

Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture

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Abstract

Species differ in vulnerability to anthropogenic land use changes. Knowledge of the mechanisms driving differential sensitivity can inform conservation strategies but is generally lacking for species-rich taxa in the tropics. The diverse bat fauna of Southeast Asia is threatened by rapid loss of forest and expanding agricultural activities, but the associations between species, traits, vulnerability to agriculture, and the underlying drivers have yet to be elucidated. We studied the responses of speciose insectivorous bat assemblages to robusta coffee cultivation in Sumatra, Indonesia. We compared abundance, species richness, and assemblage structures of bats between forests and coffee farms based on trapping data and evaluated the influence of vegetation complexity on assemblage composition and species-level reactions. Bat abundance and species richness were significantly lower in coffee farms than in forests. Bat assemblage structure differed between land uses, and the overall variation can be largely explained by vegetation simplification. Species sensitive to coffee agriculture were associated with more complex vegetation structure, whereas tolerant species were associated with simpler vegetation structure. Sensitive and tolerant species differed in the type, frequency, and bandwidth of echolocation calls and roost use. Species sensitive to coffee use broadband and high-pitched frequency-modulated calls, which are efficient at detecting insects in complex vegetation, and roost in plant structures that may be lost as vegetation is simplified. In contrast, tolerant species used lower pitched constant-frequency calls and roost in caves. We advocate for greater use of trait analyses in studies seeking to clarify the influence of agriculture on diverse tropical bat faunas.

Abstract in Indonesian is available with online material.

KEYWORDS

forest bat, Indonesia, land use change, species vulnerability, trait-based analyses, vegetation simplification

1 | INTRODUCTION

Anthropogenic land use has greatly threatened global biodiversity in the last few centuries (Ceballos et al., 2015). The processes involve loss of natural habitats and subsequent conversion of land to

human-managed habitats (Vitousek, Mooney, Lubchenco & Melillo, 1997). The expansion of human-managed habitats causes local extinction of native species via simplification of habitat structure, fragmentation, pollution, establishment of wildlife-unfriendly infrastructure including roads, hunting, human-wildlife conflict, and

introduction of alien species, among others (Owens & Bennett, 2000; Laurance, Goosem, & Laurance, 2009; Pimm et al., 2014). Species diversity declines are widespread, but species losses are not equal among evolutionary clades (Jones, Purvis & Gittleman, 2003; McKinney & Lockwood, 1999). Such phylogenetic differences in extinction rates are often strongly associated with species traits that differentiate fitness in the changing world (Flynn et al., 2009; Vandewalle et al., 2010). Consequently, it is a central goal of conservation biologists to identify species sensitive to habitat conversion and biological traits that confer resilience or vulnerability of species in human-dominated landscapes (Mace, 2014).

Relationships between traits and vulnerability influence both the probability of local extirpation of species and the distribution and abundance of traits in remnant assemblages. Trait-vulnerability relationships are especially important to elucidate in the forested habitats of the wet tropics. Not only are tropical rainforests subject to rapid rates of loss and conversion to agricultural uses (Malhi, Gardner, Goldsmith, Silman & Zelazowski, 2014), but the speciose groups they support commonly comprise diverse evolutionary clades (Mittelbach et al., 2007) and trait combinations (Stevens, Cox, Strauss & Willig, 2003). Differential vulnerability to land use change is thus expected and has been documented in several tropical agriculture systems and taxa (e.g., ants—Brühl & Eltz, 2010, bats and birds—Maas et al., 2015, amphibians and reptiles—Gallmetzer & Schulze, 2015), but the specific traits associated with sensitivity to habitat changes that derive from the establishment and intensification of agriculture are seldom identified. This constrains development of both predictive frameworks of loss and agricultural strategies and practices that might mitigate species declines.

Coffee (*Coffea* spp.) is one of the most economically significant crop species in the global market (International Coffee Organization 2015) and cultivation is widespread in montane areas (<2,000 m asl) across the tropics (Maas et al., 2015). Due to the great species diversity and high conservation relevance of wet montane forest, the biodiversity value and conservation potential of coffee agricultural systems have been extensively studied (Maas et al., 2015). The effectiveness of coffee agroecosystems in conserving biodiversity is associated with the degree of management intensification (Estrada, Damon, Hernández, Pinto & Núñez, 2006; Mendenhall, Karp, Meyer, Hadly & Daily, 2014; Williams-Guillén & Perfecto, 2010). For instance, farms in which coffee bushes are grown under native shade trees and mixed with diverse crop species retain important habitats for insects, birds, and small mammals in degraded landscapes (Harvey & Villalobos, 2007; Numa, Verdú & Sánchez-Palomino, 2005; Pineda, Moreno, Escobar & Halffter, 2005; Wordley, Sankaran, Mudappa & Altringham, 2015). Ensemble-level responses to coffee agriculture (Philpott et al. 2008, Williams-Guillén & Perfecto, 2011), and changes of functional (trait) diversity at the assemblage level have also been observed (Pineda et al., 2005; Sekercioglu, 2012). Despite the growing interest in the consequences of coffee production for biodiversity, the relationships between biological traits, species vulnerability, and cultivation management in coffee agriculture are yet to be explored.

