual sampling points, 1.75-ha rectangular plots (consisting of clusters of points), and blocks (consisting of clusters of plots). Blocks were arranged identically in old-growth forest and oil palm, and were arranged to coincide with future experimental forest fragments in logged forest. Separation between points, plots, and blocks was nonetheless similar across land uses. Shaded areas lie outside the Kalabakan Forest Reserve, consisting of a 2200-ha Virgin Jungle Reserve (Brantian-Tatulit) to the south and an extensive (>1 million ha) area of logged forest to the north (Mount Louisa Forest Reserve and connecting reserves). Insets show the location within insular Southeast Asia and the spatial proximity of the three land uses within southeast Sabah, Malaysian Borneo. Note that most camera trap locations (i.e., all those within live-trapping grids) were also sampled using live traps.



10–13 cm tall, and 28 cm in length), baited with oil palm fruit, were placed at or near ground level (0–1.5 m) within 10 m of each of the 48 grid points. Traps were checked each morning and captured individuals were anaesthetized using diethyl ether, measured, permanently marked using a subcutaneous passive inductive transponder tag (Francis Scientific Instruments, Cambridge, UK), identified to species using Payne et al. (2007), and released at the capture location. Trapping was carried out between May 2011 and March 2014, during which there were no major mast-fruited events. Some plots (eight of 31) were sampled more than once over this period (mean effort per plot = 925 trap nights).

We deployed camera traps (Reconyx HC500, Holmen, Wisconsin, USA) at a random subset of grid points within plots (mean points sampled per plot = 13), setting the cameras as close to the points as possible and strictly within 5 m. The deployment of cameras randomly with respect to space has rarely been used before, though has proven effective at these study sites for revealing species-specific patterns of space use (Wearn et al. 2013), which is a contributor toward  $\beta$ -diversity. Cameras were fixed to trees or wooden poles, or placed within locally made steel security cases in areas of high human traffic, with the camera sensors positioned at a height to maximize detection for a range of species (most often 30 cm, though this was flexible depending on the terrain encountered at each location). No bait or lure was used and disturbance to vegetation was kept to a minimum. Camera traps were active between May 2011 and April 2014, during which most plots (39 of 42) were sampled for multiple sessions (mean effort per plot = 625 trap nights). We were able to sample more plots using camera traps ( $n = 42$ ) than we could using small mammal traps ( $n = 31$ ), owing to the lower labor demands in the former case.

In total, 543 points were camera-trapped and 1488 points were live-trapped, and we used these data sets for estimating large and small mammal species richness, respectively. Both trapping protocols were used at 430 points and we used only this subset of the data for the  $\beta$ -diversity analyses. This subset included data from 31 plots nested in eight blocks (nine plots in three blocks for old-growth forest, 16 plots in three blocks for logged forest, and six plots in two blocks for oil palm).

### Data analysis

All analyses were ultimately derived from the separate community matrices from live- and camera-trapping, with trap nights forming rows of the matrices, species forming the columns, and each cell containing the number of independent capture events. Unlike live traps, camera traps are continuous-time detectors, so we considered photographic capture events to be independent if they (1) contained unambiguously different individuals or (2) were separated by >12 h, which matches the approximate minimum separation between live trap events.

Our hierarchical sampling design allowed us to partition species richness and  $\beta$ -diversity into multiple spatial grains across the three land uses, by aggregating the community matrices to the appropriate grain. However, unequal levels of effort, replication, and sample completeness across spatial grains and across land uses makes comparisons of richness and  $\beta$ -diversity problematic, an issue that has often been neglected in past studies (Beck et al. 2013).

For species richness, there are nonparametric estimators that can be used to make richness values more robust to sampling design variation. We used the abundance-based coverage estimator (ACE) to estimate overall richness in each land use, because we were confident that sufficient sampling had been done to estimate the minimum asymptotic richness (Gotelli and Chao 2013), while we standardized point richness to 90% sample coverage (Colwell et al. 2012). We hereafter refer to overall richness in each land-use and point richness as  $\gamma$ -diversity and  $\alpha$ -diversity, respectively. For both  $\gamma$ - and  $\alpha$ -diversity, we used the full camera trap and live trap data sets to make estimates for large and small mammals, respectively.

We modeled the spatial patterns in either large or small mammal  $\alpha$ -diversity as a function of land use using a Poisson generalized linear mixed-effects model, with the hierarchical sampling design specified in the random effects (points nested within plots, in turn nested within blocks), as well as an observation-level random effect to account for overdispersion. We note that, given our relatively fine-scale sampling of mammal communities, spatial variation in  $\alpha$ -diversity is due to coarse-scale species occurrence patterns, as well as finer-scale patterns of habitat use by individual animals. The random effects helped account for any spatial dependence between sampling points, caused by detections of the same individuals at multiple points. We also made estimates of  $\gamma$ - and  $\alpha$ -diversity across large and small mammals for the subset of points which had been sampled using both live traps and camera traps. In this case, we were able to model  $\alpha$ -diversity as a function of both land use and species group (large or small mammal), as well as their interaction.

