

Using Habitat Characteristics to Predict Faunal Diversity in Tropical Production Forests

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ABSTRACT

Biodiversity conservation in managed tropical forests is becoming increasingly important as forest area continues to decline. Accordingly, there is growing interest in developing conservation-driven silvicultural prescriptions and identifying indicator habitat metrics (similar to indicator taxa) that could be easily assessed via routine vegetation sampling. Successfully achieving these goals, however, requires an understanding of how habitat characteristics affect biodiversity. The purpose of this study was to determine the associations between the species diversity of three taxa (ants, insectivorous bats, and dung beetles) and the habitat characteristics of hill dipterocarp production forests. We sampled both within (three samples) and adjacent to (six samples) six Virgin Jungle Reserves distributed throughout Peninsular Malaysia, and related habitat predictors to univariate diversity metrics (species richness and Shannon diversity) as well as multivariate compositional metrics. We found that influential predictors and directional effects differed across taxa. Ant diversity was most affected by stand density and canopy cover, and positively associated with both. Bat diversity was most strongly linked to primary forest area, with smaller reserves harboring greater bat diversity. Dung beetles were most affected by canopy cover and elevation, with greater diversity at lower elevation and with less canopy cover. Our multivariate analyses did not reveal any strong relationships between species composition and habitat variables. Overall, our results provide evidence that tropical forest structure is associated with biodiversity, but also suggest that it will be difficult to identify a single silvicultural prescription or landscape management strategy to maximize the diversity of all three taxa simultaneously.

Key words: biodiversity enhancement; conservation; habitat association; moist tropical forests; Peninsular Malaysia; stand management; structural diversity.

RECENT RAPID LOSS OF FOREST AREA HAS MADE BIODIVERSITY CONSERVATION AN IMPORTANT management objective for tropical timber production forests. Sustainable forest management guidelines (e.g., ITTO 2009, FSC 2010) now include a range of stand- and landscape-level biodiversity conservation principles and guidelines. Examples include the designation of high conservation value areas within production forest landscapes (ITTO 2009) and the use of reduced-impact logging techniques to minimize disturbance (Putz *et al.* 2001). Another important but less utilized method is biodiversity-focused silvicultural prescriptions (Lindenmayer *et al.* 2006). Odion and Sarr (2007) and Getzin *et al.* (2008) argued that forest stands with heterogeneous structures better conserved biodiversity. Indeed, the diversity of many animal species is positively correlated with habitat heterogeneity, although different taxa respond to habitat heterogeneity at different spatial scales (reviewed by Tews *et al.* 2004). Similarly, retaining biological legacies such as snags and coarse woody debris has been found to enhance wildlife habitat, biodiversity, and ecosystem functions in temperate forests (Pharo & Lindenmayer 2009, Davis *et al.* 2010,

Lindenmayer *et al.* 2006). Basic knowledge of how to implement this approach in tropical production forests, however, is currently lacking. Particularly, we lack information on how different stand-level habitat characteristics in tropical forests influence biodiversity.

Many studies that compared the biodiversity of logged and unlogged tropical forests have found little difference in species richness and diversity, although some have found distinct changes in species composition (Edwards *et al.* 2009, 2011; Woodcock *et al.* 2011). The degree to which changes in forest structure drive changes in tropical forest diversity remains, however, an open question.

If diversity could be associated with specific continuous habitat characteristics, then these characteristics could be manipulated by silvicultural prescriptions. Indicator habitat metrics could be developed that are somewhat analogous to indicator taxa (Lawton *et al.* 1998, Barlow *et al.* 2007). From the perspective of feasibility, managing stands for indicator habitat metrics is attractive because vegetation sampling is already routinely incorporated into forest management planning. The Selective Management System (SMS) in Peninsular Malaysia, for example, requires a sampling intensity of ten percent of trees in every compartment prior to harvesting (Thang 1987). There are, however, few existing studies that

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provide information on how taxa are affected by particular habitat characteristics in tropical forests, and those that do usually focus only on one taxon (*e.g.*, Howlett & Davidson 2003 for pioneer vegetation; Presley *et al.* 2008 for bat populations; and Ansell *et al.* 2011 for birds). To the best of our knowledge, no study in tropical forests has examined the relationships between the diversity of multiple taxa and many continuous habitat characteristics.