Bats are generally common and diverse in coffee-dominated landscapes across tropical regions (the Neotropics—reviewed by Maas et al., 2015, the Asian tropics—Huang et al., 2014; Wordley et al., 2015). However, the abundance and species richness of bats in coffee farms decreases as management intensifies (Mendenhall et al., 2014). Bat assemblages are functionally and ecologically diverse (Kunz, de Torre, Bauer, Lobo, & Fleming, 2011; Maas et al., 2015), so trait-based differences in vulnerability and persistence are anticipated and have been observed in bat ensembles that survive the transition from forest to coffee in the Neotropics (García-Morales, Badano & Moreno, 2013; Williams-Guillén & Perfecto, 2011). Management of coffee agriculture usually involves removal of native plant species and dead parts of plants (Moguel & Toledo, 1999) and overall simplification of vegetation structure. This vegetation simplification is likely to reduce the availability of key resources (e.g., plant roosts (Cortés-Delgado & Sosa, 2014), insect diversity and abundance (Perfecto, Mas, Dietsch & Vandermeer, 2003; Perfecto & Snelling, 1995)) and increase open spaces in coffee farms. Such changes could substantially disfavor species that use plants as roosts (Cortés-Delgado & Sosa, 2014; Struebig, Kingston, Zubaid, Mohd-Adnan & Rossiter, 2008). Reduction of structural complexity would also reduce foraging efficiency of species adapted to forage for insects in cluttered vegetation (Williams-Guillén & Perfecto, 2011). Typically, insectivorous clutter specialists combine high-frequency echolocation calls for detecting prey at short range without interference from the background (Denzinger & Schnitzler, 2013) and wing morphologies that confer maneuverable flight (low wing loading and low aspect ratio) (Norberg & Rayner, 1987).

In the present study, we captured bats from the core area of robusta coffee (*Coffea canephora*) agriculture in Indonesia. We focused on understory insectivorous species because they dominate unmodified forests in Southeast Asia (Patterson, Willig, Stevens, 2003, Kingston, Francis, Zubaid & Kunz, 2003), but are proving highly vulnerable to forest loss and degradation (Kingston, 2013). The potential for agricultural activities to sustain understory insectivorous bat diversity is important. Previous studies have operated at the assemblage level (combining data across insectivorous and frugivorous ensembles) and identified negative responses to rubber plantations (Phommexay, Satasook, Bates, Pearch & Bumrungsri, 2011), neutral responses to degraded forest/agricultural mix (Furey, Mackie & Racey, 2010), and positive responses to mixed tea forest landscapes (Wordley et al., 2015). Our goals were twofold. We first evaluated the effects of coffee agriculture on bat diversity at the assemblage level and measured the associations between the changes in assemblage composition and changes in the complexity and structure of the vegetation. We then identify species in the understory insectivorous bat assemblage that are vulnerable to robusta coffee cultivation. We compared ten biological traits, including echolocation call features, body size, roost use, and flight ability, between coffee-sensitive species and coffee-tolerant species to determine if there were any common traits associated with vulnerability. We hypothesized that bat assemblages would change significantly from forest to coffee farms and such changes would be associated with

vegetation simplification in the coffee farms. We also hypothesized that species with similar levels of sensitivity to coffee agriculture would be more similar in trait values.

2 | METHODS

2.1 | Study area

Fieldwork was conducted in the Bukit Barisan Selatan landscape (5°39'S, 104° 24'E, Figure S1) in southwestern Sumatra, Indonesia between July 2011 and June 2012. The study landscape is composed of several large montane forest and lowland rainforest blocks surrounded by various anthropogenic habitats, mainly robusta coffee (*Coffea canephora*) agriculture (WWF 2007). Our surveys were conducted at three localities (Figure S1), Way Canguk-Sumber Rejo (WS: 5°37'47" S, 104°22'12" E), Sukaraja-Kuyung Arang (SK: 5°31'11" S, 104°27'00" E), and Sukabandar-Lombok (SL: 4°56'24" S, 103°52'47" E). In the study area, coffee is grown mainly under one to three crop species, including coral tree (*Erythrina subumbrans*), cacao (*Theobroma cacao*), rubber tree (*Hevea brasiliensis*), and avocado (*Persea americana*), with intermediate shade cover (Philpott et al. 2008). A few other timber trees, fruit trees, and/or bamboo stands were also grown at the borders between farms (see details in Huang et al., 2014). Based upon the classification of Moguel and Toledo (1999) that is widely applied in the Neotropics, the study coffee farms were most similar to "shade monoculture coffee" and "commercial polyculture coffee."

To ensure the independence of each locality, the minimum distance between two localities was 14 km. The distance is greater than the maximum effective distance (11 km) that understory bat assemblage structures were significantly affected by the subsidy of insectivorous bats from nearby cave roosts in Malaysia (Struebig et al., 2009). Within each locality, one forest site and two coffee sites were selected. To control potential landscape influences and to estimate the immediate influence of coffee agriculture on forest bat diversity, we selected forest sites from the largest forest block in the landscape and at least 1 km to the nearest edge. The coffee farm sites were within 2 km of the nearest edge of large forest. The two coffee sites were at least 1 km apart from each other.

2.2 | Bat diversity data

Insectivorous bats were sampled with four-bank harp traps (Francis 1989), which are effective in capturing insectivorous bats active within 5 m of the ground (Kingston, 2013). To avoid the potential influence of seasonality on responses to disturbances (Ferreira et al., 2017), the trapping sessions were conducted in two consecutive dry seasons (July–September 2011 and late February–June 2012) during the survey period, avoiding the monsoon rains of October–mid February. Five to seven harp traps were placed at approximate 50-m intervals along existing trails each night and moved to new points in the next morning. Captures from trap nights interrupted by rain, or from traps closed early because of actual or potential ant attacks

were excluded from analysis. At each site, 22–32 harp trap-nights were completed. To reduce the influence of rare species to incidence-based analysis (see data analysis 2.8 section), we also included additional species occurrence data of understory insectivorous bats from literature (Huang et al., 2014) and by acoustics (4 hr per site) in our parallel project in incidence-based analyses (see Table S1 for details).