Commonly used metrics of  $\beta$ -diversity are also sensitive to the specific sampling design employed (Appendix S2). Instead of using  $\beta$ -diversity values directly, we compared observations ( $\beta_{\text{obs}}$ ) with an appropriate null model ( $\beta_{\text{null}}$ ), an approach which has been underexploited to date (Lessard et al. 2012). Differences from the null model, calculated using simple subtraction ( $\beta_{\text{obs}} - \beta_{\text{null}}$ ), can be interpreted as a measure of  $\beta$ -diversity due to nonrandom community assembly processes (including those of intraspecific aggregation, environmental filtering, and dispersal limitation), over and above that due to the vagaries of the sampling process itself. We refer to this difference between observed and null  $\beta$ -diversity as the  $\beta$ -diversity signal (as opposed to the random  $\beta$ -diversity noise). Observed  $\beta$ -diversities were calculated

using Lande's (1996) additive formulation, in which  $\beta$ -diversity at a given level,  $i$ , in a hierarchy is the average richness at the given level subtracted from that in the level above:  $\beta_i = \alpha_{i+1} - \alpha_i$ . This was done for each combination of land use (old-growth forest, logged forest, and oil palm) and species group (small mammals, large mammals, or both combined), for each of three spatial grains: points (camera detection zone = 0.02 ha), plots (1.75 ha) and blocks (25 ha). It follows from Lande's (1996) additive diversity partitioning that overall observed  $\gamma$ -diversity of each land-use is:  $\alpha_{\text{point}} + \beta_{\text{point}} + \beta_{\text{plot}} + \beta_{\text{block}}$ . We used additive partitioning because  $\beta$ -diversity is in units of species richness in this framework, which means differences from null models are also in units of species richness, allowing more straightforward comparisons between land uses, between species groups, and between hierarchical levels.

To estimate null  $\beta$ -diversities, we used null models based on the sample-based randomizations of Crist et al. (2003). For each spatial grain  $i$  in the hierarchy, we randomly shuffled (without replacement) the community samples at the level below ( $i - 1$ ), while constraining the random placements to maintain the integrity of any higher-level ( $i + 1$ ) spatial nesting. For example, null  $\beta$ -diversity for the plot level was derived by randomly shuffling point-level communities among plots, but only among plots within the same block. By constraining the null model in this way, we were able to test for differences from null at the specific spatial grain of interest. We extended this to the case of multiple sampling methods, by keeping the matrices derived from live- and camera-trapping separate and conducting the randomizations in parallel, mimicking how the data were generated. This also allowed us to specifically control for the different sampling efforts achieved during live- and camera-trapping. Despite our large sampling efforts, mammal communities were likely to be under-sampled due to imperfect detection, but this affects our observed and null data sets equally (poorly detected species in the observed data set remain as poorly detected species in the null data sets), and therefore we do not expect substantial bias in our  $\beta$ -diversity measure due to this.

By repeating the randomization process, we obtained distributions of differences from the null. We calculated the 95% quantiles of these distributions and deemed differences to be significant if the quantiles did not overlap zero. Sample size necessarily declines at the higher spatial levels of a fractal sampling design, causing a loss in the precision of  $\beta$ -diversity estimates (Marsh and Ewers 2012). This was also true of our null model approach, because we had fewer community samples to shuffle at higher levels. We used 1000 randomizations in all cases, except for our oil palm sampling design, in which there were few possible combinations of placing plots within blocks. In this case we restricted the number of randomizations to the number of combinations ( $n = 40$ ).

We modeled the differences from null using linear mixed-effects models in order to explore differences

across land use, across spatial grains, and across the two species groups. Since  $\beta$ -diversity at a given hierarchical level is, in the additive framework, the mean of the number of "missing" species in each sample (species which are absent from a sample but present at the level above), we took advantage of this by extracting the un-averaged number of missing species for each sample. We calculated the difference from null for each of these observed values and accounted for the lack of independence between values by specifying the hierarchical sampling design in the random effects structure. Point-level values were nested within plots and blocks, while plot-level values were nested within blocks. For the block-level model, no random effects were specified because this was the highest level in the hierarchy.

Finally, using the approach outlined by Baselga (2010), we differentiated between the two broad proximate causes of  $\beta$ -diversity (species turnover and nestedness; Appendix S2) to investigate which was primarily responsible for  $\beta$ -diversity at each spatial grain in the three land uses. Species turnover (the replacement of some species by others) can be calculated using a multiple-site generalization of the Simpson index ( $\beta_{\text{Simp}}$ ), while the  $\beta$ -diversity generated by nestedness (variation in species richness without turnover,  $\beta_{\text{nest}}$ ) can be calculated by subtracting the Simpson measure from the total  $\beta$ -diversity, as measured using a multiple-site Sørensen index ( $\beta_{\text{Sor}}$ ), i.e.  $\beta_{\text{nest}} = \beta_{\text{Sor}} - \beta_{\text{Simp}}$ . Given the dependence on sample size of these measures, we calculated them over 100 random subsamples of our data (Baselga 2010), taking the minimum sample sizes at each hierarchical level across the whole data set each time (eight points per plot, three plots per block, and two blocks per land use). This would still not enable fair comparisons across spatial grains, so we calculated values as a proportion of the total  $\beta$ -diversity,  $\beta_{\text{Sor}}$  (Baselga 2010). We modeled the proportion of  $\beta$ -diversity in the nestedness component using beta regression models with a log link and constant dispersion parameter, constructing separate models with land use, species group, or spatial grain as the explanatory variable. We used the combined live and camera trap data set for this analysis, removing 12 points which had been camera-trapped for less than 7 d.

All analyses were done in R version 3.1.0 (R Core Team 2014), using the additional packages *vegan* 2.0-10 (Oksanen et al. 2013), *iNEXT* 1.0 (Hsieh 2013), *lme4* 1.1-6 (Bates et al. 2014), and *betareg* 3.0-5 (Cribari-Neto and Zeileis 2010).

## RESULTS

Live-trapping resulted in a total of 4046 captures (1905 unique individuals) of 25 mammal species over 28681 trap nights, while camera-trapping resulted in a total of 12788 independent captures of 58 mammal species over 26251 trap nights. This gave a total of 65 mammal species (Appendix S5), of which 19 species were captured

using both protocols. Over the points sampled using both live and camera traps ( $n = 430$ ), we obtained 11579 captures of 61 species over a combined effort of 27176 trap nights.

