

Multiple dimensions of biodiversity in paleotropical hotspots reveal comparable bat diversity

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ABSTRACT

Bat species commonly comprise at least 50% of tropical mammalian assemblages, but Afrotropical bat faunas have been little studied leading to perceptions that they are depauperate. Here, we compare alpha taxonomic, functional, and phylogenetic diversity of insectivorous bats belonging to the narrow-space foraging ensemble from a bat diversity hotspot in Nigeria to species-rich sites in Indonesia and Malaysia, using previously published data. The Nigerian site is protected unlogged forests at Afi Mountain Wildlife Sanctuary and Cross River National Park. For comparison, we targeted similar unlogged forest sites in Southeast Asia: Indonesia—Bukit Barisan Selatan National Park Forest in Sumatra; and Kakenauwe Forest Reserve on Buton Island, Sulawesi; and another in Malaysia—Krau Wildlife Reserve. All sites were sampled using comparable methods, with an emphasis on harp traps that effectively capture the forest-interior ensembles. We also compare regional beta diversity of bat assemblages in ecoregions using occurrence data (literature, unpublished records, and online natural history collections) from the

Lower Guinean Forest and the Malay Peninsula. We demonstrate comparable alpha taxonomic, functional, and phylogenetic diversity of narrow-space bats among sites in Nigeria and Indonesia, but greater diversity in Malaysia. Turnover and overall beta diversity of bats among ecoregions was comparable between the Lower Guinean Forest and the Malay Peninsula, but nestedness was higher in the latter. Our results reiterate the value of harp traps in generating bat survey data that allows equatable comparisons of “mist net avoiders” in the Paleotropical forest understory. Our findings have implications for regional and local bat conservation.

Keywords: Chiroptera, alpha diversity, beta diversity, ecoregion, Nigeria, Afrotropics, Paleotropics

1. INTRODUCTION

Species richness peaks in the tropics, yet differences in diversity patterns exist between tropical regions, even for globally distributed taxa such as bats (Hillebrand, 2004; Procheş, 2005; Rohde, 1992). Patterns of species diversity are driven by multiple interacting processes, such as climate, biotic interactions, dispersal, and environmental heterogeneity (Ricklefs, 1987). However, observed patterns are influenced by sampling effort and bias (Fisher-Phelps et al., 2017; Meyer et al., 2011; Rahbek, 1995) that are mediated by the scale of observation (Wiens, 1989), all of which must be considered to ensure robustness of diversity comparisons (Magurran, 2004).

Bats often comprise half the mammalian diversity of the wet tropics (Findley, 1993). Findley (1993) was the first to map the global distribution of bat species richness, and in the Paleotropics, which are largely populated by the same nine families (Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Nycteridae, Emballonuridae, Miniopteridae, Vespertilionidae, and Molossidae) of bats, identified peaks of species richness in Equatorial Africa and the Indo-Malayan region. However, he concluded, based on data available at the time, that Afrotropical bat faunas were depauperate relative to those in Indo-Malaya. This perspective was something of a dogma until more recent surveys pointed to the cryptic diversity within species complexes (Demos et al., 2020; Demos, Webala, Goodman, et al., 2019; Demos, Webala, Kerbis Peterhans, et al., 2019; Hassanin et al., 2015; Hassanin et al., 2018; Monadjem, Richards, Taylor, & Stoffberg, 2013; Monadjem et al., 2019; Patterson et al., 2020; Vallo et al., 2008) and the importance of multi-faceted survey methods in inventorying Paleotropical bat faunas (Fahr & Kalko, 2011; Kingston et al., 2003).

Findley (1993) primarily had access to bat survey data that were based on mist net captures. Mist nets underrepresent bat diversity in Paleotropical forests because the dominant insectivorous ensemble of the forest understorey comprises species of the families Rhinolophidae, Hipposideridae, and Nycteridae, and the vespertilionid subfamilies Kerivoulinae and Murininae, all of which are adept at negotiating dense clutter (Kingston et al., 2003; Senawi & Kingston, 2019) and tend to evade capture in mist nets a.k.a. blindspot diversity (Tanshi et al., 2021). This trapping bias presented Findley with low estimates of Afrotropical alpha diversity between 22 and 38 species (Brosset, 1966; Jones, 1971). Subsequent studies have demonstrated the importance of representing Paleotropical bat faunas through the deployment of complementary capture techniques that target specific ensembles (Francis, 1989; Kingston et al., 2003). Most notable has been the use of harp traps to capture and better represent the forest understory insectivores (also known as “narrow-space” ensemble), and this has been further complemented by deployment of canopy-level mist nets (Fahr & Kalko, 2011; Kingston et al., 2003; Monadjem et al., 2016; Sedlock et al., 2008). The highest species richness from a single Paleotropical forest site of >72 bat species from Krau Wildlife Reserve, Peninsular Malaysia is based on long-term intensive use of harp traps and mist netting surveys to capture high-flying frugivorous and insectivorous bats (Kingston et al., 2003; Kingston et al., 2006). Although intense multi-method sampling with rigorous harp trapping is limited across Africa (Tanshi & Kingston, 2021), Afrotropical forest bat assemblages are suggested to be more diverse than previously believed (Decher et al., 2015; Fahr & Kalko, 2011), and equatorial forest-savanna mosaic assemblages in West Africa report 57 and 60 species at Comoe National Park and Mt Nimba, respectively (Fahr & Kalko, 2011; Monadjem et al., 2016). Yet, equatable contemporary comparisons based on comparable sampling data across Paleotropical regions are lacking. To revisit comparisons between Afrotropical and Indo-Malayan fauna, our study uses recently published data that focused on species that are missed in mist net surveys—forest understorey bats, thereby accounting for the underrepresentation that has limited equatable comparisons between both regions.