2.3 | Biological traits

To assess the associations between sensitivity and species traits, we extracted data of five echolocation call features (call category, frequency of maximum energy (kHz), highest frequency (kHz), frequency bandwidth (kHz) and call duration (ms)), forearm length (mm), and body mass (g) roost use and flight maneuverability score (see below). Echolocation and morphological features were extracted from our empirical data (Huang, 2015; Huang et al., 2014) and literature (Kingston, Jones, Zubaid & Kunz, 1999; Schmieder, Kingston, Hashim & Siemers, 2010, 2012). Species were assigned to one of the four call type categories based on the major echolocation call types used, namely constant frequency (CF), multiharmonic frequency-modulated (MFM), broadband frequency-modulated (BFM), and FM-quasi-CF (FQ) primarily following Jones and Teeling (2006). Roost use was assigned based on Kingston, Lim and Zubaid (2006) and Huang et al. (2014). Six species lacking data were assigned based on the major trend among congeners if possible (see Table S3 for details). All species were assigned to one of the following roosting ensembles (a) plant-roosting specialist, (b) cave-roosting specialist, and (c) roosting generalist. Flight maneuverability was estimated from log body mass using a linear equation based on 25 Malaysian insectivorous bats (Senawi, 2015).

2.4 | Vegetation structure assessment

We measured vegetation structure using a categorical approach for capturing vegetation composition through rapid ground assessments across sites (Gibbons & Freudenberger 2006). We visually identified presence or absence (as 1 and 0, respectively) of (a) shrubs (height 0.5–5 m), (b) understory plants (5–10 m), (c) canopy tree (>10 m and tree crown connected and formed a continuous cover), (d) emergent tree (taller than canopy level and with a crown that did not connect with neighbors), (e) large fallen logs (fallen tree trunk with a diameter > 30 cm), and (f) arboreal liana within a 7-m radius of each harp trap point. We then estimated vegetation stratification by calculating the proportion of the summed vegetation strata over the maximum number of strata (shrub, understory, canopy, emergent plants, and arboreal liana) for each survey point. For example, a value of 40% indicates two strata, regardless of strata type, out of the five strata measured were recorded at a point. We also measured shade cover at the survey point by estimating proportional coverage of vegetation directly above the point viewed through a 50 × 50 cm quadrat divided into 25 10 × 10 cm grids. The quadrat was held 2 m above ground. The eight parameters are not only used as indicators of vegetation complexity but can be also considered indicators of

plant roost availability, foraging habitat diversity, and associated with insect diversity.

2.5 | Data analysis

We performed all analyses in the environment of R version 3.5.3 (R Core Team 2019) and used the *vegan* package 2.5.4 (Oksanen et al., 2019) unless stated otherwise.

2.6 | Assemblage level: abundance, species richness, assemblage structure

The three study localities differed in elevation ranges (WS: 0–50 m, SK: 360–640 m, SL: 595–1,045 m, asl) and known cave roost abundance (within 11-km radius, WS: 6 roosts, SK: 3 roosts, SL: none, Huang et al., 2014, MN unpublished data). To avoid confounding the effects of coffee agriculture with the potential effects of elevation (McCain, 2007) and subsidy of individuals from local caves (Struebig et al., 2009), we adopted a block design for the comparisons of bat assemblages, treating localities as the blocks and land use as the fixed factor. We used permuted one-way analysis of variance (ANOVA) tests with a block design based on 4,999 iterations to estimate the significance levels of differences of abundance and rarefied richness between groups (land uses: forest vs. coffee) and blocks (localities) (Anderson, 2001). We used EstimateS version 9.1 (Colwell, 2013) to calculate sample-based rarefied species richness to that of the lowest harp trap effort across sites (22 trap-nights) with MaoTau estimator based on 1,000 randomizations. To estimate the effects of land use and locality on assemblage structure, we used non-metric multi-dimensional scaling (NMDS) with the function *metaMDS* to project the dissimilarity of assemblage structures (McGarigal, Cushman & Stafford, 2000). Then, we measured the differences in species composition as the variance of distances between group centroids in the selected NMDS space (Warton, Wright & Wang, 2012) and beta diversity as the deviation of distances from samples to group centroid (Anderson, Ellingsen & McArdle, 2006). We used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) with block design and permuted ANOVA tests on 4,999 iterations with the functions *adonis* to test the differences of species composition and beta diversity, respectively, between land uses and among localities.

2.7 | Correlations between species composition, and vegetation structure, elevation and cave roost

Vegetation variables were averaged across all points for each study site and standardized to a scale of 0.0–100.0, which gave equal weight to all variables. Bootstrapped 95% confidence intervals on 1,000 randomizations were estimated for between-site comparisons. Bio-env analysis was used to find a subset of vegetation variables that had the maximum rank correlation with the variations in species composition among sites (Clarke & Ainsworth, 1993). We

also included the lowest, highest, and midpoint measures of elevation, number of cave roosts and the distance to the nearest cave roost within the 11 km radius, across all trap points for each site in a second bio-env analysis to determine the contribution of the two landscape factors for the among-locality variations of species composition.

2.8 | Species level: identifying sensitive and tolerant species to robusta coffee agriculture

We carried out Indicator Species Analysis (ISA) on abundance data and Pearson's correlation with Phi coefficient (PcP) on species presence-absence data to determine associations between species and land use types using the *indicspecies* package in R. The significance of the tests was assessed with Monte Carlo procedure (Dufrene & Legendre, 1997). We assigned species with strong positive correlations ($IV \geq 0.70$) with forest by ISA and/or negative correlations (R^2 value ≤ -0.70) with coffee farm by PcP to “sensitive species” to coffee agriculture, and *vice versa* for “tolerant species.” Species with IV values ≥ 0.70 for both land uses were also assigned to coffee agriculture-tolerant species.

2.9 | Relationships between coffee agriculture sensitivity, species traits, and vegetation structure

We performed permuted unpaired t tests on 4,999 iterations and Pearson's chi-square tests with corrected *p*-value estimation via 2,000 Monte Carlo simulations to compare trait differences between coffee sensitive and tolerant species for quantitative and qualitative measures, respectively. We used smoothing function-based generalized additive models (GAMs) with *ordisurf* function to predict the summed values of selected vegetation factors by Bio-env analysis in *vegan* for each sensitive and tolerant species. The GAM model with a knot number greater than the degree of freedom and with a minimized value of restricted maximum likelihood (REML) was selected as the best-fitted model (Oksanen et al. 2019). We then tested the correlations between the predicted vegetation complexity score and quantitative and traits using permuted Pearson linear correlation and permuted one-way ANOVA on 4,999 iterations, respectively. We provide further details of the statistical analyses in the Supplementary Information (Appendix S1).