The goal of this study was to determine the associations between the species diversity of three taxa (ants, understory insectivorous bats, and dung beetles) and the habitat characteristics of hill dipterocarp production forests in Peninsular Malaysia. Currently, Virgin Jungle Reserves (VJRs) and the SMS are used in conjunction to conserve biodiversity in these forests. VJRs are areas of primary forest that are established to protect biodiversity, conserve gene pools, and provide sources of natural regeneration within landscapes managed intensively for timber production (Wyatt-Smith 1950, Laidlaw 1999). SMS is a diameter cutting limit silvicultural system designed to conserve advance regeneration, enhance soil and water protection, and enable wood production from a wider spectrum of timber species (Thang 1987). Neither strategy directly manages habitat characteristics to conserve the biodiversity of taxa other than vegetation.

To meet our objective of developing diversity–habitat relationships for each taxon, we first employed a variable selection method to identify habitat characteristics that influence biodiversity. We then developed biodiversity–habitat prediction models to quantify the degree of influence of each predictor on the diversity of each taxon. Finally, to further explore diversity patterns in these forests, we analyzed relationships between species composition and habitat characteristics.

METHODS

STUDY SITES.—This study was conducted between September 2007 and June 2009 within and around six VJRs varying in size (28 to 1834 ha) and distributed throughout Peninsular Malaysia (Fig. S1). A study site refers to a VJR and its surrounding production forests. All sites are located in undulating lowland and hill forests and are dominated by large, high-value timber trees in the Dipterocarpaceae family. The six VJRs are surrounded by forest stands harvested under SMS in late 1960s and early 1970s. The SMS requires that felled trees from the Dipterocarpaceae family to be at least 50 cm diameter at breast height (dbh), and non-dipterocarp trees must be at least 45 cm dbh. The SMS also requires retention of at least 32 trees/ha that are sound, marketable, and have a dbh between 30 and 45 cm (Thang 1987). Numerous VJRs were screened based on both logging records and field visits to ensure that the six selected sites were representative of logging as prescribed under the SMS system.

DATA COLLECTION.—A 3 × 3 systematic grid was established at each study site with sampling conducted at each grid point. One axis of the grid corresponded to topographic class ('ridge', 'mid-slope', and 'valley'). The other axis corresponded to relative

position to the interior of the VJR ('in', 'near', 'out'), where 'in' refers to the primary forest interior of a VJR, 'near' refers to areas of logged forest approximately 200 m from a VJR boundary, and 'out' refers to areas of logged forest approximately 600 m away from the boundary of a VJR. Thus, each one of the nine grid points is a combination of topographic class and position relative to the interior of the VJR. The motivation behind this set up was to capture as much variation in forest structure and biodiversity as possible. Both a 20 × 80 m plot (0.16 ha) and a 300-m transect were set up at each grid point to sample the different taxa. As a result, a total of 54 plots and transects were established in this study. Basic information on the geographical features and forest stand structures of each site is provided in Table 1.

Ants, understory insectivorous bats, and dung beetles were sampled at each grid point, either in the plot or along the transect, using accepted taxon-specific capture methods. These three taxa were chosen to span a range of mobility, logging sensitivities, and habitat requirements, and to serve as indicators of other taxa and environmental conditions. For example, dung beetles are a good indicator of mammal diversity, *e.g.*, elephants (Hanski & Cambefort 1991), and understory insectivorous bat activity may reflect the degree of overstory canopy removal (Peters *et al.* 2006).

Ants were sampled in the 0.16-ha plots with four trapping methods to cover a range of habitats (ground pitfall traps, arboreal pitfall traps, bait stations, and leaf litter sifting). All traps were deployed for 48 h, and baiting and sifting took place for 30 min. Understory insectivorous bats were trapped along the 300-m transects using three harp traps placed 50 to 75 m apart. Bat trapping was carried out for three consecutive nights. Dung beetles were pitfall-trapped along the transects using elephant dung as bait. Nine traps were set up approximately 30 m apart. Trapping was carried out for 48 h. More detailed sampling and collection protocols for all three taxa are provided in the Supporting Information. Lastly, vegetation structure was assessed in the 0.16-ha plots, where height and dbh of all trees >5 cm dbh were measured. A GRS densitometer was also used to estimate overstory canopy cover with 80 readings evenly distributed across the plot. Finally, litter cover representing forest floor conditions was measured.