Taxonomic diversity is a poor proxy for other forms of biodiversity, for example, phylogenetic and functional diversity (Cisneros et al., 2014; Herrera et al., 2018; Pérez-Sánchez et al., 2021; Webb et al., 2004), limiting our understanding of differences in alpha diversity. Phylogenetic diversity is the total branch length of species on a phylogeny and represents evolutionary relatedness at a given site (Faith, 1992; Scherson & Faith, 2018). Functional diversity refers to total differences or distance between species in functionally relevant trait space (Mason et al., 2005; Villéger et al., 2008). Despite a shared evolutionary history, phylogenetic diversity of Paleotropical bat faunas should differ between Afro- and Indo-Malayan sites because of significant isolation and radiation of Old World bat families that has resulted in distinct regional species pools and local assemblages. Although functional diversity reflects the phylogenetic template, traits are phylogenetically conserved, one is not a reliable proxy for the other due to community processes (Devictor et al., 2010; Swenson & Enquist, 2009).

Turnover increases regional species richness, whereas absolute nestedness has no effect (Baselga, 2012; Whittaker, 1960). As previous comparisons of bat diversity among tropical areas (Findley, 1993) have focused on local richness, the role of turnover in structuring differential

regional richness patterns remains unknown. In addition, comparisons of beta diversity patterns are subject to scale (Olivier & Van Aarde, 2014). Due to the species-area effect, beta diversity tends to be exaggerated at smaller spatial scales (Olivier & Van Aarde, 2014), for example, site level. Conversely, beta diversity values are conservative at larger spatial scales such as ecoregions. Thus, ecoregion-level datasets potentially cover larger spatial extents and represent biologically relevant units for comparing beta diversity between regions.

We hypothesize that the perception of depauperate Afrotropical bat diversity is a consequence of limited sampling effort and biases in capture techniques. We compare multiple dimensions of bat diversity in Nigeria versus Malaysia, and Indonesia. To measure alpha diversity, we used published data from a multi-method (ground and canopy-level mist netting and harp traps) survey (reported in Tanshi et al., 2021) in the largest predicted hotspot of bat diversity in Africa (Herkt et al., 2016) with a focus on two Key Biodiversity Areas (KBAs) of the Lower Guinean Forest of West Africa (hereafter “Lower Guinean Forest”) (Bakarr et al., 2004) in southeastern Nigeria. To compare alpha diversity of Afrotropical bats with the Indo-Malayan tropics, we compared taxonomic, phylogenetic, and functional diversity from sites that were predicted by Findley to hold vastly different richness in Nigeria (40) to data from Malaysia (80) and Indonesia, Sumatra (80). A third site in Indonesia, from Sulawesi, falls within the Australasian realm, predicted by Findley to support 80 species. To compare beta diversity of bat assemblages between both regions, we compiled presence data from literature, the SEABCRU database (Fisher-Phelps et al., 2017), and online databases (GBIF.org, 2019; ACR, 2018) for ecoregions in the Lower Guinean Forest and an area of comparable spatial extent in the Malay Peninsula.

2 METHODS

Site-level survey data

2.1.1 Nigerian sites

We recently published data from the first harp trap survey conducted in Nigeria (Tanshi et al., 2021). Specific survey localities were lowland and montane areas of Afi Mountain Wildlife Sanctuary, (hereafter “Afi Mtn WS”) and Cross River National Park (hereafter “Cross River NP”). Afi Mtn WS (150–1300) m above sea level (a.s.l.) and Cross River NP (150–1800) m a.s.l. are Key Biodiversity Areas (KBA) in Southeastern Nigeria that hold over 50% of forest, and the last unlogged forest in Nigeria. Both areas are part of a larger network of contiguous or partially connected protected areas with other nearby forests in Nigeria and Cameroon that comprise the largest protected area of forest in West Africa (Oates et al., 2004). Both KBAs fall within the Cross-Sanaga-Bioko Coastal Forest ecoregion that is in turn part of the Lower Guinean Forest— one of two forest blocks in the Guinean Forest of West Africa (hereafter “Guinean Forest”). The Guinean Forest is one of 25 global biodiversity hotspots (Myers et al., 2000) and covers an original area of 620,314 km², spanning Guinea to the Sanaga River in Cameroon. The vegetation has a closed canopy formed by broadleaf evergreen trees, with emergent trees ≥60 m tall in the lowland. Bats were trapped using harp traps and mistnets set for two consecutive nights along existing trails, at 50 m intervals on 200 m transects (see Tanshi et al., 2021 for details). Field

trapping spanned the elevational gradient at both survey localities, but only data collected from lowland areas (150–400 m a.s.l.) were used in the current analysis.

Southeast Asian sites

We compiled published survey data for insectivorous bats trapped in harp traps in the forest understorey for one locality in Malaysia—Krau Wildlife Reserve, hereafter Krau WR (Kingston et al., 2003) and two in Indonesia: Bukit Barisan Selatan National Park (Suka Raja and Way Canguk forests) Forest, Sumatra (Huang et al., 2019a, 2019b) and Kakenauwe Forest Reserve on Buton Island, Southeast Sulawesi (T.K. and S.R., unpubl. data), hereafter Bukit Barisan NP and Kakenauwe FR, respectively. These sites comprise lowland unmodified dipterocarp forests within relatively large forest blocks, often with karst caves that offer abundant roosting opportunities. Seasonality varies from distinct dry and rainy seasons in Indonesia to two short (1–2 months) relatively dry periods at Krau WR (Huang et al., 2014; Kingston et al., 2003; Nurul-Ain et al., 2017; Patterson et al., 2017). We selected these sites due to availability of bat abundance data from comparable intensive surveys that deployed multiple harp traps per night to target bats in the forest understorey (Table 1). Bat surveys at each site in Southeast Asia involved the use of 5–10 harp traps placed at 30–50 m interval along suspected flight paths (Indonesia) or long-term grid system (Malaysia). Trapping was conducted for two consecutive nights at each trap point.