3 | RESULTS

3.1 | Abundance and species richness

In total, 836 individuals of 25 insectivorous bat species were captured with harp traps (709.6 STUs) (see Table S1 for species accounts). Abundance of insectivorous bats were significantly different between land uses ($p < .001$, permuted one-way ANOVA), with more individuals captured in the forest sites than in the coffee sites (Figure 1a). However, this pattern was largely driven by the abundance of individuals in the

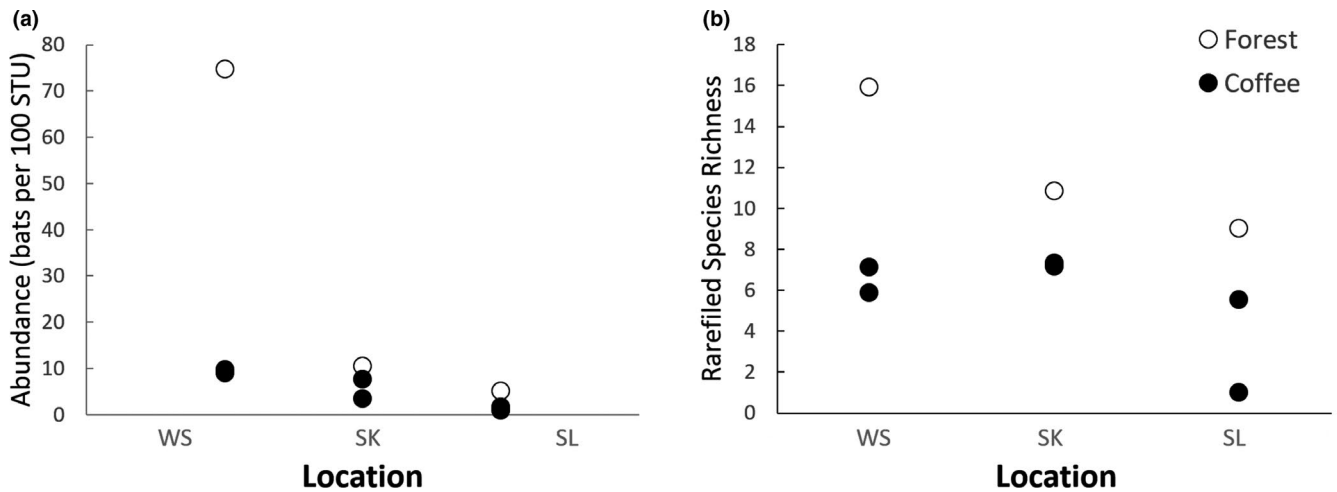


FIGURE 1 Abundance (a) and rarefied species richness at 22 trap-nights (b) of insectivorous bats at the nine study sites in Bukit Barisan Selatan Landscape, Sumatra. Locality abbreviations—WS: Way Canguk-Sumber Rejo; SK: Sukaraja-Kuyung Arang; SK: Sukabanjar-Lombok. In the Y axis title, STU stands for the standard trap unit, which is calculated as one m² area of a trap opened per 12 hr

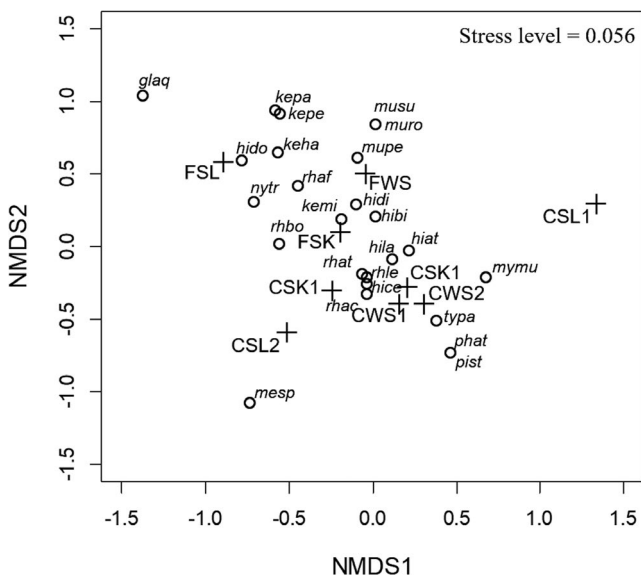


FIGURE 2 Non-metric multidimensional scaling ordination of insectivorous bat assemblages at the nine study sites showing associations between species and sites. Crosses denote sites and unfilled circles denote species. Uppercase letters are abbreviated site names, of which the first letter indicates the landuse (F: forest; C: coffee farm), the next two letters indicate the locality, and the number indicates the field number of coffee farm sites. Lowercase letters are abbreviated species names, of which the first two letters indicate the genus and the next two letters the specific epithet. Genus abbreviations—gl: Glischropus, hi: Hipposideros, ke: Kerivoula, me: Megaderma, mu: Murina, my: Myotis, ny: Nycteris, pi: Pipistrellus, ph: Phoniscus, rh: Rhinolophus, ty: Tylonycteris. See Figure 1 for locality abbreviations and Table S1 for full species abbreviations

forest of the locality WS and abundance of insectivorous bats was significantly different among localities ($p < .001$, permuted one-way ANOVA). More species were recorded in forest sites than in coffee sites ($p < .001$, permuted one-way ANOVA) and this was consistent across localities ($p = .104$) (Figure 1b).