Species accumulation curves in each land-use closely approached asymptotes (Appendix S3: Fig. S1), all with an estimated sample coverage >98%. Logged forest had the highest observed and estimated mammal  $\gamma$ -diversity, though the 95% confidence intervals overlapped with those for old-growth forest (Fig. 2). Of the 44 species found in old-growth forest, 39 species (89%) were also detected in the logged habitats. Oil palm plantations were a significantly depauperate habitat (Fig. 2), harboring just 22 of the 63 species (35%) found in the forest habitats, in addition to the invasive domestic dog (*Canis familiaris*) and plantain squirrel (*Callosciurus notatus*). Three of these species were recorded only within a 200 m wide margin of forest-scrub habitat connected to a 45 km<sup>2</sup> block of logged forest, meaning that just 19 forest species (31%) were found in the oil palm crop itself.

The overall  $\gamma$ -diversity differences between land uses were in large part due to the small mammals. Observed and estimated large mammal  $\gamma$ -diversities were very similar for old-growth and logged habitats (Fig. 2) and, for the full camera trap data set, the 95% confidence intervals for oil palm overlap, albeit slightly, with those of

old-growth forest (Appendix S4: Table S1). In contrast, small mammal estimated  $\gamma$ -diversity was significantly different among all three land-use contrasts, except for a slight overlap in 95% confidence intervals between old-growth forest and oil palm in the combined live and camera trap data set (Fig. 2; Appendix S4: Table S1).

Mixed-effects models of  $\alpha$ -diversity (standardized to 90% sample coverage) indicated a significant (i.e.  $p < 0.05$ ) effect of land use, for both small mammals from the live trap data ( $\chi^2_2 = 119$ ,  $P < 0.0001$ ) and large mammals from the camera trap data ( $\chi^2_2 = 21.7$ ,  $P < 0.0001$ ). As with  $\gamma$ -diversity, large and small mammals showed markedly different responses for  $\alpha$ -diversity (Fig. 2), which resulted in a significant interaction term between land use and species group using the combined live and camera trap data set ( $\chi^2_2 = 251$ ,  $P < 0.0001$ ). In this model, logged forest had a significantly higher  $\alpha$ -diversity than old-growth forest for small mammals (3.7 times higher,  $z = 14.2$ ,  $P < 0.0001$ ) and a significantly lower  $\alpha$ -diversity for large mammals (24% lower,  $z = -2.51$ ,  $P = 0.01$ ). This difference between the two forest habitats was also significant for small mammal  $\alpha$ -diversity with the full live trap data set (five times higher in logged forest,  $z = 6.76$ ,  $P < 0.0001$ ), but was not significant for large mammals when the full camera trap data set was used (19% lower in logged forest,  $z = -1.54$ ,  $P = 0.12$ ). Oil palm was, again, highly

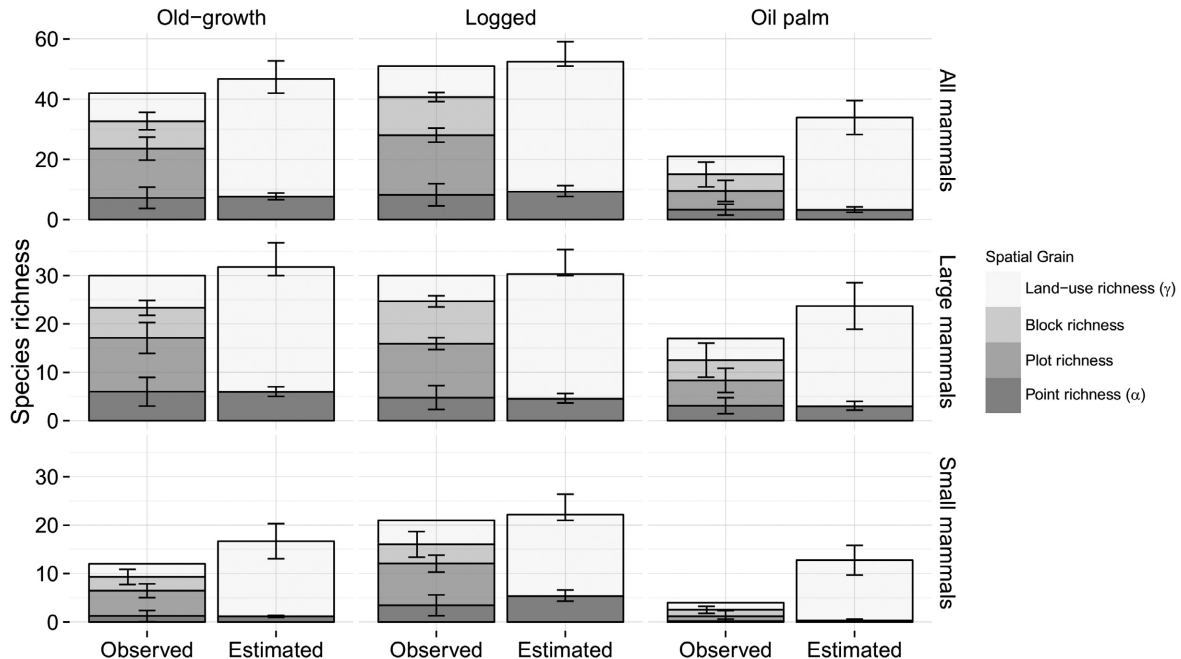


FIG. 2. Diversity partitions for all mammals, large mammals, and small mammals across a gradient of land uses, including observed values ( $\pm$  standard deviation) at four spatial grains and estimated  $\alpha$ - and  $\gamma$ -diversities ( $\pm$  95% confidence intervals [CI]). Estimates of  $\alpha$ -diversity (standardized to 90% sample coverage) are predictions from a mixed-effects model which accounted for the hierarchical nested sampling design. Estimates of  $\gamma$ -diversity were calculated using the abundance-based coverage estimator (ACE). Observed  $\beta$ -diversity at a given spatial grain is the average richness at the given grain subtracted from that in the grain above (for example,  $\beta_{\text{plot}} = \alpha_{\text{block}} - \alpha_{\text{plot}}$ ). Only data from sampling points which were both camera- and live-trapped were used in this figure (see Appendix S4 for full results).

depauperate compared to the forest habitats (either with or without the points in the forest–scrub boundary; Appendix S4: Table S2), and this difference was significant for both small mammals from the live trap data (compared to old-growth forest:  $z = 4.61$ ,  $P < 0.0001$ ) and large mammals from the camera trap data (compared to logged forest:  $z = -3.47$ ,  $P < 0.01$ ).