TABLE 1. Bat abundance of ensembles varied by trapping technique across field sites examined in the current study. Site abbreviations are same as Figure 1.

| | Harp trap | | | | Mist net | | | |
|--------------|-----------|-------|------|------------------|----------|--------|-----|-------------------|
| | Afi/CRNP | BBSNP | KFR | KWR | Afi/CRNP | BBSNP | KFR | KWR |
| Trap effort | 8693.5 | 702.8 | - | 837 ^a | 2809.7 | 2519.4 | - | 1573 ^a |
| Edge space | 33 | 4 | 28 | 97 | 2 | 2 | - | 21 |
| Narrow space | 1028 | 595 | 1397 | 1790 | 8 | 70 | - | 61 |
| Open space | - | - | - | - | 6 | - | - | 46 |

^a Trap effort is harp trap hours and mist net meter² hours for all but Krau Wildlife Reserve (harp trap nights and mist net hours).

Ecoregion data compilation

To compare the contribution of turnover among ecoregions to bat regional diversity in the Afrotropics and Indo-Malayan tropics, we compiled bat species incidence data for the Lower Guinean Forest and the Malay Peninsula. We compiled data from three sources: published literature, online sources (GBIF and ACR) and the SEABCRU database (Fisher-Phelps et al., 2017). For published sources, we restricted our search to Google Scholar and Biodiversity Heritage Library, using the terms “Chiroptera” OR “bat”, AND any of “Africa”, “Nigeria”, “Cameroon”, “Malaysia”, “Thailand”. To assign locality records to ecoregions, we used geographic coordinates provided by the databases, or where absent, obtained coordinates from Google Earth based on locality names and/or descriptions. All records without a verifiable geographic coordinate, or locality data were removed from further analysis. Incidence data was

compiled from literature, but online databases report individual capture/specimen records. As a result, we did not account for number of records recovered for each ecoregion in further analysis.

2.3.1 Lower Guinean Forest of West Africa

The Guinean Forest is divided into the Lower and Upper Forest blocks, which are separated by the Dahomey Gap - a ca. 200 km wide savanna corridor that extends to the coast in parts of Ghana, Togo, and Benin Republic (Figure S1). Of the original forests within these blocks, about 15% remain and the remnants are highly fragmented and under intense human pressure (Bakarr et al., 2004). The Lower Guinean Forest comprises six ecoregions (Burgess et al., 2004; Olson et al., 2001): (a) Nigerian Lowland Forests (NLF) stretch from southwestern Benin Republic, through southern Nigeria and east to the River Niger; (b) Niger Delta Swamp Forests (ND) cover the delta formed by the River Niger as it empties into the Atlantic Ocean; (c) Cross-Niger Transition Forests (CN) spans areas east of the River Niger and east to the River Cross; (d) Cross-Sanaga-Bioko Coastal Forest (CS) is delimited by the River Cross in southeastern Nigeria and Sanaga River in southwestern Cameroon, and includes lowland areas of Bioko in the Gulf of Guinea—a land bridge island that was connected to the mainland (Cameroon) during the last ice age; (e) Cameroon Highlands Forests (CH) covers highland areas of western Cameroon and Nigeria, mostly formed along the Cameroon Volcanic Line, excluding Mount Cameroon; and (f) Mount Cameroon and Bioko Montane Forests (MCB) that includes Mount Cameroon and montane areas of Bioko. Due to limited data and non-contiguity, we excluded bat records from small portions of some ecoregions: (a) Bioko coastal forests in the Cross-Sanaga-Bioko Coastal Forest ecoregion; (b) Bioko montane forest in the Mount Cameroon-Bioko Montane Forest; and (c) eastern Benin Republic in the Nigeria Lowland Forest ecoregion.

2.3.2 Malay Peninsula

Here, we define the Malay Peninsula as Malaysia through to southern Thailand—south of the Isthmus of Kra, an important biogeographic break on the Malay Peninsula (Wikramanayake et al., 2002). Hereafter, we refer to this area as the Malay Peninsula although it includes a small area of Thailand. The Malay Peninsula is an appropriate comparison for the Lower Guinean Forest because it is of similar size (ca. 190,000 km²) and latitude, has been intensively surveyed for bats, and comprises several ecoregions. These ecoregions are as follows: (a) Peninsular Malaysian rain forest (MRF); (b) Peninsular Malaysian Montane rain forest (MmRF); (c) Peninsular Malaysian peat swamp forests (PSF); and (d) Tenasserim-South Thailand semi-evergreen rain forest (TRF) (Wikramanayake et al., 2002).

Data analysis

2.4.1 Alpha taxonomic diversity

All statistical data analysis were conducted in R (R Core Team, 2016). To compare species richness of bats captured in harp traps in the lowland (≤ 400 m a.s.l.) forest understorey, that is, narrow-space ensemble, we computed sample-size-based rarefaction and extrapolation curves

from species abundance data, using the R package iNEXT (Hsieh et al., 2016). As the Nigerian localities were <30 km apart, we pooled lowland captures from both Afi Mtn WS and Cross River NP. We extrapolated the species richness estimates of Afi Mtn WS and Cross River NP (pooled), Bukit Barisan NP, and Kakenauwe FR to 1570 individuals (total captures at Krau WR) to allow comparisons between low abundance sites and the highest one. We computed 95% Confidence Intervals (CI) for all rarefaction/extrapolation curves to allow for pairwise test of significant difference between sites.

2.4.2 Alpha phylogenetic diversity

We compared phylogenetic diversity of narrow-space bat ensembles between captures from Afi Mtn WS and Cross River NP, with sites in SEA—Krau WR, Bukit Barisan NP, and Kakenauwe FR. We calculated Faith's PD (Faith, 1992) using the *pd* function in the picante package (Kembel, 2010). To represent the phylogenetic relationships between species known from each of the Paleotropical sites, we pruned a species-level phylogeny of bats (Upham et al., 2019), retaining those found at each site. Faith's PD is a sum of branch lengths of all species in a community.