3.2 | Assemblage structure

A two-dimensional NMDS model with a stress level of 0.056 was selected (Figure 2). Models with three or more dimensions all had stress levels nearly 0 and were not considered improvements over the two-dimensional model. In general, most *Hipposideros* and *Rhinolophus* species and most coffee sites were distributed close to the origin of the NMDS space. Forest sites (top left quadrant) were generally characterized by species of vespertilionid genera *Kerivoula* and *Murina*. Species compositions of insectivorous bats varied significantly between land uses ($p = .002$, PERMANOVA) and among localities ($p = .013$, PERMANOVA). Homogeneity tests suggest beta diversity of insectivorous bat assemblages was differed significantly among localities ($p = .033$, permuted one-way ANOVA) but not between land uses ($p = .976$, permuted one-way ANOVA). Lower beta diversity among sites were detected at localities WS and SK than at locality SL (average distance to centroid: 0.288, 0.271 and 0.532, respectively).

3.3 | Correlations between species composition, and vegetation structure, elevation, and cave roost

All forest sites had higher occurrences of canopy tree, emergent, and arboreal liana and higher shade cover and vegetation complexity than coffee farm sites. Coffee sites in the same locality also differed in the presence of canopy trees and arboreal lianas, shade cover, and vegetation complexity, but there was no consistent pattern across localities (see Table S2 for details). Bio-env analysis suggested shade-cover level and presence of fallen logs as the most influential factors for insectivorous bats, explaining 44.9% of the overall variation of species compositions (Table 1). With the additional measures of elevation and cave abundance gradients, the best model was described by presence of fallen log, number of cave roosts within 11 km, and distance to nearest cave roost, explaining 61.2% of the overall variation in species composition (Table 2).

3.4 | Identifying coffee sensitive and tolerant species

Eight species showed high positive correlations with forest sites by the Indicator Species Analysis (ISA): all three *Kerivoula* species, *Murina peninsularis*, *Rhinolophus trifolius*, *Hipposideros bicolor*, and *H. doriae*. Only the associations of *Kerivoula hardwickii* were considered significant by both ISA and PcP (Table 3). Among the eight ISA-selected forest species (hence coffee agriculture sensitive), *R. trifolius* was the only species that showed intermediate correlations with both land uses by PcP analysis. PcP did not support the significance of other suggested coffee-sensitive species despite generally high (≥ 0.75 , Table 3) IV values. Seven species, namely *Hipposideros cervinus*, *H. larvatus*, all other *Rhinolophus* species and *Myotis muricola*, were identified as coffee agriculture-tolerant species by ISA. The PcP test did not detect a strong correlation between any of the ISA coffee-tolerant species and coffee farms in general (Table 3).

3.5 | Biological traits of coffee sensitive and tolerant species

Sensitive species averaged smaller body size, better flight maneuverability, and echolocation calls with shorter duration, higher frequency and broader frequency bandwidth (Figure 3, Table S3). However, only differences in the highest frequency (HF) and bandwidth (BW) were significant ($p = .007$ and 0.012 for HF and BW, respectively, permuted t test). The sensitive and tolerant species also differed in the use of roost type and call category ($p = .012$ and $.013$, respectively, permuted chi-square test). All sensitive species, except the *Hipposideros bicolor*, mainly use plants as day roosts. In contrast, all tolerant species, except *Myotis muricola*, are either cave-roosting specialists ($n = 4$) or roost generalists ($n = 3$). All tolerant species, except *M. muricola*, use echolocation calls characterized

TABLE 1 Maximum rank correlations between species composition in non-metric multidimensional scaling space and subsets of eight vegetation characters by bio-env analysis

Variable(s) included	No. of variable	Correlation (%)
Log	1	34.94
Log, shade	2	44.87
Log, shade, emergent	3	44.88
Log, shade, emergent, strata	4	42.34
Log, shade, emergent, strata, liana	5	39.94
Log, shade, emergent, strata, liana, canopy	6	35.90
Log, shade, emergent, strata, liana, canopy, understory	7	27.74
Log, shade, emergent, strata, liana, canopy, understory, shrub	8	20.40

Note: Boldface indicates the subset used in GAM predictions.

by a constant-frequency component (CF), whereas five of the sensitive species use broadband frequency-modulated calls and only three use CF calls (see Table S3 for species trait details).

3.6 | Predicted associations between species traits and vegetation complexity

A two-variable GAM on the two selected vegetation measures (shade cover and fallen log) with five knots for the smoothing function was selected to predict species' responses to vegetation structure ($y = \text{smooth}[x_1, x_2], \text{knot} = 5, \text{REML score} = 35.4$). The ISA-selected species sensitive to coffee have significantly higher predicted values of vegetation complexity than the coffee tolerant species ($p < .001$, permuted t test) (Table 4, Figure 3I). Generally, species that use frequency-modulated calls with higher frequency and broader frequency bandwidth, and exclusively use plant roosts are associated with higher vegetation scores than cave-dwelling species that use constant-frequency calls with lower frequency and narrow bandwidth ($p = .014$ and $.009$ for HF and BW, respectively, permuted Pearson Linear Correlation; $p = .011$ and $.002$ for roost use and call category, respectively, permuted one-way ANOVA).

TABLE 2 Maximum rank correlations between species composition in non-metric multidimensional scaling space and subsets of all 13 environmental characters by bio-env analysis

Variable(s) included	No. of variable	Correlation (%)
D_{Cave}	1	37.01
D_{Cave}, \log	2	59.68
$D_{\text{Cave}}, \log, N_{\text{Cave}}$	3	61.22
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}$	4	61.17
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}$	5	58.09
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{strata}$	6	55.31
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{strata}, \text{liana}$	7	54.42
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{emergent}$	8	50.43
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{emergent}, \text{strata}$	9	47.80
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{strata}, E_{\text{Min}}, E_{\text{Avg}}$	10	45.28
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{strata}, E_{\text{Min}}, E_{\text{Avg}}, \text{emergent}$	11	42.24
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{strata}, E_{\text{Min}}, E_{\text{Avg}}, \text{emergent}, \text{understory}$	12	37.69
$D_{\text{Cave}}, \log, N_{\text{Cave}}, \text{shade}, E_{\text{Max}}, \text{liana}, \text{canopy}, \text{strata}, E_{\text{Min}}, E_{\text{Avg}}, \text{emergent}, \text{understory}, \text{shrubs}$	13	30.20

Note: Boldface indicates the subset with maximum correlation and used in GAM predictions.