BIODIVERSITY MEASURES AND HABITAT CHARACTERISTICS.—A multitude of measures (Krebs 1999) exist to quantify biodiversity from raw species abundance or presence–absence data. The two measures we used are simple and intuitive: species richness (*S*) defined as the number of observed species from a sample (Lam & Kleinn 2008) and the Shannon diversity index (*H*) that incorporates both richness and evenness of species distributions (Krebs 1999),

$$H = - \sum_{i=1}^S p_i \log p_i \quad (1)$$

where p_i is the proportion of individuals of species i , S is the number of species observed in a sample, and \log is logarithm with

TABLE 1. Descriptions and stand structures of the six sites, *i.e.*, Virgin Jungle Reserves (VJRs) and corresponding adjacent logged forests, in Peninsular Malaysia.^a

Site ^b	Size (ha)	Elevation (m)	Forest type ^c	Tree density (trees/ha)		Basal Area (m ² /ha)		Mean DBH (cm)		Top height ^d (m)	
				Pri	Log	Pri	Log	Pri	Log	Pri	Log
SFR	28.0	379–472	H	985	876	38.98	27.88	20.34	19.48	30.25	23.91
GTFR	50.0	244–472	L, H	915	762	31.91	44.35	21.12	26.90	28.66	30.16
GAFR	143.3	200–500	L, H	850	706	56.90	30.69	29.51	23.81	30.12	24.52
UGFR	449.0	457–1128	H, U	944	819	30.10	40.37	19.97	25.32	24.00	26.93
KSFR	814.0	100–600	L, H	1183	1344	42.50	31.36	21.50	17.92	31.89	26.79
BFR	1834.3	200–700	L, H	631	708	24.30	26.64	21.76	21.77	25.90	26.06

^aAll values for structural variables were plot-level means across all topographic positions. ‘Pri’ characterized plots within the VJR (3 per site, 18 in total); ‘Log’ characterized plots within the logged forest adjacent to the VJR (6 per site, 36 in total).

^bSFR—Semangkok Forest Reserve, GTFR—Gunung Tebu Forest Reserve, GAFR—Gunung Angsi Forest Reserve, UGFR—Ulu Gombak Forest Reserve, KSFR—Kledang Saiong Forest Reserve, BFR—Berembun Forest Reserve.

^cL—Lowland Dipterocarp Forest, H—Hill Dipterocarp Forest, U—Upper Hill Dipterocarp Forest (Whitmore 1990).

^dTop height was defined as the mean height of the largest 100 trees/ha (*i.e.*, the largest 16 trees in each plot).

base *e*. Both biodiversity metrics were calculated for each taxon: (i) Shannon diversity index (H_{ants} , H_{bat} , H_{beetle}) and (ii) species richness (S_{ants} , S_{bat} , S_{beetle}).

The habitat characteristics investigated were as follows: (1) topographic category (TOPO, ‘ridge’, ‘mid-slope’, ‘valley’); (2) distance to the interior of the VJR, with distance of zero representing primary forest (D_{int} , m); (3) distance to the nearest river (D_{river} , m); (4) mean elevation within each site (Elev, m); (5) size of the VJR (VJR_{size} , ha); (6) stand density (TPH, trees/ha); (7) mean dbh (dbh_{mean} , cm); (8) horizontal structural heterogeneity (dbh_{H}); (9) mean tree height (ht_{mean} , m); (10) vertical structural heterogeneity (ht_{H}); (11) overstorey canopy cover (CC, %); and (12) forest floor litter cover (LC, %). Minimum, mean, and maximum values for each habitat characteristic are summarized in Table S1.