2.4.3 Alpha functional diversity

We examined functional diversity of narrow-space bat ensembles between captures from Afi Mtn WS and Cross River NP with sites in Southeast Asia (SEA)—Krau WR, Bukit Barisan NP, and Kakenauwe FR. We calculated functional diversity (functional richness) using the function *dbfd* in the FD package (Laliberté et al., 2010). We used forearm length (mm) and body mass (g) collected during field surveys at each site and from the literature. Traits represent mean values for each species. We used only these two traits because of limited data for other functional traits such as wing morphology and biteforce. Moreso, body mass is a predictor of wing morphology and biteforce (Senawi et al., 2015).

2.4.4 Standardized effect sizes (SES) of alpha phylogenetic and functional diversity

Mean Nearest taxon Distance (MNTD) and Mean Pairwise Distance (MPD) are metrics used to examine relatedness and similarity between species in an assemblage. MNTD and MPD use a distance-based approach to calculate the phylogenetic relationship and functional similarity in a community (Kembel, 2010). MNTD and MPD values are not useful for comparing ensembles drawn from different species pools. Therefore, we did not quantify observed values of both metrics. Furthermore, MNTD and MPD are highly impacted by species richness, but rectified by standardized effect sizes that compare observed to null communities, allowing site comparisons. We calculated the SES for MNTD and MPD across each community phylogeny and functional space using the *ses_mntd* and *ses_mpd* functions in the Picante package (Kembel et al., 2010). SES values are calculated as the difference between observed and null values (*mntd* and *mpd*), divided by the standard deviation of null values. Null models and a distribution of ses values were based on 1000 randomizations.

2.4.5 Beta diversity

Approximately 10,000 and 20,000 records were recovered across data sources for Lower Guinean Forest and Malay Peninsula, respectively. Post cleanup, only 1128 unique locality records (literature: 270; ACR: 222; GBIF: 597; MANIS: 9; Vertnet: 30) for the Lower Guinean Forest and 2082 (SEABCRU: 2032; literature: 50) records for Malay Peninsula were used in further analysis. We calculated turnover, nestedness, and overall beta diversity between ecoregions in the Lower Guinean Forest and the Malay Peninsula. We used the *betasample* function in the *betapart* package (Baselga & Orme, 2012) to compute turnover, nestedness, and total beta diversity for multiple ecoregions. *Betasample* creates a distribution of multi-site beta diversity values from a randomized sample ($n-1$, where n = ecoregion) and additively partitions total dissimilarity (sensu Jaccard and Sorensen dissimilarity indices) into independent components—turnover and nestedness. For any number of sites, *betasample* iteratively takes incidence and computes three components of beta diversity as dissimilarity in species composition due to: (a) turnover (Simpson dissimilarity index); (b) nestedness; and (c) total beta diversity (Sorensen dissimilarity index). To ensure unbiased comparison between both regions, we calculated beta diversity using only three ecoregions, randomly drawn from four (Malay Peninsula) and six (Lower Guinean Forest) ecoregions. We repeated the analysis at the ensemble level in order to examine the contribution of each bat foraging ensemble recognized in Paleotropical forests: (a) plant-visiting—frugivores and nectarivores foraging above and below canopy; (b) open-space insectivores—foraging in open/uncluttered space above the canopy or over large clearings; (c) edge and gap space insectivores—foraging in background clutter/edge space near to vegetation; and (d) narrow-space insectivores—foraging in narrow or highly cluttered space within stands of vegetation (Kingston, 2013; Monadjem et al., 2010; Schnitzler & Kalko, 2001).

We calculated ecoregion dissimilarity in bat species composition using the *betadiver* function in the *Vegan* package (Oksanen et al., 2019). We computed the Bray–Curtis dissimilarity index and plotted a dendrogram using the *hclust* function in *Vegan* and overlaid on a map of each region, to visualize ecoregion clustering.

3 RESULTS

Alpha diversity

3.1.1 Taxonomic diversity

Species richness in southeastern Nigeria was not significantly different from the two sites in Indonesia (Kakenauwe FR and Bukit Barisan NP). However, species richness at Krau WR, Malaysia was significantly greater (Figure 1, Table 2) than sites in Indonesia and Nigeria. The 95% confidence interval of the rarefaction curve for narrow-space bats at Krau WR was clearly separated from rarefied observed and extrapolated curves of the three other sites, showing significant difference.

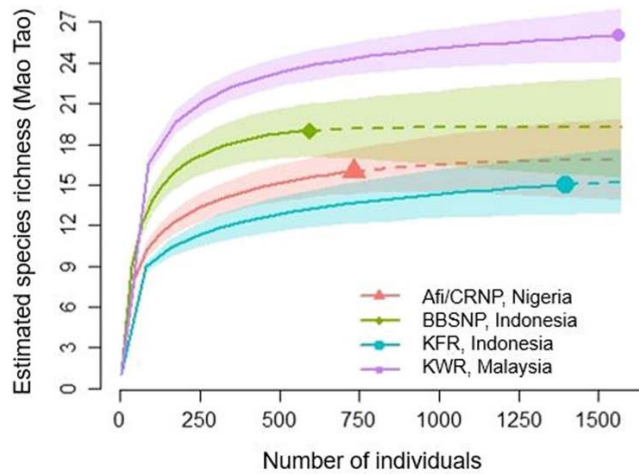


FIGURE 1. Sample-size-based rarefaction/extrapolation curves of lowland narrow-space bats of the forest understory captured in harp traps shows estimated species richness (alpha diversity) is significantly higher at KWR than three other Paleotropical sites, but there is no significant difference between our study area (pooled for Afi Mtn WS and Cross River NP) in Nigeria and two sites in Indonesia. Solid lines = rarefaction, broken lines = extrapolation. Line markers (circle, triangle, and diamond) represent total number of individuals captured. Extrapolation endpoint set to 1570—the highest observed number of individuals at KWR. Shaded areas represent 95% Confidence Intervals based on 1000 bootstrap replicates. KWR = Krau WR; BBSNP = Bukit Barisan Selatan National Park, Indonesia; KFR = Kakenauwe Forest Reserve, Indonesia; Afi/CRNP = Afi Mountain Wildlife Sanctuary and Cross River National Park.