Diversity partitioning suggested that the majority of the  $\gamma$ -diversity was contained in the  $\beta$ -diversity components (Fig. 2): 83% in old-growth forest and 84% in both logged forest and oil palm. The percentages for each of the spatial grains also appear broadly similar for overall mammal diversity (Fig. 2): 38%, 38%, and 30% as  $\beta_{\text{point}}$ -diversity; 20%, 25%, and 27% as  $\beta_{\text{plot}}$ -diversity, and 25%, 20%, and 28% as  $\beta_{\text{block}}$ -diversity for old-growth forest, logged forest, and oil palm, respectively. However, the proportion of diversity contained within the  $\beta$  components across land use, especially  $\beta_{\text{plot}}$  and  $\beta_{\text{block}}$ , is markedly different for large and small mammals (Fig. 2).

Null model comparisons demonstrated that most community samples had a significant signal of nonrandom assembly processes (as evidenced by 95% confidence intervals which did not overlap zero; Appendix S4: Table S3). In old-growth forest, the  $\beta$ -diversity signal at large spatial grains was increasingly strong for large mammals and increasingly weak for small mammals, while this pattern was reversed in logged forest (Fig. 3). The  $\beta$ -diversity signal in oil palm was found to be much lower overall, due in part to the depauperate nature of the mammal community that exists there, especially for small mammals. However, the  $\beta$ -diversity signal for large mammals in oil palm was still comparable

at the point level to that found in old-growth forest, and did not decline at the block level as it did in logged forest (Fig. 3).

Mixed-effects models of  $\beta_{\text{point}}$  differences from null showed significant differences among the land-uses ( $\chi^2_2 = 7.70$ ,  $P = 0.02$ ) and among the species groups ( $\chi^2_1 = 13.94$ ,  $P < 0.001$ ). These significant differences were due to: larger differences from null in logged compared to old-growth forest (showing support for  $H_1$ ); smaller differences from null in oil palm (showing support for  $H_2$ ), and the consistently higher differences from null, irrespective of land use, for large mammals (showing no support for  $H_3$ ). The interaction between land use and species group was not significant at this spatial grain ( $\chi^2_2 = 3.31$ ,  $P = 0.19$ ). There were no consistent differences in  $\beta_{\text{plot}}$  or  $\beta_{\text{block}}$  differences from null, either between land uses (plot level,  $\chi^2_2 = 0.87$ ,  $P = 0.65$ ; block level,  $F_{2,10} = 0.30$ ,  $P = 0.75$ ) or species groups (plot level,  $\chi^2_1 = 0.92$ ,  $P = 0.34$ ; block level,  $F_{1,10} = 1.17$ ,  $P = 0.30$ ), showing no support at these spatial grains for any of  $H_1$  to  $H_3$ . The interaction terms in both models were also not significant (plot level,  $\chi^2_2 = 0.28$ ,  $P = 0.87$ ; block level,  $F_{2,10} = 0.63$ ,  $P = 0.55$ ).

Beta diversity was predominantly generated by species turnover rather than nestedness, with turnover forming the larger component in all cases except for small mammals at the plot level in oil palm and block level in logged forest (Fig. 4). Nestedness formed a larger component of  $\beta$ -diversity for small mammals compared to large mammals ( $z = 2.09$ ,  $P = 0.04$ ). There was a trend for nestedness to be more important in oil palm (compared to logged forest:  $z = 1.68$ ,  $P = 0.093$ ), but no

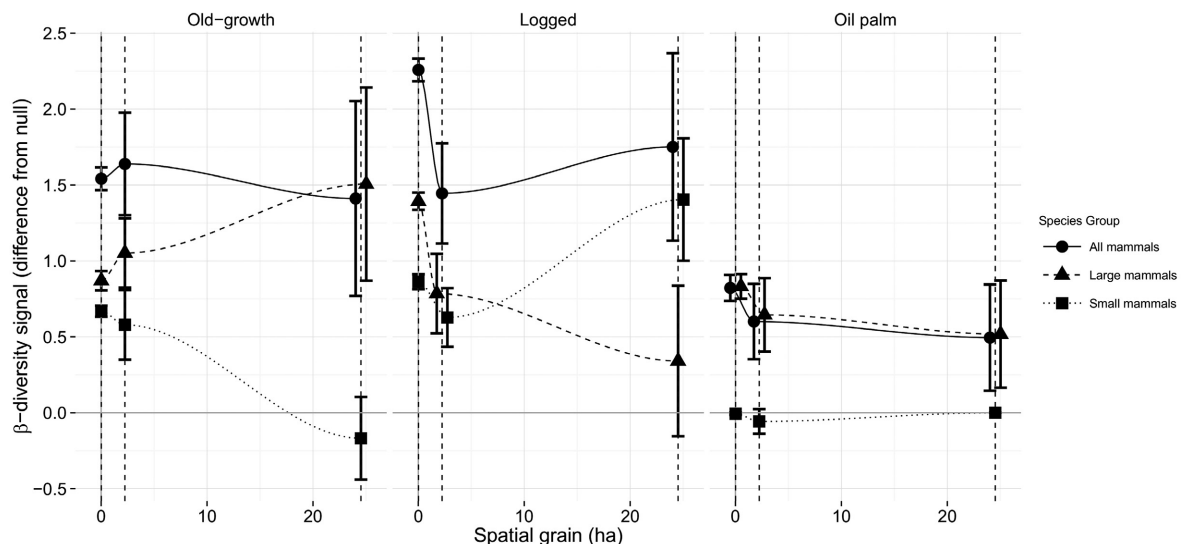


FIG. 3. Beta diversity differences from null models ( $\pm$  standard error) with increasing spatial grain, for all mammals, large mammals, and small mammals. Panels show results across a gradient of land uses. The horizontal line at  $y = 0$  represents the case of no difference between observed  $\beta$ -diversity and expected  $\beta$ -diversity from null models. Dashed vertical lines show the three spatial grains of  $\beta$ -diversity sampling within each land use (points, plots, and blocks). Smoothed lines between data points are to aid interpretation. Overlapping data points have been spaced apart slightly. See Appendix S4: Table S3 for 95% CIs.