Horizontal structural heterogeneity (dbh_{H}) quantified the distribution of dbh among trees in a plot, whereas vertical structural heterogeneity (ht_{H}) quantified the distribution of height. Both were estimated using the Shannon index (Staudhammer & LeMay 2001, Maguire *et al.* 2007). The dbh and height data of each plot were grouped into classes of 5-cm and 2-m intervals, respectively, and the number of trees in each size class was tallied. Each discrete dbh and height class was treated as a ‘species’, and thus the number of trees in a class was analogous to the abundance of a ‘species’. Hence, dbh_{H} and ht_{H} were estimated using eqn. (1). A high value implied a diverse stand structure with a large number of structural classes and a relatively even distribution, and a low value implied low structural diversity with the presence of dominant structural classes and relatively few trees in other classes.

DATA ANALYSIS.—Our analyses can be divided into two main categories defined by the nature of the response variable: univariate diversity metrics (species richness or Shannon diversity) or multivariate compositional distances. In both cases, the same 12 habitat variables were used as predictors. Development of the

univariate models consisted of two steps: (1) identifying habitat characteristics that influenced the biodiversity of each taxon; and (2) quantifying the effects of the influential habitat characteristics on biodiversity.

Step 1 consisted of a variable selection method to remove non-influential predictors and thereby construct models with greater parsimony (Ginzburg & Jensen 2004). Boosted Regression Trees (BRT) was the method of choice in this study (Leathwick *et al.* 2006). BRT is a more robust alternative to methods that are commonly used but widely criticized such as stepwise selection (Whittingham *et al.* 2006). Briefly, BRT has two interacting components: regression trees and stochastic gradient boosting (Friedman 2002, Elith *et al.* 2008). The regression tree method partitions multidimensional predictor spaces into disjoint regions by making the values of a response variable in a region as homogenous as possible. Stochastic gradient boosting combines a collection of simple and weak trees with large prediction error to form a final strong tree with a lower prediction error (De’ath 2007). The final output is the degree of influence of a predictor on the response variable. In this study, the BRT for Shannon diversity was specified with a Gaussian distribution, whereas a Poisson distribution was specified for species richness. The BRT was also specified to have a learning rate of 0.001, a tree complexity of 1, a bag fraction of 0.5, and a number of cross-validation of 6. BRT analysis was carried out for each combination of taxa (three taxa) and biodiversity measures (two measures), resulting in a total of six BRT analyses. For each analysis, we ran BRT ten times to get ten values of relative importance for each predictor (the relative amount of the total variance explained by the predictor, *i.e.*, the degree of influence of the predictor on the response variable). We classified a predictor to be influential if it had relative importance averaged over the ten BRT runs ≥ 4 percent. Additional details on BRT procedures are provided in the Supporting Information.

Step 2 consisted of fitting models for each taxon with either Shannon diversity or species richness as the response variable, and the corresponding set of BRT-selected influential predictors as the explanatory variables. Linear Mixed Models (LMMs) were used for the Shannon diversity analyses, whereas Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution and a log-transformed response variable were used for the species richness analyses. In all cases, a random effect for study site was applied to the intercept term to account for the nested sampling design. We also tried adding random site effects to the parameters of influential predictors, but Analysis of Variance (ANOVA) suggested that all such terms were insignificant. Thus, they were omitted in the interest of parsimony. All modeling was done in the R statistical software (R Development Core Team 2010) using *gbm* and *lme4* packages.

Unlike many studies, we did not use *p*-values for variable selection (*e.g.*, as is done with stepwise selection) or for assessing the significance of parameter estimates. We made this decision because stepwise methods have inherent issues and are widely criticized (Whittingham *et al.* 2006), and accurate estimation of *p*-values for individual predictors in mixed effect models, especially GLMMs, is controversial and elusive (Zuur *et al.* 2009). Instead, we applied a more robust approach that combined BRT and LMMs or GLMMs. BRT replaced common variable selection methods to select significant predictors, and once that was done, LMMs or GLMMs estimated the parameters and direction of these predictors.