TABLE 2. Taxonomic diversity patterns of narrow-space bat assemblages in the Afrotropical site in Nigeria fall within a continuum for sites in Southeast Asia, that is, Malaysia and Indonesia.

| Diversity metrics | Afi/CRNP | Krau WR | BBSNP | Kakenauwe |
|-------------------|----------|---------|-------|-----------|
| Species richness | 17 | 27 | 18 | 14 |
| Shannon Div. | 1.40 | 2.34 | 1.28 | 1.32 |

3.1.2 Phylogenetic diversity (PD)

Bootstrapped values of phylogenetic diversity showed that Krau WR is different (higher) than all three sites from Nigeria and Indonesia (Figure 2a), which all had similar values of PD.

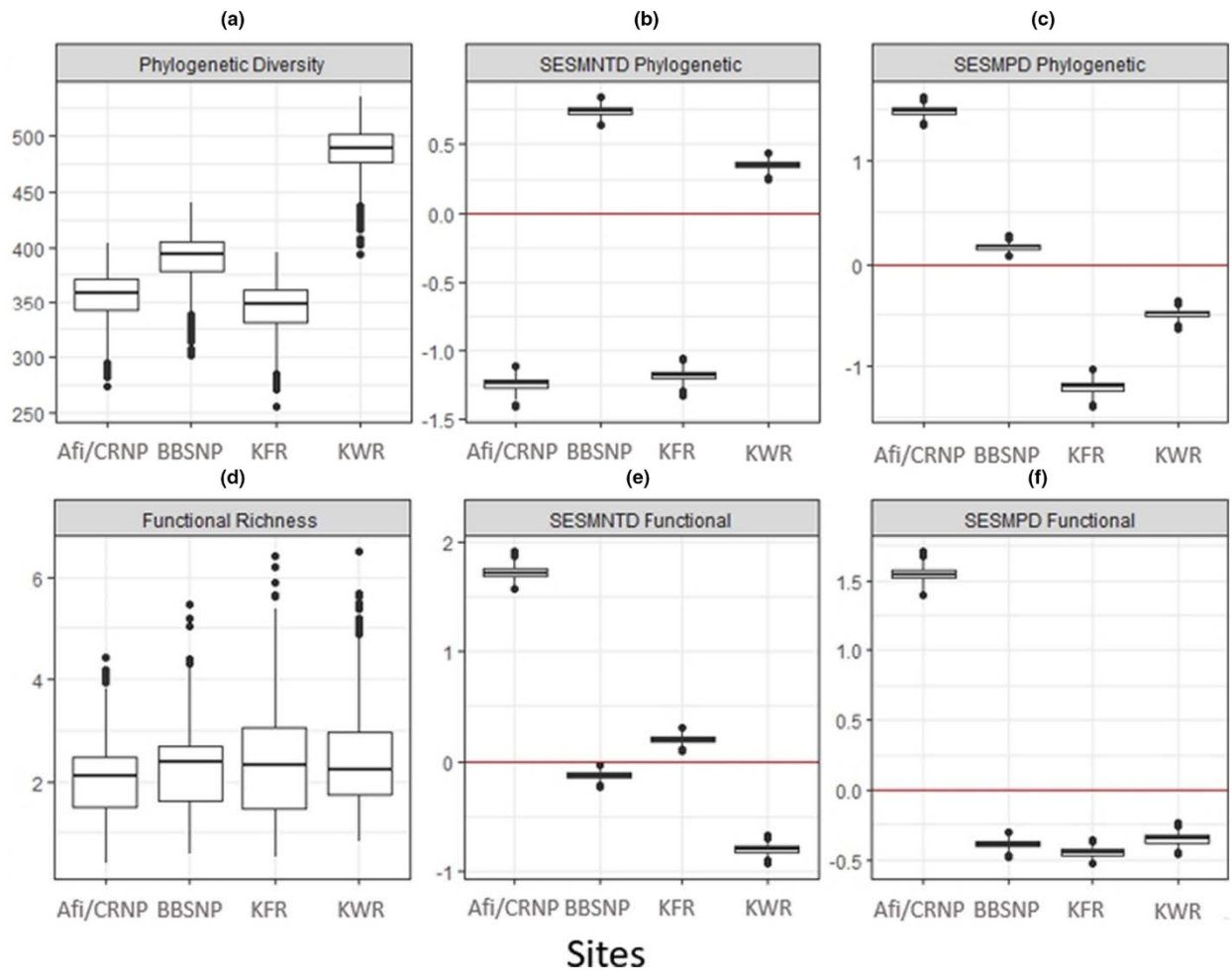


FIGURE 2. Phylogenetic diversity (a) but not functional (richness) diversity (d) of bat assemblage is higher at Krau Wildlife Reserve (KWR), Malaysia than sites in Indonesia and Nigeria. Relative to null communities, phylogenetic and functional diversity of bat assemblages. Boxplot of bootstrapped values of (a) phylogenetic diversity and functional richness (d) and associated SES-MNTD (standardized effect size of mean nearest taxon distance) (b, e) and SES-MPD (standardized effect size of mean pairwise distance) (c, f). Quartiles represent 95% confidence intervals based on 1000 bootstrap replicates. Red line represents null in plots b, c, e, f. Site abbreviations are the same as Figure 1. Note different scales.

3.1.3 Functional diversity

Bootstrapped values of functional richness (FRic) were not significantly different between sites across all four sites examined in this study (Figure 2c). Near complete overlap in the distribution and 95% confidence intervals of functional diversity values showed that functional richness was similar across sites.