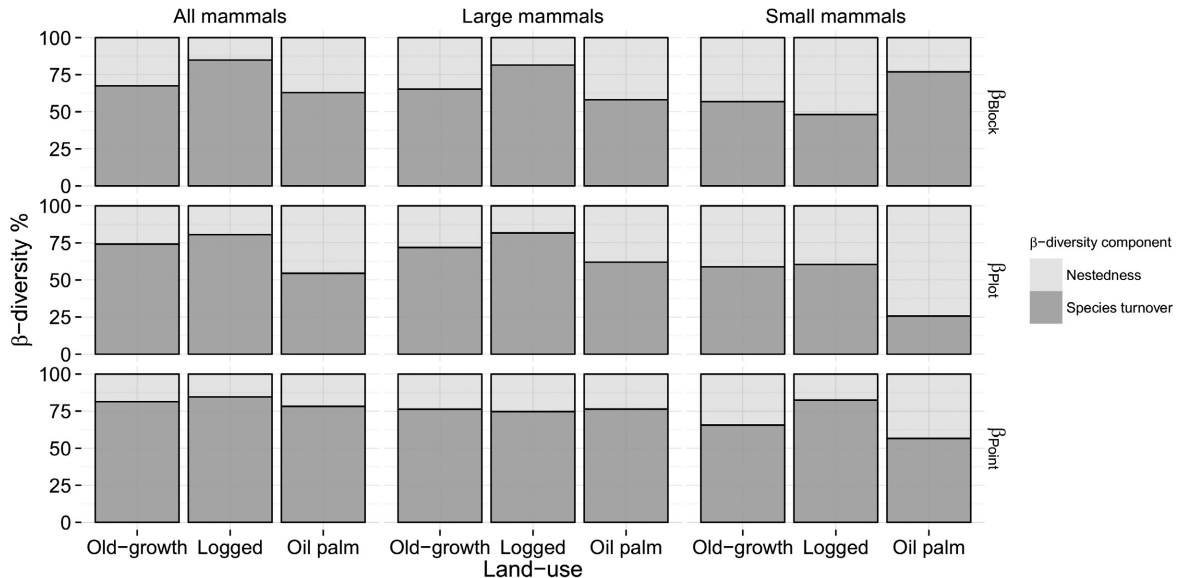


FIG. 4. Percentage of overall  $\beta$ -diversity generated by nestedness (variation in species richness without species composition changes) and species turnover (changes in species composition) across species groups and land-use types.

obvious patterns across spatial grains ( $\chi^2_2 = 2.28$ ,  $P = 0.32$ ).

#### DISCUSSION

Our finding that the vast majority of old-growth species are retained in logged forest is in agreement with the emerging consensus, from studies of a large variety of taxa, that logged forest has substantial conservation value (Putz et al. 2012, Edwards et al. 2014). Logging responses are strongly taxon- and continent-specific (Burivalova et al. 2014), and our study also adds to a relatively small body of literature on Southeast Asian mammals, supporting the general notion that large areas of logged forest in the region retain much of the terrestrial mammal diversity of old-growth forest (Wells et al. 2007, Bernard et al. 2009, Brodie et al. 2015), despite timber extraction rates that may be an order of magnitude higher than on other continents (Putz et al. 2012).

While supporting this general notion, our study also offers a more comprehensive assessment of mammal community responses to logging than has been possible before. For the first time, we were able to examine mammal diversity responses at multiple spatial grains, and across the whole terrestrial mammal community, including both large and small mammals. This revealed a more nuanced view of community responses to logging: logged habitats had either a higher or lower richness of large mammals depending on spatial grain, while small mammals were richer in logged forest across all spatial grains. Moreover, large mammal communities became more heterogeneous at increasing spatial grains in old-growth forest but more homogeneous in logged forest, while the reverse pattern was seen in small mammal communities.

Large mammal richness at small spatial grains was reduced by 19–24% in logged forest, even though species richness at larger spatial grains was maintained. Similarly, Brodie et al. (2015) found a reduction in large mammal richness of 11% at the sampling point level in recently logged (<10 yr) areas, similar to our logged areas (last logged 3–6 yr before data collection). Therefore, while logged forests in the region do appear to retain much of the mammal  $\gamma$ -diversity of old-growth forest, logging may in fact be having subtle but pervasive impacts on the diversity of mammals utilizing resources within any given forest patch, with unknown consequences for ecosystem functioning. We also note that many of the large mammal species in our study are long-lived, and therefore there is the potential that a long-term extinction debt remains to be paid off, with communities gradually “relaxing” to a lower equilibrium richness in logged forest compared to old-growth forest.

Small mammals, on the other hand, appeared to respond positively to logging, which is consistent with the broader literature from across the tropics (Isabirye-Basuta and Kasenene 1987, Lambert et al. 2006). Small mammals may be resilient to logging due to their apparently high dietary flexibility (Langham 1983, Munshi-South et al. 2007) and to the greater availability of their preferred microhabitats post-logging (Cusack et al. 2015). Small mammal communities in old-growth habitats are also likely constrained by supra-annual cycles of mast-fruiting in dipterocarp forests (Curran and Leighton 2000), in contrast to more consistent food resources in logged forests (Munshi-South et al. 2007).

