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RESEARCH ARTICLE

Biotic interactions are the dominant drivers of phylogenetic and functional structure in bird communities along a tropical elevational gradient

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ABSTRACT

Understanding how biotic and abiotic interactions influence community assembly and composition is a fundamental goal in community ecology. Addressing this issue is particularly tractable along elevational gradients in tropical mountains that feature substantial abiotic gradients and rates of species turnover. We examined elevational patterns of avian community structure on 2 mountains in Malaysian Borneo to assess changes in the relative strength of biotic interactions and abiotic constraints. In particular, we used metrics based on (1) phylogenetic relatedness and (2) functional traits associated with both resource acquisition and tolerance of abiotic challenges to identify patterns and causes of elevational differences in community structure. High elevation communities were composed of more phylogenetically and functionally similar species than would be expected by chance. Resource acquisition traits, in particular, were clustered at high elevations, suggesting low resource and habitat diversity were important drivers of those communities. Traits typically associated with tolerance of cold temperatures and low atmospheric pressure showed no elevational patterns. All traits were neutral or overdispersed at low elevations suggesting an absence of strong abiotic filters or an increased influence of interspecific competition. However, relative bill size, which is important for thermoregulation, was larger in low elevation communities, suggesting abiotic factors were also influential there. Regardless of metric, clustered and neutral communities were more frequent than overdispersed communities overall, implying that interspecific competition among close relatives may not be a pervasive driver of elevational distribution and community structure of tropical birds. Overall, our analyses reveal that a diverse set of predominantly biotic factors underlie elevational variation in community structure on tropical mountains.

Keywords: abiotic, biodiversity, competition, environmental filtering, mountains, niche conservatism

Las interacciones bióticas son los causantes principales de la estructura filogenética y funcional en las comunidades de aves a lo largo de un gradiente altitudinal tropical

RESUMEN

Entender cómo las interacciones bióticas y abióticas influencian los ensambles y la composición de las comunidades es un objetivo fundamental de la ecología de comunidades. Este problema es particularmente abordable a lo largo de gradientes ambientales en las montañas tropicales que presentan marcados gradientes abióticos y tasas de recambio de especies. Examinamos patrones altitudinales de la estructura de las comunidades de aves en dos montañas de Borneo malayo para evaluar cambios en las importancias relativas de las interacciones bióticas y las restricciones abióticas. En particular, usamos métricas basadas en (1) la relación filogenética y (2) los rasgos funcionales asociados a la adquisición de recursos y a la tolerancia a las limitantes abióticos para identificar los patrones y las causas de las diferencias altitudinales en la estructura de las comunidades. Las comunidades de los sitios de elevaciones altas estuvieron compuestas por especies más similares filogenética y funcionalmente que lo esperado por azar. En particular, los rasgos de adquisición de recursos estuvieron agrupados en las elevaciones altas, sugiriendo que la baja diversidad de recursos y de hábitats fueron causantes importantes de estas comunidades. Los rasgos típicamente asociados a la tolerancia a las bajas temperaturas y a la baja presión atmosférica no mostraron un patrón altitudinal. Todos los rasgos fueron neutros o estuvieron sobre-dispersos en las elevaciones bajas, sugiriendo una ausencia de filtros abióticos fuertes o un aumento en la influencia de la competencia inter-específica. Sin embargo, el tamaño relativo del pico, que es importante para la termorregulación, fue más grande en las comunidades de elevaciones bajas, sugiriendo que los factores abióticos también tuvieron influencia allí. Sin importar la métrica, las comunidades agrupadas o neutrales fueron más frecuentes que las comunidades sobre-dispersadas en general, implicando que la competencia inter-específica entre parientes cercanos puede no ser un causante generalizado de la distribución altitudinal y la estructura de las comunidades de aves

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tropicales. De modo general, nuestros análisis revelan que un conjunto diverso de factores predominantemente bióticos subyace la variación altitudinal en la estructura de las comunidades en las montañas tropicales.

Palabras clave: abiótico, biodiversidad, competencia, conservadurismo de nicho, filtros ambientales, montañas

INTRODUCTION

Understanding the ecological processes that influence community assembly and composition across geographic gradients is a fundamental goal in ecology (MacArthur and Levins 1967, Diamond 1975, Hubbell 1979). Community structure, or the relative similarity or dissimilarity of species in a community relative to that expected by chance, is thought to reflect the ecological and historical processes shaping community composition (Ricklefs 1987). Of ecological factors, competition among species is the most commonly invoked process underlying community structure (Schoener 1983) and is thought to explain adjacent, but generally non-overlapping, elevational ranges of tropical congeners (Terborgh and Weske 1975, Remsen and Graves 1995, Jankowski et al. 2010, Freeman 2015). Specifically, species that are similar in resource use are thought to compete most intensely and are less likely to coexist (Connell 1961, MacArthur and Levins 1967, Diamond 1975, Gilpin and Diamond 1982). Abiotic conditions are also thought to affect the composition of species assemblages by limiting species or lineages present in a community to those with traits necessary to colonize and persist in a given set of abiotic conditions (Grinnell 1917, Connell 1961, Webb 2000, Graham et al. 2009). Physiology can limit elevational ranges of congeneric species when they differ in tolerance to abiotic factors such as temperature, moisture, and atmospheric conditions that vary with elevation (Gifford and Kozak 2011, Graham et al. 2012).