3.1.4 Standardized effect sizes (SES)

Relative to null communities (red horizontal line) (Figure 2b,c,e,f), tree-tip (MNTD) phylogenetic distances of observed communities were underdispersed (species are more related) at

Afi/Cross River NP, and Kakenauwe FR, but overdispersed (less related) at Bukit Barisan NP, Indonesia and random at Krau WR, Malaysia. Tree-wide (MPD) phylogenetic distance of bat assemblages was overdispersed at Afi/Cross River NP, but underdispersed at Kakenauwe FR and random at Bukit Barisan NP, Indonesia and Krau WR, Malaysia. Functional traits of similar bat species at Afi/Cross River NP were overdispersed (Figure 2e) relative to null communities. Conversely, Krau WR was underdispersed relative to null communities, but Bukit Barisan NP and Kakenauwe FR are random relative to chance (Figure 2e). Functional traits of all bat species at Afi/Cross River NP are overdispersed (Figure 2f) relative to null expectations, suggesting less trait similarity than expected by chance. In contrast, functional traits of all species at Bukit Barisan NP, Kakenauwe FR, Indonesia, and Krau WR, Malaysia, are underdispersed relative to null communities (Figure 2f), suggesting a higher trait similarity than expected by chance.

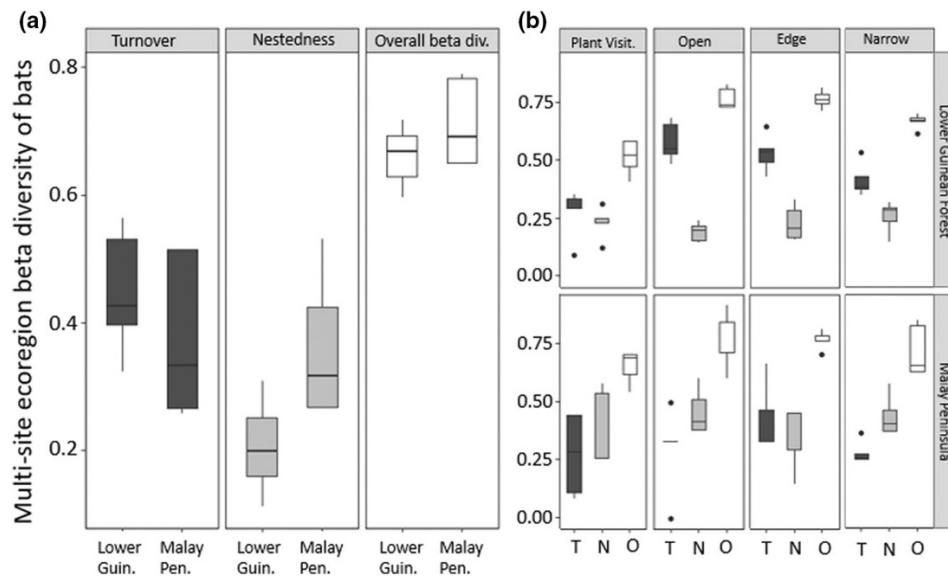


FIGURE 3. Beta diversity of ecoregion bat assemblages partitioned into turnover (T) and nestedness (N) components and overall (O) is comparable between both sub-regions (although Malaya Peninsula is significantly more nested) for (a) all species but varies across (b) foraging ensembles. Multi-site dissimilarity computed using the *betasample* function for n-1 ecoregions.

Beta diversity

Multi-ecoregion turnover was comparable between the Lower Guinean Forest and the Malay Peninsula. Turnover was significantly higher than nestedness in the Lower Guinean Forest, whereas turnover was similar to nestedness in the Malay Peninsula (Figure 3a). Turnover was significantly higher in the Lower Guinean Forest than Malay Peninsula ($t_{\text{turnover}} = 24.45$, p -value $<.001$). Conversely, nestedness and overall beta diversity were significantly higher in the Malay Peninsula than the Lower Guinean Forest ($t_{\text{nestedness}} = 42.78$, p -value $<.001$; $t_{\text{overall betadiv}} = 28.61$, p -value $<.001$). Compositional turnover between ecoregions in the Lower Guinean Forest was significantly higher than nestedness across all ensembles but plant-visiting bats (Figure 3b), suggesting that insectivores contribute equally to turnover. In the Malay Peninsula, turnover and nestedness were similar for the plant-visiting and edge insectivore ensembles, but

nestedness was significantly greater than turnover for the narrow- and open-space. Regardless of beta diversity patterns between sub-regions, total species richness across the Malay Peninsula (117) is greater than that of the Lower Guinean Forest (93) (Table S1).

Ecoregion assemblage dissimilarity

3.3.1 Lower Guinean Forest

In the Lower Guinean Forest, the Cross-Sanaga-Bioko Forest ecoregion was the most species-rich with 67 species (Table S1). Dissimilarity between ecoregions appears to be in part spatially driven, as closest neighbors share more species. The Niger Delta Swamp Forest appears distinct from other ecoregions. The two most similar ecoregions are Cross-Sanaga-Bioko and Mount Cameroon Forest (Figure 4a). The 36 species reported in Tanshi et al. (2021) represent 30% of the species known from the Lower Guinean Forest (Table S1).