Abbreviations: D_{Cave} , distance to nearest cave roost; N_{Cave} , number of cave roosts; E_{Max} , maximum elevation; E_{Min} , minimum elevation; E_{Avg} , average elevation.

TABLE 3 Results of Indicator Species Analysis and Pearson correlation with Phi coefficient for 22 study bat species sampled across the Bukit Barisan Selatan Landscape, Sumatra

	Forest		Coffee farm		Pooled data of both land uses
	IV	R ² _{phi}	IV	R ² _{phi}	IV
<i>Hipposideros ater</i>	0.45	0.00	0.36	0.00	0.58
<i>H. bicolor</i>	0.75	0.50	0.16	-0.50	0.58
<i>H. cervinus</i>	0.46	-0.32	0.49	0.32	0.75
<i>H. diadema</i> ^a	0.58	0.16	0.18	-0.16	0.47
<i>H. doriae</i>	0.82	0.76	0.00	-0.76	0.47
<i>H. larvatus</i> ^a	0.69	-0.19	0.44	0.19	0.82
<i>Rhinolophus acuminatus</i>	0.48	0.25	0.74	-0.25	0.88
<i>R. affinis</i>	0.58	0.25	0.74	-0.25	0.94
<i>R. borneensis/celebensis</i>	0.66	0.16	0.41	-0.16	0.75
<i>R. lepidus/pusillus</i>	0.53	-0.19	0.59	0.19	0.88
<i>R. trifoliatus</i> ^a	0.95*	0.50	0.16	-0.50	0.67
<i>Megaderma spasma</i> ^a	0.00	0.32	0.41	-0.32	0.33
<i>Nycteris tragata</i>	0.69	0.63	0.22	-0.63	0.58
<i>Kerivoula hardwickii</i>	1.00*	1.00*	0.00	-1.00*	0.58
<i>K. minuta</i>	0.77	0.50	0.13	-0.50	0.58
<i>K. papillosa</i>	0.82	0.76	0.00	-0.76	0.47
<i>K. pellucida</i>	0.82	0.76	0.00	-0.76	0.47
<i>Phoniscus atrox</i> ^a	0.00	-0.19	0.41	0.19	0.33
<i>Murina peninsularis</i>	0.82	0.76	0.00	-0.76	0.47
<i>M. rozendaali</i>	0.58	0.50	0.00	-0.50	0.33
<i>M. suilla</i>	0.58	0.50	0.00	-0.50	0.33
<i>Myotis muricola</i>	0.30	-0.32	0.69	0.32	0.75
<i>Glischropus aquilis</i>	0.58	0.50	0.00	-0.50	0.33
<i>Pipistrellus sthenopterus</i>	0.00	-0.25	0.41	0.25	0.33
<i>Tylonycteris pachypus</i>	0.00	-0.25	0.41	0.25	0.33

Note: IV and R²_{phi} denote indicator value and Pearson correlation, respectively. Species in boldface denote species with absolute values of IVs or R²_{phi} ≥ 0.70. Significant values are marked with asterisks.

^aSpecies with additional occurrence data from mist netting and museum records in Huang et al. (2014) and acoustic monitoring (JCCH and TK unpublished data).

4 | DISCUSSIONS

We demonstrated that robusta coffee agriculture significantly shaped understory insectivorous bat assemblages in southwestern Sumatra, and that the patterns were mainly driven by trait-based species reactions to vegetation simplification in coffee farms. Species with similar responses to coffee agriculture and vegetation simplification generally shared similar biological traits, which suggests that biological traits are useful predictors of species vulnerability for tropical bats. Our findings suggest that extirpation of Southeast Asian bats from coffee landscapes is non-random among ecological groups. As a result, we predict large-scale decreases in functional diversity of bat assemblages as coffee agriculture expands and intensifies throughout the region.

Seven of the eight coffee-sensitive species are generally characterized by small body size and use of short and high-frequency

echolocation calls and are predicted to be associated with complex vegetation. All sensitive species, except *Rhinolophus trigoliatus* and two *Hipposideros* species, also showed convergence of plant-roosting habit and short and broadband calls. The commonality of traits and strong correlations with complex vegetation in our samples may explain why these species were sensitive to coffee agriculture. Vegetation simplification could disfavor sensitive species by reducing plant roost availability (Cortés-Delgado & Sosa, 2014; Struebig et al., 2013), prey availability (Phommexay et al., 2011; Wickramasinghe & Harris, 2004), degrading roost quality (e.g., through changes in roost microclimate as shade cover is lost Barradas & Fanjul, 1986), or increasing predation pressure (Gardner, 1998). Although not yet documented, vegetation simplification may also provide fewer quality foraging microhabitats for the sensitive species in our study. The high-frequency calls used rapidly attenuate in air (Denzinger & Schnitzler, 2013) and disfavor targeting prey in more open