Oil palm mammal communities were highly depauperate for both large and small mammals at all spatial grains, even when including nonnative species and



species occurring in plantation margins. This finding agrees with studies of a range of other taxa (Foster et al. 2011), as well as a small number of studies on mammals (Maddox et al. 2007, Bernard et al. 2009, Yue et al. 2015), and underlines the grave threat to wildlife populations that oil palm expansion represents (Wilcove et al. 2013). This is especially the case given that our results likely represent something of a best-case scenario for oil palm biodiversity: plantations were in close proximity to a large block of well-protected forest, riparian forest margins existed in the broader landscape, and hunting levels were relatively low (only three incidences of hunting activity were photographed in 3104 camera trap nights).

We hypothesized that logged forest would be more environmentally heterogeneous than old-growth forest, giving rise to higher  $\beta$ -diversity ( $H_1$ ). We found that the  $\beta$ -diversity signal was more strongly evident in logged forests compared to the other land-uses consistently only at the smallest grains, though small mammal communities showed a stronger  $\beta$ -diversity signal in logged forest compared to the other land-uses at more coarse spatial grains as well. This appears to match with the spatial grain of heterogeneity imparted by the logging process: felling of individual dipterocarp trees usually creates initial canopy gaps of less than 600 m<sup>2</sup> (Sist et al. 2003) and these gaps are mostly less than 10 m in length (i.e., 100 m<sup>2</sup>) after a decade or more of regeneration (Bebber et al. 2002). In contrast, gaps are rare in old-growth forest, typically occupying less than 1% of forest area (Sist et al. 2003). Other forms of disturbance, e.g., the creation of skid-trails, roads, and log landings, also impart heterogeneity at a more coarse grain than the felling process, as does variation among logging compartments in the intensity of extraction (Cannon et al. 1994). This variation may be by as much as an order of magnitude (Berry et al. 2008). For small mammals, which show strong preferences for specific microhabitats (Cusack et al. 2015), this latter source of environmental heterogeneity may have driven the strong signal of  $\beta$ -diversity we observed at larger spatial grains. Note, however, that small mammal  $\beta$ -diversity at the block level was primarily driven by nestedness rather than turnover in logged forest, which may suggest that the processes of local extinction and dispersal limitation are also important at this scale. For large mammals, communities may not respond as strongly to forest structure per se, and the greater homogeneity at coarse grains may reflect the greater homogeneity of tree communities in logged forest at coarse grains, overwhelmingly dominated by a single pioneer species, *Macaranga pearsonii*, in this forest.

We also hypothesized that oil palm would be environmentally homogeneous, giving rise to lower  $\beta$ -diversity ( $H_2$ ). Oil palm communities, overall, were more homogeneous than forest communities, but this was not consistently the case: large mammal communities at the block level showed a stronger  $\beta$ -diversity signal

in oil palm compared to logged forest. This was likely due to the substantial differences in management practices between blocks, for example in the year of planting and the extent of undergrowth clearance, and, perhaps more crucially, due to differences in the proximity to forest across blocks. Beta diversity in oil palm was also generated comparatively more by nestedness than in the other land-uses.

Our final hypothesis was that small mammal communities would be more dispersal-limited than large mammal communities, and would therefore show higher levels of  $\beta$ -diversity ( $H_3$ ). Support for this hypothesis was only found at the block level in logged forest and large mammals otherwise showed a stronger signal of  $\beta$ -diversity. Given the greater dispersal abilities expected of larger-bodied mammals (Sutherland et al. 2000), this does not suggest a primary role for local-scale dispersal limitation in the assembly of communities in these systems, and niche-based assembly may prevail.

Our findings have implications for the management and conservation of mammal biodiversity at local scales. In the context of logging, our results point to the importance of spatial heterogeneity, particularly at fine grains, in maintaining the diversity of mammal communities at similar levels to old-growth forest. Small mammal diversity may also be increased by heterogeneity in forest structure at larger spatial grains, but the high levels of nestedness at this scale also suggests that populations could benefit from interventions to increase connectivity among populations. For large mammals, heterogeneity in forest structure at larger spatial grains was apparently less important, and the maintenance instead of floristically diverse areas of old-growth forest may have greater benefits for large mammal diversity. In the context of plantation landscapes, our findings point to the key role that the maintenance of heterogeneity could play in improving biodiversity values, for example by deliberately varying the year of planting across management blocks ("coupes") within a concession and, more importantly, by retaining forested areas in the broader landscape.

An understanding of  $\beta$ -diversity patterns is essential for the effective identification of HCV set-aside in forest landscapes. In Southeast Asia, these forest landscapes are overwhelmingly composed of logged and degraded forest (Margono et al. 2012, Bryan et al. 2013), and HCV assessments are made in the context of reentry logging under sustainable certification or conversion to tree plantation. Typically ~10% or more of a concession may be considered for set-aside (WWF-Malaysia, 2009), in patches of ~30 ha (Tawatao et al. 2014) or more. Given this, our results suggest that the specific placement of set-aside for the conservation of large mammal communities, which we have shown are homogeneous in logged forest at spatial grains <30 ha, will be less critical and we would tentatively suggest an approach of maximizing the size of set-aside patches. Such patches, even when isolated from surrounding natural forest, may have

considerable value for mammals (McShea et al. 2009, Bernard et al. 2014). For small mammals, on the other hand, logged forest communities showed substantial heterogeneity at the scale of conservation set-aside (i.e., tens of hectares), which may favor a distributed network of patches. Although the long-term viability of these meta-populations is largely unknown, patches would ideally be connected, for example by riparian margins, and positioned according to robust HCV baseline surveys. Trade-offs in the most effective spatial arrangement of conservation areas often exist between different species groups (Schwenk and Donovan 2011), and our findings for large and small mammals suggest that a diversified strategy including a small number of large patches and a network of smaller stepping-stone patches would be necessary for the conservation of both groups. These recommendations for large and small mammals are supported by simulation studies, albeit of sessile taxa, of randomly occurring and aggregated species communities undergoing logging, in which a single large set-aside patch was optimal for maximizing yield and biodiversity in the case of homogeneous communities, but multiple smaller reserves were favored for aggregated communities (Potts and Vincent 2008). We should underline that our results are relevant for set-aside at the local scale, for example of a single concession, and a different approach may be necessary at the regional scale of large forest management units or other administrative regions.