To investigate relationships between species composition and habitat characteristics, we used Multiple Regression on Distance Matrices (MRDM), which is conceptually similar to but more flexible than Mantel tests (Lichstein 2007). As in Mantel tests, MRDM significance is determined via permutations. In the current context, significance levels were calculated after 1000 permutations as: (the number of permutations with slope \geq actual slope)/the number of permutations. Due to the lack of independence among values in a distance matrix, the raw data are shuffled (not the distances) and distance matrices are re-calculated for each permutation (Lichstein 2007). Predictor distance matrices can be calculated from multiple variables (*e.g.*, several habitat variables) or from a single variable; we calculated separate distance matrices (Euclidean in all cases) for each predictor and analyzed each individually. Note that topographic classes were converted to numerical values (Ridge = 1, Slope = 2, and Valley = 3) to yield a single topographic distance variable ranging from 0 to 2. We investigated two different compositional distance matrices (as MRDM response variables): Sorensen and Morisita-Horn, representing presence-absence and abundance-based analyses, respectively.

To account for the nested sampling design, as well as the fact that composition varied substantially from site to site (results not shown), permutations for most variables were stratified by site (*i.e.*, plots shuffled within but not between sites); the only exceptions were VJR_{size} and Elev, which have only one value per site (rendering intra-site shuffling moot). With the exception of VJR_{size} and Elev, compositional and predictor distances were

calculated only within sites, resulting in six separate single-site distance matrices for each variable. For model fitting, each set of six distance matrices was collapsed into a single vector, and statistical significance was determined across all sites simultaneously. Note that this analytical approach (distances calculated and shuffled only within sites) eliminates replication with regard to logging effects and thereby prevents the disentanglement of logging effects from underlying compositional gradients (Ramage *et al.* 2013). This was necessary due to the overwhelming compositional variation across sites; analyses across all sites failed to reveal a single significant relationship between composition and any of our predictor variables (results not shown).

RESULTS

ANTS.—The BRT analyses indicated that all predictors combined explained an average of 27.8 percent of the total variance in ant Shannon index (H_{ant}). CC and TPH were the two major contributors to the total explained variance (29.7% and 23.3% of the explained variance, respectively; Fig. 1). Both predictors were positively associated with H_{ant} , with increases of 10 percent canopy cover and 100 trees/ha stand density being associated with 0.062 and 0.02 unit increases in H_{ant} , respectively (Table 2). Each of all remaining predictors contributed <11 percent (individually) of the explained variance.

By contrast, the BRT analyses using ant species richness (S_{ant}) showed that all predictors were only able to account for an average of 9.1 percent of the total variance. Unlike H_{ant} , the two strongest predictors of S_{ant} were ht_{mean} and VJR_{size}, accounting for 26.3 and 20.0 percent of the explained variance, respectively (Fig. 1). Both predictors had a negative effect on S_{ant} (Table 2). All other predictors accounted for <12 percent (individually) of the explained variance.

INSECTIVOROUS BATS.—All predictors on average explained 18.1 percent of the total variance in bat Shannon index (H_{bat}). VJR_{size} was the single major contributor to the explained variance (39.7%), while all other influential predictors contributed <11 percent (individually) to the explained variance (Fig. 1). With a 100 ha increase in VJR_{size}, H_{bat} was predicted to decrease by 0.02 units (Table 2).

Unlike S_{ant} , all predictors combined explained on average almost half of the total variance (43.8%) in bat species richness (S_{bat}). Consistent with H_{bat} , the largest contribution to the explained variance came from the VJR_{size} (32.3%; Fig. 1). An increase of 100 ha in VJR_{size} was associated with a decrease of 0.03 log-transformed units of species richness (Table 2). Also in agreement with the H_{bat} results, all other predictors contributed less than 13 percent to the explained variance for S_{bat} (Fig. 1).

DUNG BEETLES.—BRT analyses indicated that all predictors combined explained about 31.2 percent of the total variance in dung beetle Shannon index (H_{beetle}). TOPO was found to be the only non-influential predictor (Fig. 1). CC and ELEV contributed the most to the explained variance (21.5% and 17.5%, respectively).