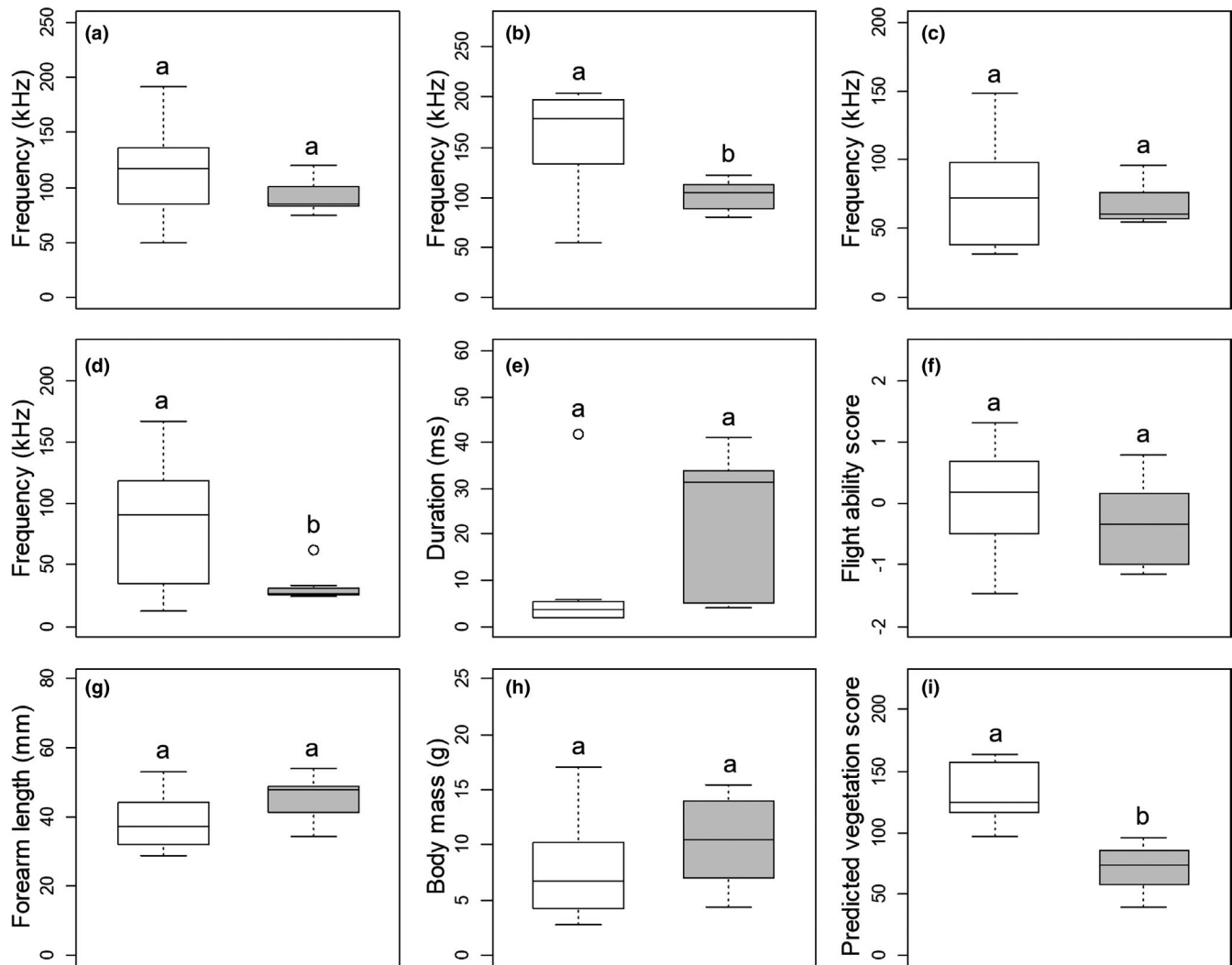


FIGURE 3 Comparisons of eight biological traits (a–h) and the predicted vegetation complexity score (i) of coffee-sensitive species (white boxes) and coffee-tolerant species (light gray boxes). Frequency with maximum energy (a), highest frequency (b), lowest frequency (c), frequency bandwidth (d), call duration (e), predicted flight maneuverability (f), forearm length (g) and body mass (H). The sections of the box represent upper quartile, median, and lower quartile; the open dots represent outliers, which are more than 1.5 times the value of the upper quartile or <1.5 times value of the lower quartile; the upper and lower whiskers represent values outside the inter-quartile range, excluding outliers. In each pair-wise comparison, species groups that do not share the same letter are statistically different in permuted unpaired t test, whereas those that share the same letter are not statistically different

microhabitats. Flight constraints might also preclude these species from hunting fast-flying insects in open habitats because their wing morphologies are more suitable for slow and maneuverable flight in cluttered environments (Furey & Racey, 2016; Senawi, 2015).

Six of the seven coffee tolerant species, except *Myotis muricola*, were intermediate size bat species characterized by cave specialization (Kingston et al., 2006; Struebig et al., 2009) and lower pitch constant-frequency (CF) calls (Kingston, Jones, Zubaid & Kunz, 2000). Although CF bats are referred as forest-interior species in Asia (Kingston et al., 2003; Wordley et al., 2015), the recent records of these bats from disturbed habitats (Furey et al., 2010; Graf, 2010; Kusuminda, Mannakkara, Patterson & Yapa, 2018; Phommexay et al., 2011; Struebig et al., 2013; Wordley et al., 2015) suggest they might be tolerant of some degree of disturbance. The abundance of these cave specialists at the study sites reflects the relationship

between cave availability and commuting distances, suggesting the ability of these bats to travel from roosts to foraging grounds in disturbed landscapes and highlighting the role of caves in maintaining bat diversity at landscape scale (Struebig et al., 2009). Constant-frequency calls enable bats to detect wing fluttering of insects, a distinctive acoustic signature in cluttered environments (Denzinger & Schnitzler, 2013) but also one that is apparent in semi-cluttered habitats. Moreover, lower frequency calls attenuate relatively slowly and may allow bats to forage by aerial-hawking and perching-hunting (Jones & Rayner, 1989; Neuweiler et al., 1987) in the gaps and vegetation edge of coffee farms. However, decreasing abundance and activity of CF bats in other agriculture types with less vegetative complexity (Furey et al., 2010; Phommexay et al., 2011; Wordley et al., 2015), indicate that these bats are sensitive to high agricultural management intensity.