#### CONCLUSION

We have shown that diversity responses are strongly grain-dependent and that patterns of  $\beta$ -diversity at each spatial grain play a fundamental role in this. Better forecasting of local-scale responses to land-use will require consideration of this grain-dependency. Our data also suggest that management decisions taken at the local scale, including optimizing the spatial arrangement of conservation set-aside, may be made more effective by considering patterns of  $\beta$ -diversity. Given the increased uptake of sustainable forestry principles, in particular FSC, in the management of logged forests in the region (Dennis et al. 2008), as well as rising membership of the RSPO and other crop certification schemes (Edwards et al. 2012), it is now critical that the scientific underpinnings of HCV are improved, and this should include consideration of  $\beta$ -diversity at a range of spatial grains.

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#### LITERATURE CITED

- Asner, G. P., T. K. Rudel, T. M. Aide, R. Defries, and R. Emerson. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23:1386–1395.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134–143.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-6. <http://cran.r-project.org/package=lme4>.
- Bebber, D., N. Brown, M. Speight, P. Moura-Costa, and Y. S. Wai. 2002. Spatial structure of light and dipterocarp seedling growth in a tropical secondary forest. *Forest Ecology and Management* 157:65–75.
- Beck, J., J. D. Holloway, and W. Schwanghart. 2013. Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution* 4:370–382.
- Bernard, H., J. Fjelds , and M. Mohamed. 2009. A case study on the effects of disturbance and conversion of tropical lowland rain forest on the non-volant small mammals in north Borneo: management implications. *Mammal Study* 34:85–96.
- Bernard, H., E. L. Baking, A. J. Giordano, O. R. Wearn, A. Hamid, and A. H. Ahmad. 2014. Terrestrial mammal species richness and composition in three small forest patches within an oil palm landscape in Sabah, Malaysian Borneo. *Mammal Study* 39:141–154.
- Berry, N. J., O. L. Phillips, R. C. Ong, and K. C. Hamer. 2008. Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape Ecology* 23:915–929.
- Brodie, J. F., A. J. Giordano, E. F. Zipkin, H. Bernard, J. Mohd-Azlan, and L. Ambu. 2015. Correlation and persistence of hunting and logging impacts on tropical rainforest mammals. *Conservation Biology* 29:110–121.
- Bryan, J. E., P. L. Shearman, G. P. Asner, D. E. Knapp, G. Aoro, and B. Lokes. 2013. Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PLoS One* 8:e69679.
- Burivalova, Z.,  . H.  ekerci  lu, and L. P. Koh. 2014. Thresholds of logging intensity to maintain tropical forest biodiversity. *Current Biology* 24:1893–1898.
- Cannon, C. H., D. R. Peart, M. Leighton, and K. Kartawinata. 1994. The structure of lowland rainforest after selective logging in West Kalimantan, Indonesia. *Forest Ecology and Management* 67:49–68.
- Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3–21.
- Cribari-Neto, F., and A. Zeileis. 2010. Beta Regression in R. *Journal of Statistical Software* 34:1–24.
- Crist, T. O., J. A. Veech, J. C. Gering, and K. S. Summerville. 2003. Partitioning species diversity across landscapes and