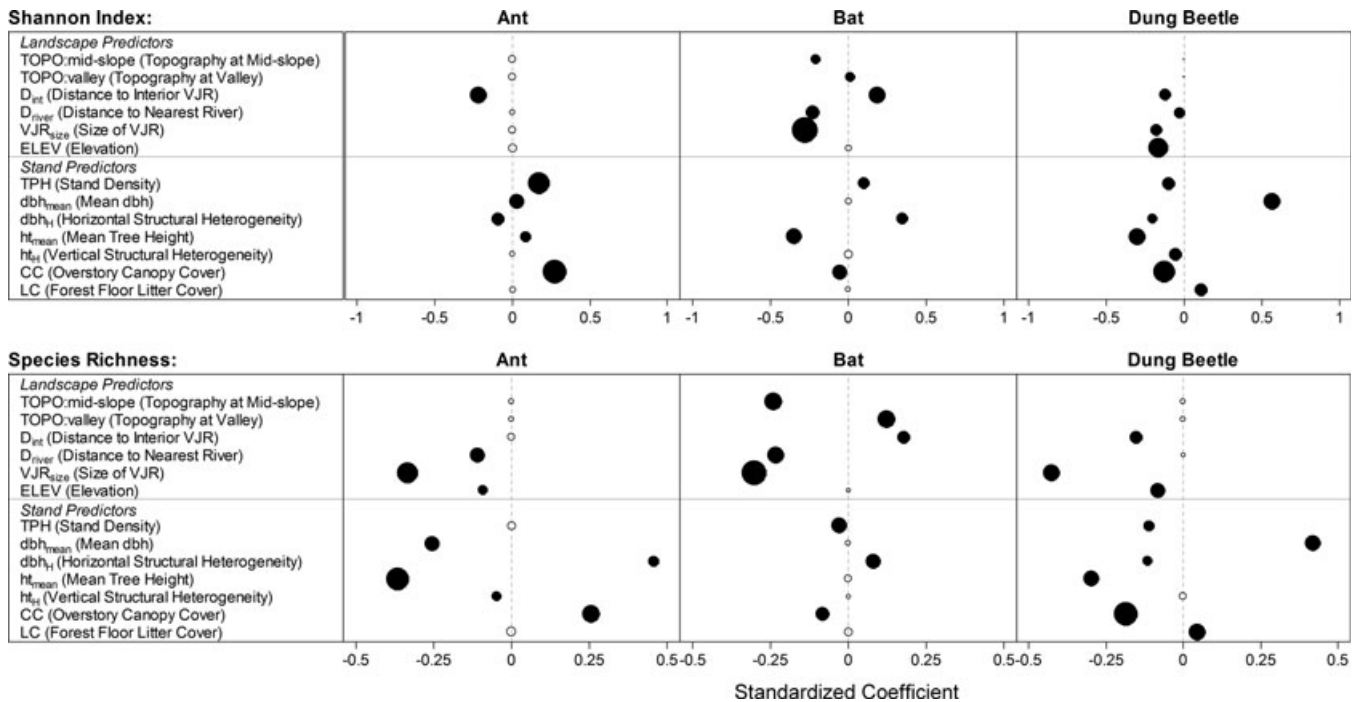


FIGURE 1. Relative importance and directional effects of predictors on Shannon index and species richness of ants, bats, and dung beetles. The size of circles reflects the relative importance. Black circles depict influential predictors, whereas white circles depict non-influential predictors. The position of a circle on the horizontal axis reflects standardized parameter estimates. Standardized parameter estimates for non-influential predictors are displayed as zeros.

A 10 percent increase in canopy cover was predicted to decrease H_{beetle} by 0.076 units, and a 100-meter increase in elevation was predicted to decrease H_{beetle} by 0.09 units (Table 2). All other predictors accounted for less than 11 percent (individually) of the explained variance.

All predictors combined explained only 11.8 percent of the total variance in dung beetle species richness (S_{beetle}). All predictors were influential ($>4\%$ of explained variance) except TOPO, D_{river} , and ht_{H} (Fig. 1). Similar to H_{beetle} , CC contributed the most to the explained variance (29.3%), but unlike H_{beetle} , ELEV was not particularly influential. All predictors other than CC accounted for <12 percent (individually) of the explained variance.