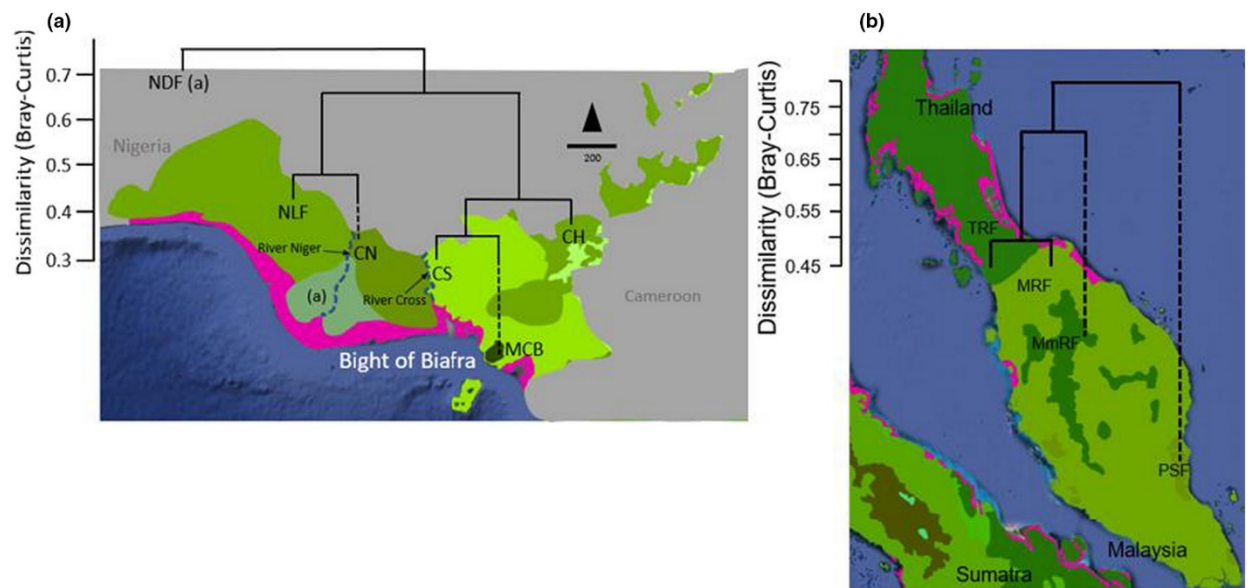


FIGURE 4. Dissimilarity (Bray-Curtis) between ecoregions of the Lower Guinean Forest (a), and Malay Peninsula (b). Lower Guinean Forest assemblages show a split in bat assemblages at Cross River. The Niger Delta Swamp Forest is the most dissimilar ecoregion from others, which split into two clusters that are separated by the River Cross. In the Malay Peninsula, the two largest ecoregions are the least dissimilar i.e., MRF and TRF. Ecoregions codes represent Lower Guinean Forest: Nigeria Lowland Forests (NLF), Niger Delta Swamp Forests (ND), Cross-Niger Transition Forests (CN), Cross-Sanaga-Bioko Forests (CS), Cameroon Highlands Forests (CH), Mount Cameroon-Bioko Montane Forests (MCB), and Malay Peninsula: Peninsular Malaysian rain forest (MRF); Peninsular Malaysian Montane rain forest (MmRF); Peninsular Malaysian peat swamp forests (PSF); and Tenasserim-South Thailand semi-evergreen rain forest (TRF). Rivers (blue broken lines) were hand traced to provide a general position. Continuous lines correspond to dissimilarity values, black broken lines are drawn to indicate ecoregion. Map source: <https://ecoregions2017.appspot.com/> (Dinerstein et al., 2017).

3.3.2 Malay Peninsula

The Peninsular Malaysian Rain Forest ecoregion is the largest (Figure 4b) in the subregion that surrounds the two smallest ecoregions: Peninsular Malaysian Montane Rain Forest and Peninsular Malaysian Peat Swamp Forest. Despite acting as a matrix to these two small ecoregions, the Peninsular Malaysian Rain Forest ecoregion is least dissimilar from the Tenasserim-South Thailand semi-evergreen Rain Forest, suggesting that regional bat occurrence depends on contiguity despite distinctiveness of ecoregion biotype.

4 DISCUSSION

Multiple dimensions of alpha bat diversity

We hypothesized that the perception of depauperate Afrotropical bat fauna is a consequence of limited sampling effort and biases in capture techniques. Our approach was to compare multiple dimensions of bat diversity from sites with comparable trapping effort in Nigeria versus Malaysia, and Indonesia. We compared alpha diversity of narrow-space insectivorous bats that forage in the forest understory at four sites. Alpha taxonomic diversity of narrow-space bats was comparable between Nigeria and two sites in Indonesia, but was lower than at Krau WR, Malaysia. Functional diversity was similar between sites in both regions. Conversely, phylogenetic diversity differed between the most species-rich site—Krau WR and the two least diverse sites. Note that lower (relative to Krau WR) alpha taxonomic richness from the two Indo-Malayan sites may be a combination of island (as islands are typically less species-rich than mainland sites) and sampling effects, as Krau WR is the best sampled of all three sites.

Despite comparable alpha diversity of narrow-space bats between sites in Nigeria and Southeast Asian sites, we found differences in family-level richness between sub-regions. For example, four species of *Nycteris* are known from the Nigerian site, versus two allopatric species known across Southeast Asia. Conversely, Indonesian, and Malaysian sites reported here support more species of Kerivoulinae (4–9) than the Nigerian site (4). In addition, *Phonicus* spp. (subfamily Kerivoulinae) and the subfamily Murininae that are endemic to Asia and Australasia contributed to the high alpha diversity of Krau WR in Malaysia. Similarly, fewer species of Rhinolophidae (4) and Hipposideridae (6) are known from the Nigerian site relative to the Indo-Malayan sites where 5–8 rhinolophids and 6–11 hipposiderids have been reported. Nonetheless, recent work from East Africa demonstrates high levels of cryptic diversity within African rhinolophids and hipposiderids (Demos, Webala, Goodman, et al., 2019; Patterson et al., 2020) that may rival the Indo-Malayan diversity within both families.

Regardless of high levels of phylogenetic diversity at Krau WR, relationships between bat species were random relative to null communities. Despite comparable levels of functional richness among sites in this study, traits across ensemble and between the most similar species at Afi/CRNP were overdispersed unlike other sites that were underdispersed or random. The results suggest that phylogenetic and functional diversity at the Nigerian site occurs along a continuum of sites in Southeast Asia.

Ecoregion-level beta taxonomic bat diversity and biogeography

Although overall ecoregion-level beta diversity was comparable across regions, turnover was greater in the Lower Guinean Forest and nestedness in the Malay Peninsula indicating distinctiveness and similarity of bat assemblages, respectively, and likely reflecting regional differences in heterogeneity and spatial configuration of ecoregions. Similar turnover across bat ensembles (edge/gap, open-space, and narrow-space) in the Lower Guinean Forest suggests heterogeneity of ecoregions created by multiple biogeographical systems, that is, delta (Niger Delta), major rivers (River Niger, Cross and Sanaga rivers) and mountain chain (Cameroon Volcanic Mountain). Conversely, nestedness, highest in the narrow-space ensemble of the Malay Peninsula indicates homogeneity of forests between ecoregions that are dipterocarp dominated with limited influence on bat assemblages of major rivers and mountains. Moreover, the two smallest ecoregions (Peninsular Malaysian montane rain forest, and Peninsular Malaysian peat swamp) are embedded in the large Peninsular Malaysian rain forest.