- regions: a hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist* 162:734–743.
- Curran, L., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruited Dipterocarpaceae. *Ecological Monographs* 70:101–128.
- Cusack, J. J., O. R. Wearn, H. Bernard, and R. M. Ewers. 2015. Influence of microhabitat structure and disturbance on detection of native and non-native murids in logged and unlogged forests of northern Borneo. *Journal of Tropical Ecology* 31:25–25.
- Dennis, R. A., E. Meijaard, R. Nasi, and L. Gustafsson. 2008. Biodiversity conservation in Southeast Asian timber concessions: a critical evaluation of policy mechanisms and guidelines. *Ecology and Society* 13:25.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296–299.
- Dunn, R. R. 2004. Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera. *Forest Ecology and Management* 191:215–224.
- Edwards, D. P., B. Fisher, and D. S. Wilcove. 2012. High Conservation Value or high confusion value? Sustainable agriculture and biodiversity conservation in the tropics. *Conservation Letters* 5:20–27.
- Edwards, D. P., et al. 2014. Selective-logging and oil palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications* 24:2029–2049.
- Ewers, R. M., et al. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366:3292–3302.
- Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology* 51:331–363.
- Foster, W. A., et al. 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366:3277–3291.
- Gibson, L., et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–381.
- Gossner, M. M., S. Getzin, M. Lange, E. Pašalić, M. Türke, K. Wiegand, and W. W. Weisser. 2013. The importance of heterogeneity revisited from a multiscale and multitaxa approach. *Biological Conservation* 166:212–220.
- Gotelli, N. J., and A. Chao. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Pages 195–211 in S. A. Levin, editor. *Encyclopedia of biodiversity*, Second edition. Academic Press, Waltham, Massachusetts, USA.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.
- Hardwick, S. R., R. Toumi, M. Pfeifer, E. C. Turner, R. Nilus, and R. M. Ewers. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology* 201:187–195.
- Hill, J., and K. Hamer. 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41:744–754.
- Hsieh, T. C. 2013. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 1.0. <http://chao.stat.nthu.edu.tw/blog/software-download/>.
- Isabirye-Basuta, G., and J. M. Kasenene. 1987. Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. *Biotropica* 19:260–266.
- Johns, A. D. 1988. Effects of “selective” timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20:31–37.
- Kessler, M., et al. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. *Ecological Applications* 19:2142–2156.
- Kitching, R. L., L. A. Ashton, A. Nakamura, T. Whitaker, and C. V. Khen. 2013. Distance-driven species turnover in Bornean rainforests: homogeneity and heterogeneity in primary and post-logging forests. *Ecography* 36:675–682.
- Koh, L. P., and J. Ghazoul. 2010. Spatially explicit scenario analysis for reconciling agricultural expansion, forest protection, and carbon conservation in Indonesia. *Proceedings of the National Academy of Sciences of the United States of America* 107:11140–11144.
- Lambert, T. D., J. R. Malcolm, and B. L. Zimmerman. 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. *Journal of Mammalogy* 87:766–776.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Langham, N. 1983. Distribution and ecology of small mammals in three rain forest localities of Peninsula Malaysia with particular references to Kedah Peak. *Biotropica* 15:199–206.
- Lessard, J.-P., J. Belmaker, J. A. Myers, J. M. Chase, and C. Rahbek. 2012. Inferring local ecological processes amid species pool influences. *Trends in Ecology & Evolution* 27:600–607.
- Lindenmayer, D. B., et al. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters* 5:421–431.
- Luskin, M. S., and M. D. Potts. 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. *Basic and Applied Ecology* 12:540–551.
- Maddox, T., D. Priatna, E. Gemita, and A. Salampey. 2007. The conservation of tigers and other wildlife in oil palm plantations. *Zoological Society of London, London, UK*.
- Margono, B. A., S. Turubanova, I. Zhuravleva, P. Potapov, A. Tyukavina, A. Baccini, S. Goetz, and M. C. Hansen. 2012. Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. *Environmental Research Letters* 7:034010.
- Marsh, C. J., and R. M. Ewers. 2012. A fractal-based sampling design for ecological surveys quantifying  $\beta$ -diversity. *Methods in Ecology and Evolution* 4:63–72.
- McShea, W. J., C. Stewart, L. Peterson, P. Erb, R. Stuebing, and B. Gimán. 2009. The importance of secondary forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. *Biological Conservation* 142:3108–3119.
- Munshi-South, J., L. H. Emmons, and H. Bernard. 2007. Behavioral monogamy and fruit availability in the large treeshrew (*Tupaia tana*) in Sabah, Malaysia. *Journal of Mammalogy* 88:1427–1438.
- Nekola, J., and P. White. 2002. Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal* 22:305–310.
- Oksanen, J., et al. 2013. vegan: community ecology package. R package version 2.0-10. <http://cran.r-project.org/package=vegan>.
- Payne, J., C. M. Francis, and K. Philipps. 2007. A field guide to the mammals of Borneo, Fourth edition. The Sabah Society, Kota Kinabalu, Malaysia.

- Potts, M. D., and J. R. Vincent. 2008. Spatial distribution of species populations, relative economic values, and the optimal size and number of reserves. *Environmental and Resource Economics* 39:91–112.
- Putz, F. E., et al. 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conservation Letters* 5:296–303.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Sax, D. F., and S. D. Gaines. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18:561–566.
- Scales, B. R., and S. J. Marsden. 2008. Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. *Environmental Conservation* 35:160–172.
- Scheiner, S. 2004. A mélange of curves—further dialogue about species–area relationships. *Global Ecology and Biogeography* 13:479–484.
- Schwenk, W. S., and T. M. Donovan. 2011. A multispecies framework for landscape conservation planning. *Conservation Biology* 25:1010–1021.
- Sist, P., R. Fimbel, D. Sheil, R. Nasi, and M.-H. Chevallier. 2003. Towards sustainable management of mixed dipterocarp forests of South-east Asia: moving beyond minimum diameter cutting limits. *Environmental Conservation* 30:364–374.
- Sodhi, N. S., L. P. Koh, B. W. Brook, and P. K. L. Ng. 2004. Southeast Asian biodiversity: an impending disaster. *Trends in Ecology & Evolution* 19:654–660.
- Soininen, J., J. Lennon, and H. Hillebrand. 2007. A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88:2830–2838.
- Sutherland, G., A. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* 4:16.
- Tawatiao, N., J. M. Lucey, M. Senior, S. Benedick, C. Vun Khen, J. K. Hill, and K. C. Hamer. 2014. Biodiversity of leaf-litter ants in fragmented tropical rainforests of Borneo: the value of publically and privately managed forest fragments. *Biodiversity and Conservation* 23:3113–3126.
- Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beauséjour, C. D. Brown, P. De Frenne, K. Verheyen, and S. Wipf. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences of the United States of America* 110:19456–19459.
- Wearn, O. R., D. C. Reuman, and R. M. Ewers. 2012. Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* 337:228–232.
- Wearn, O. R., J. M. Rowcliffe, C. Carbone, H. Bernard, and R. M. Ewers. 2013. Assessing the status of wild felids in a highly disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One* 8:e77598.
- Wells, K., E. K. V. Kalko, M. B. Lakim, and M. Pfeiffer. 2007. Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. *Journal of Biogeography* 34:1087–1099.
- Wilcove, D. S., X. Giam, D. P. Edwards, B. Fisher, and L. P. Koh. 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution* 28:531–540.
- Woodcock, P., D. P. Edwards, T. M. Fayle, R. J. Newton, C. V. Khen, S. H. Bottrell, and K. C. Hamer. 2011. The conservation value of South East Asia's highly degraded forests: evidence from leaf-litter ants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 366:3256–3264.
- WWF-Malaysia. 2009. High Conservation Value Forest (HCVF) toolkit for Malaysia: a national guide for identifying, managing and monitoring High Conservation Value Forests. WWF-Malaysia, Kuala Lumpur, Malaysia.
- Yue, S., J. F. Brodie, E. F. Zipkin, and H. Bernard. 2015. Oil palm plantations fail to support mammal diversity. *Ecological Applications* 25:2285–2292.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/15-1363/supinfo>

## DATA AVAILABILITY

Data associated with this paper have been deposited in Zenodo: <http://dx.doi.org/10.5281/zenodo.44545>