SPECIES COMPOSITION.—We detected very few relationships between species composition and our habitat predictor variables (Table S2). Furthermore, across all taxa, compositional distance metrics, and predictor variables, the proportion of variance explained never exceeded 0.05. D_{int} exhibited the greatest number of significant and borderline significant associations, but caution is needed when interpreting these results (see Discussion).

DISCUSSION

We have systematically modeled the diversity of ants, bats, and dung beetles as a function of local stand structural and environmental variables across six dipterocarp forests. We are unaware of any previous study in tropical forests that simultaneously

sampled several animal taxa and predicted the diversity of these taxa from continuous structural variables. One advantage of simultaneously sampling several forest taxa in one location is that responses to influential predictors can be readily compared across taxa. Our results indicate that multiple taxa do not share the same set of influential predictors. For example, VJR size was the most influential predictor of Shannon diversity for bats, but had very little effect on dung beetle Shannon diversity. Similarly, mean tree height was associated with ant species richness, but not with bat species richness. Furthermore, in some cases, the predicted directional effects were contradictory; for instance, canopy cover was positively associated with ant diversity, but negatively associated with dung beetle diversity. These findings suggest that it might not be possible to design one single silvicultural prescription to conserve all three taxa simultaneously in the production forests of Peninsular Malaysia. Cushman *et al.* (2008) similarly concluded that generalized characterization of habitat was unlikely to provide a reliable basis for multi-species conservation of birds in western Oregon, U.S.A. Thus, silvicultural prescriptions may need to be customized for each taxon of concern.

Ants are the most dominant forest arthropod in terms of animal biomass, and they play a major role in forest ecosystems as predators, facilitators of soil turnover, nutrient carriers, and environment manipulators (Gunadi & Verhoef 1993, Adis *et al.* 1998). Our results suggest that habitat characteristics are better predictors of ant biodiversity in terms of Shannon diversity than species richness. Thus, we limit the following discussion of ant diversity to our Shannon index analyses, which indicate that

TABLE 2. Estimated effects of predictors on Shannon index and species richness of ants, bats, and dung beetles.

Predictors	Shannon index			Species richness ^a		
	Ant	Bat	Dung beetle	Ant	Bat	Dung beetle
Intercept	1.9139	1.3553	3.4412	3.1584	1.8218	4.6089
TOPO: midslope	ns ^b	-0.2780	ns	ns	-0.2933	ns
TOPO: valley	ns	0.0141	ns	ns	0.1509	ns
D _{int}	-0.0001	0.0001	-0.0001	ns	0.0001	-0.0002
D _{river}	ns	-0.0012	-0.0002	-0.0002	-0.0011	ns
VJR _{size}	ns	-0.0003	-0.0002	-0.0001	-0.0003	-0.0007
ELEV	ns	ns	-0.0009	-0.0001	ns	-0.0005
TPH	0.0002	0.0002	-0.0003	ns	-0.00005	-0.0004
dbh _{mean}	0.0017	ns	0.1007	-0.0121	ns	0.0902
dbh _H	-0.1369	1.0546	-0.8174	0.4943	0.2155	-0.5700
ht _{mean}	0.0148	-0.1249	-0.1476	-0.0472	ns	-0.1747
ht _H	ns	ns	-0.2593	-0.0592	ns	ns
CC	0.0062	-0.0025	-0.0076	0.0041	-0.0033	-0.0137
LC	ns	ns	0.0108	ns	ns	0.0052
Site Effect ^c	0.0184	0.1073	0.4027	0.0001	0.0864	0.2858

^aSpecies richness was log-transformed prior to analysis and thus all estimated effects apply to log(species richness).

^bns—non-influential predictor (*i.e.*, relative importance <4%).

^cRandom study site effects for LMM (Shannon diversity index) and GLMM (species richness).

forest stands with higher stand density and greater canopy cover had higher ant diversity. This suggests that ant diversity may decrease with disturbances that remove enough trees to open up the forest canopy, which agrees with the findings of Burbidge *et al.* (1992), Watt *et al.* (2002), and Woodcock *et al.* (2011).