High bat assemblage turnover due to heterogeneity in the Afrotropics has typically been associated with drier habitat types, that is, forest and savanna mosaic landscapes in West Africa (Fahr & Kalko, 2011), East Africa (Herkt et al., 2016), and Southern Africa (Schoeman et al., 2013). Our results suggest that heterogeneity in wet forest landscapes like the Lower Guinean drive bat assemblage turnover and regional diversity.

Afrotropical narrow-space bat ensembles and capture techniques

Bat capture techniques are designed to target different bat foraging ensembles and harp traps are more effective than mist nets for trapping narrow-space bats (Francis, 1989; Kingston, 2016; Kingston et al., 2003). Previous conclusions that Afrotropical bats are depauperate were based on mist nets surveys that reported fewer narrow-space bats than our study. For example, Tanshi et al. (2021) reported 18 narrow-space species (primarily members of Rhinolophidae, Hipposideridae, Nycteridae, Kerivoulinae), of which 14 species were exclusively captured in harp traps (Figure 1). In comparison, older studies of forest bat assemblages summarized by Findley (1993) reported only nine at Haute Inwindo, Gabon (Brosset, 1966) and six at Rio Muni, Equatorial Guinea (Jones, 1971). Similarly, more recent work based exclusively or predominantly on mist nets in the Guinean Forest of West Africa report fewer narrow-space bats than the current Nigerian survey: 0 at Okomu National Park (Tanshi et al., 2019); 14 at Tai National Park, Ivory Coast (Fahr & Kalko, 2011); two at Draw River, four at Boi-Tano and six at Krokosua Hills, Ghana (Decher & Fahr, 2007).

Despite the high diversity of forest understorey bat species recorded at Afi/CRNP, limited deployment of canopy and ground-level nets likely resulted in under sampling of the full diversity of edge and open space bats present (Tanshi et al., 2021). Of the 72 bat species predicted for the study area, over 70% are expected to belong to the edge and open space ensemble, yet the Nigerian survey reported only 42%.

For Afrotropical bats, inventories miss hard-to-catch bats, especially narrow-space bats that avoid mist nets, and open space bats that are best sampled with acoustic detectors (Kingston, 2016). Underrepresentation of these blindspot diversity in local inventories has raised questions about the assertions that Afrotropical bats are depauperate (Decher & Fahr, 2007; Fahr & Kalko, 2011). To resolve this question, contemporary surveys must deploy appropriate sampling techniques especially harp trap, ground and canopy mist nets, acoustic surveys/libraries (Görföl et al., 2022) and comparable protocols that are rigorous, standardized, and quantify effort.

No reported surveys have deployed intensive harp trapping efforts across the Afrotropics. Furthermore, as the Southeast Asian sites with comparable sampling are hyper-diverse, we targeted a potentially hyper-diverse site in Nigeria to maximize capture effort. Therefore, the extent to which our conclusions hold true across Afrotropical sites remains to be seen.

Conservation implications and conclusions

High diversity of narrow-space bats at the site level, and high turnover at the regional level confirm Herkt's prediction that southeastern Nigerian forests and the Lower Guinean Forests are hyper-diverse for bats (Herkt et al., 2016), and thus, should be prioritized for global bat protection. Our study highlights the significance of ecoregion contributions to regional diversity. Except for the Cross-Sanaga-Bioko ecoregion (Afi Mtn WS and Cross River NP) southeastern Nigeria remains a conservation void, with no operational federally protected areas in the Cross-Niger Transition Forests. To ensure representation of these diverse forests and sustain integrity of the region's biodiversity, secure protected areas need to be established in each ecoregion and managed as a network. Similarly, the region should be prioritized for investigation on the role of biogeography on speciation patterns and assemblage structure of bats in Africa. This study and the discovery of the rare range-restricted Endangered *Hipposideros curtus* (Tanshi et al., 2021) highlights the value of conserving Nigerian forests through long-term Government-NGO (Pandrillus Foundation, Small Mammal Conservation Organization, and Wildlife Conservation Society) partnerships.

With the highest recorded bat diversity in the Paleotropics, Krau WR is critical for the conservation of many globally important species. Indeed, without strict protection for this forest, knowledge of the true diversity of Malaysia would be difficult, if not impossible to decipher. Therefore, ongoing protection efforts by managers is commendable and deserving of more support against all encroachment and illegal exploitation or development plans for the park.

In conclusion, our results indicate that Afrotropical bat assemblages are not depauperate; rather, that the species-rich, narrow-space ensemble has been under-sampled. With modern sampling methodologies, we show that there is comparable alpha diversity of narrow-space bats of the forest understorey among sites in Nigeria and Indonesia, but not in Malaysia. More diverse sampling methodologies and refined systematic analyses of African bats might substantially increase knowledge of local-scale faunal diversity. Therefore, we recommend

detailed multi-faceted bat surveys, that include extensive use of harp traps, of other recognized and putative hotspots across Africa, to provide full representation of the distribution of Afrotropical bat diversity.

AUTHOR CONTRIBUTION

IT and TK designed the project; IT and BO conducted field surveys in Nigeria; TK and SR conducted field surveys in Sulawesi, Indonesia; IT and AM identified bat species; MFP and IT compiled regional bat incidence data; IT wrote manuscript draft; IT, TK, BO, AM, SR, and MFP revised and edited manuscript.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

ETHICAL GUIDELINES

Permission for this survey was granted by the Institutional Animal Care and Use Committee (IACUC, approval number: 15077–12) of Texas Tech University, Lubbock Texas.

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