TABLE 4 Summary of sensitivity to coffee agriculture for 15 selected species with summed value of shade cover and occurrences of fallen log predicted by generalized additive model (GAM)

Taxon	ISA	PcP	GAM prediction
<i>Kerivoula pellucida</i>	Sensitive	Sensitive	164.0
<i>Kerivoula papillosa</i>	Sensitive	Sensitive	163.3
<i>Murina peninsularis</i>	Sensitive	Sensitive	151.6
<i>Kerivoula hardwickii</i>	Sensitive	Sensitive	128.2
<i>Rhinolophus trifoliatus</i>	Sensitive	-	121.8
<i>Hipposideros doriae</i>	Sensitive	Sensitive	121.1
<i>Hipposideros bicolor</i>	Sensitive	-	112.3
<i>Kerivoula minuta</i>	Sensitive	Sensitive	97.2
<i>Rhinolophus borneensis/celebensis</i>	Tolerant	-	95.1
<i>Hipposideros larvatus</i>	Tolerant	-	93.6
<i>Hipposideros cervinus</i>	Tolerant	-	76.6
<i>Rhinolophus lepidus/pusillus</i>	Tolerant	-	73.7
<i>Rhinolophus affinis</i>	Tolerant	-	62.7
<i>Rhinolophus acuminatus</i>	Tolerant	-	51.4
<i>Myotis muricola</i>	Tolerant	-	39.5

Note: Only species considered sensitive and tolerant to coffee agriculture by one or more of the analytical techniques are listed. Analysis abbreviations: ISA, Indicator Species Analysis; PcP, Pearson correlation with Phi coefficient. "sensitive" and "tolerant" denotes high and low sensitivity to coffee agriculture regardless management intensity, respectively. "-" denotes no or low correlation for both all landuse types by PcP.

All species of Kerivoulinae (five species) and Murininae (three species) in our studies were either sensitive to coffee farms or only found in forests, whereas tolerant species were largely drawn from the Rhinolophidae and Hipposideridae. This suggests a strong phylogenetic signal to sensitivity. Given the decline of species richness and abundance of Kerivoulinae and Murininae in other agricultural types (Furey et al., 2010; Phommexay et al., 2011) and disturbed habitats (Struebig et al., 2008), a directional shift of phylogenetic diversity of bats in SE Asia as landscapes are modified is to be expected (Kingston, 2013). Despite the phylogenetic component to vulnerability in our samples, our finding of trait convergence—to small size and high frequencies—across families precludes reliance on phylogeny alone and highlights the importance of trait-based analyses for studying responses of bats to disturbances, particularly if predictive frameworks are to be developed (Furey & Racey, 2016).

We found clear evidence that local vegetation structure influenced bat diversity. The two influential vegetation measures in our study, shade cover and the presence of fallen logs, have also been identified as important to local bat diversity in other disturbed landscapes. Shade cover is an important predictor of insect diversity in neotropical arabica coffee (*Coffea arabica*) farms (Perfecto & Snelling, 1995; Perfecto et al., 2003). Abundance of large fallen logs (and dead standing tree trunks), an indicator of cavity roost

availability, was positively associated with insectivorous bat diversity in a logging forest landscape in Borneo (Struebig et al., 2013). Our findings could explain why studies of bat communities from the Neotropics frequently report greater abundance and unchanged species richness in arabica coffee farms (Mendenhall et al., 2014; Numa et al., 2005; Pineda et al., 2005; Williams-Guillén & Perfecto, 2010). Arabica coffee is commonly grown as an understory shade crop, a practice that retains much of the structural complexity of unmodified forests (Moguel & Toledo, 1999). In contrast, robusta coffee is shade intolerant, so is cultivated under limited canopy cover and in association with lower diversity and complexity of vegetation (Philpott et al. 2008). The more vegetative diverse arabica coffee farms in the Neotropics may support more insects and plant roosts to bats (Cortés-Delgado & Sosa, 2014; Williams-Guillén & Perfecto, 2011).

Roost ecology may provide a partial explanation of the greater bat diversity in Neotropical coffee farms, but there is also an interaction with another biological trait, trophic level. Whereas insectivorous bats dominate local bat diversity in the Paleotropical rainforests, there is much greater diversity of understory herbivorous and omnivorous species in the Neotropics and relatively few understory insectivorous species (Kingston et al., 2003; Maas et al., 2015). The shade coffee farms of the Neotropics provide a diversity of fruiting plant species that may provide more predictable and high-density food to herbivorous generalists and omnivorous species and thus support higher bat populations. Similar responses of herbivorous bats to agriculture systems have also been found in the Asian tropics (Fukuda, Tisen, Momose & Sakai, 2009; Furey et al., 2010; Graf, 2010; Wordley, Sankaran, Mudappa & Altringham, 2017). Like our findings, understory carnivorous and insectivorous bats in the Neotropics also showed decreased species richness (Estrada & Coates-Estrada, 2002) and activity (Farneda et al., 2015; Williams-Guillén & Perfecto, 2011) in disturbed habitats, including high management arabica coffee. The convergence in the responses to agricultural activities of different trophic ensembles between the two regions suggests a non-random shift of dietary composition to more herbivorous and less insectivorous assemblages across tropical agricultural landscapes.

At least one landscape feature, the presence and abundance of caves in the landscape, further shaped ensembles at localities. We followed a block design intended to minimize landscape effects at each locality—coffee sites were within 1 km of the forest sites so were part of the same landscape. However, the responses of bats to robusta coffee agriculture may further be modulated by other landscape-scale habitat features, such as habitat size, configuration and isolation, as has been seen in experimental fragmentation systems in the Neotropics (Estrada, Coates-Estrada & Meritt, 1993; Rocha et al., 2017), suggesting an avenue for future research.

Our results support previous suggestions that trait-based evaluations are useful in understanding the complicated reactions of diverse bat assemblages to land uses in tropical areas (Farneda et al., 2015; García-Morales et al., 2013; Struebig et al., 2013). Disturbance studies of tropical bats commonly focus on the consequences at the

assemblage level. Trait-based evaluations are thus critical if comparisons of assemblages that differ in functional trait composition are to be made. Critically, trait-based approaches hold predictive power because traits conferring vulnerability can be identified in species prior to disturbance and population decline. We advocate for further research on a greater diversity of species and land uses to encompass greater trait and disturbance gradients and refine assessments of bat vulnerability in the tropics.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gj34813> (Huang, Rustiati, Nusalawo & Kingston, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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