Our analyses reveal that habitat characteristics were good predictors of both bat Shannon index diversity and bat species richness, but they were much better for the latter. VJR size was consistently the main determinant of bat diversity for both biodiversity measures. Contrary to our expectations, smaller VJRs were predicted to host greater bat diversity than larger VJRs. Small VJRs may act as sink habitats (Dias 1996) for insectivorous bats moving in from surrounding logged forest areas. Thus, bat density and diversity may increase in small forest fragments even if habitat conditions there are not optimal.

Dung beetles primarily feed, live, and breed in mammal dung, and they are found in high diversity and abundance in areas rich in mammals (Hanski & Cambefort 1991). Thus, this taxon is increasingly being used as a bioindicator of mammal assemblages (Davis *et al.* 2001). Our analyses indicated that habitat characteristics can be used as predictors of dung beetle Shannon diversity and, to a lesser extent, species richness. Forest

canopy cover was the strongest contributor to both dung beetle diversity measures, with a negative association between canopy cover and beetle diversity. Elevation was also associated with dung beetle Shannon diversity (but not species richness), with higher diversity predicted at lower elevations. Due to the strong association between large herbivores and dung beetles (Hanski & Cambefort 1991), it is generally assumed that the habitat requirements of large herbivores match those of dung beetles. This assumption has not, however, been rigorously tested, and little is known about the specific requirements of dung beetles in Peninsular Malaysia.

We found very little evidence that species composition is related to any of the habitat variables we investigated. Although a few significant associations were detected, r^2 values were consistently very low (<0.05), suggesting that any such effects were not particularly strong. The predictor that seemed to have the greatest influence was distance to the interior of the primary forest (*i.e.*, logging status), suggesting perhaps a slight compositional effect of logging (despite the complete absence of detectable relationships between logging status and any of our environmental or stand structural predictors; results not shown). Because compositional distance matrices were calculated and permuted separately for each site, effectively eliminating replication with regard to logging status (see Methods), we cannot distinguish logging effects from underlying compositional turnover across space (Ramage *et al.* 2013). Furthermore, even if the observed compositional variation resulted entirely from logging, the very low proportion of explained variation, across all taxa, suggests that biodiversity was minimally impacted in the long-term by logging, which occurred more than 30 yr prior to data collection. This assertion is aligned with our other analyses, which show weak and inconsistent relationships between logging status and biodiversity (species richness and Shannon diversity). Furthermore, all of our findings are consistent with a growing body of literature (Edwards *et al.* 2009, 2011; Woodcock *et al.* 2011) that indicates the high conservation value of selectively logged tropical forests. We caution that our results should not be generalized to forests that were logged more recently and/or more intensively.

As alluded to in the introduction, in addition to advancing our understanding of how biodiversity is associated with habitat characteristics in tropical forests, predictive models such as ours can be used for forest management planning. Although the sampling protocols for our three studied taxa are relatively straightforward, they are more time consuming than sampling vegetation, and few trained experts are available for reliable species identification of most tropical taxa. Furthermore, vegetation sampling is routinely incorporated into forest management planning and more frequently done than faunal sampling (*e.g.*, the SMS in Peninsular Malaysia requires a sampling intensity of 10 percent for trees in every compartment prior to harvesting; Thang 1987). Thus, models similar to those we developed can be used to predict the diversity of animal taxa from vegetation characteristics when faunal sampling is not feasible due to operational or financial issues.

These suggested applications of our biodiversity–habitat models are based on the premise that the models can be extrapolated to other forest compartments throughout Peninsular Malaysia or in the region. Furthermore, one has to judge whether the variances explained by the influential predictors produced from the BRT analyses are operationally acceptable for the suggested applications. Nonetheless, the predictive models we developed can be continuously updated when additional information from new study sites becomes available, and such models could have broad utility for conservation management in diverse tropical forests.

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SUPPORTING INFORMATION

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

TABLE S1. Mean, minimum, and maximum values of the 12 habitat characteristics.

TABLE S2. Relationships between predictor variables and species composition of ants, bats, and dung beetles.

FIGURE S1. Locations of the six study sites in Peninsular Malaysia.

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