Theory predicts that the relative importance of biotic and abiotic factors will vary across environmental gradients, but evidence is limited. For example, interspecific competition is thought to be most important in abiotically benign environments, whereas abiotic factors become increasingly important in the harsher or more variable climates of temperate regions or high elevations in the tropics (Dobzhansky 1950, MacArthur 1972, Schemske et al. 2009, Sexton et al. 2009). The shift from biotic to abiotic drivers of community structure along latitudinal gradients has limited support (Schemske et al. 2009), but tests across elevational gradients have produced inconsistent results (Bryant et al. 2008, Graham et al. 2009, Gifford and Kozak 2011). Cold temperatures and low partial-pressure of oxygen make high elevation environments physiologically challenging to endotherms. Such harsh abiotic conditions may restrict the availability of such habitats to species or clades with traits necessary to cope with their challenges. Conversely, interspecific competition and other biotic interactions are thought to be a dominant force at low elevations due to the general lack of strong abiotic filters (Janzen 1967, MacArthur 1972). Thus, theory predicts that low elevation communities should be structured largely by competition and high elevation largely by abiotic filtering. This view is supported by studies of hummingbirds and ants (Graham et al. 2009, 2012, Machac et al. 2011), but the opposite pattern has been observed in plants (Bryant et al. 2008), and abiotic conditions appear to influence microbial communities at all elevations (Bryant et al. 2008). It is also possible that different members of groups of organisms may respond differently to ecological mechanisms, and in some cases the methods for determining the factors underlying community structure may simply be inappropriate.

The synthesis of community ecology and phylogenetics has provided a quantitative framework to infer the relative importance of biotic and abiotic forces in determining community composition (Webb 2000, Webb et al. 2002). The phylogenetic structure of communities is thought to reflect the relative importance of biotic (competition, facilitation) vs. abiotic filtering in determining community composition. Such interpretation is based on the assumption that traits important for resource exploitation and tolerance of abiotic conditions are phylogenetically conserved (Webb 2000, Webb et al. 2002, Wiens and Graham 2005, Lovette and Hochachka 2006, Hardy and Senterre 2007, Kraft et al. 2007, but see Gerhold et al. 2015). Specifically, closely related species should compete more strongly due to their similarity in traits related to resource use (MacArthur and Levins 1967, Wiens and Graham 2005). Accordingly, when interspecific competition dominates the determination of community composition, communities should be composed of species that are more distantly related than expected by chance (phylogenetic overdispersion). In contrast, when harsh abiotic conditions select for a narrow range of adaptive traits, communities should consist of species that are more closely related than expected by chance (phylogenetic clustering) (Losos 1996, Webb 2000, Webb et al. 2002, Graham et al. 2009). However, clustering may not always indicate abiotic filtering. Clustering may also result when there is phylogenetic signal in competitive ability (Mayfield and Levine 2010), or when the biotic environment is simplified, such that it restricts overall niche space (Hanz et al. 2018). In such cases, biotic interactions may cause clustered communities.

An alternative way of detecting the influence of abiotic filtering and/or biotic interactions on community structure is by the distribution of functional traits among co-occurring species. Phylogenetic methods use relatedness as a proxy for niche similarity, but we can also directly measure traits that are likely to be important to resource or habitat use and compare the distribution of these traits within and across communities (Ricklefs and Travis 1980, Weiher et al. 1998). In communities in which interspecific competition is a dominant assembly mechanism, functional traits should be distributed such that maximal trait-distance exists between species (overdispersion) (MacArthur and Levins 1967, Hespenheide 1973), reflecting minimal overlap in ecological niches and alleviating competition between similar species. By contrast, if environmental filtering by harsh abiotic conditions is dominant, traits that confer an advantage in such conditions should be similar among species, or clustered relative to a null model of community assembly. If low resource or habitat complexity is driving clustered community structure, traits related to resource acquisition or habitat use/locomotion should also be clustered in those communities.

Applying phylogenetic and trait-based methods simultaneously to the same dataset is advantageous because each method is based on assumptions that may be violated in some cases. First, if traits that are important to either competition or habitat filtering are not phylogenetically conserved, phylogenetic structure alone will not explain the community assembly process. In such cases, an absence of phylogenetic community structure might occur even if abiotic filtering or competition are strong drivers of community structure. However, as long as measured traits are important for competition or abiotic tolerance, trait-based methods should detect either overdispersion or clustering of communities, even if traits do not show phylogenetic signal (Cavender-Bares et al. 2004). Second, trait-based methods depend on the assumption that measured traits are important for community assembly processes. However, many traits are difficult to measure, and integrating numerous complex traits into a framework suitable for analysis is not always straightforward (but see Villéger et al. 2008), so this assumption may be frequently violated. In such cases, as long as the relevant (unmeasured) traits display phylogenetic signal, phylogeny-based methods can reveal patterns in community structure when trait-based methods do not (Cadotte et al. 2008, 2009). Despite the clear benefits of combining phylogenetic and trait-based methods to investigate community assembly mechanisms, relatively few studies have done so (Cavender-Bares et al. 2004, Kraft and Ackerly 2010).

Here, we examine patterns of phylogenetic and functional community structure of bird communities across 2 elevational gradients on adjacent tropical mountains in Borneo to assess how competition and abiotic filtering may influence community assembly across elevations. If competition determines community structure at low elevations and abiotic conditions are dominant at high elevations, we expect both phylogenetic and trait-based metrics to indicate overdispersed communities at low elevations and more clustered communities with increasing elevation. We also expect overdispersion in specific traits related to resource competition at low elevations and clustering in traits related to physiological tolerance at high elevations (Figure 1). Alternatively, if high elevation communities are composed of similar species due to restricted niche space, we expect clustering in traits associated with locomotion or resource acquisition (Figure 1). Finally, forces driving assembly may not vary appreciably across elevations in the tropics. In such cases, the potential causes of community structure should show no change across elevations.

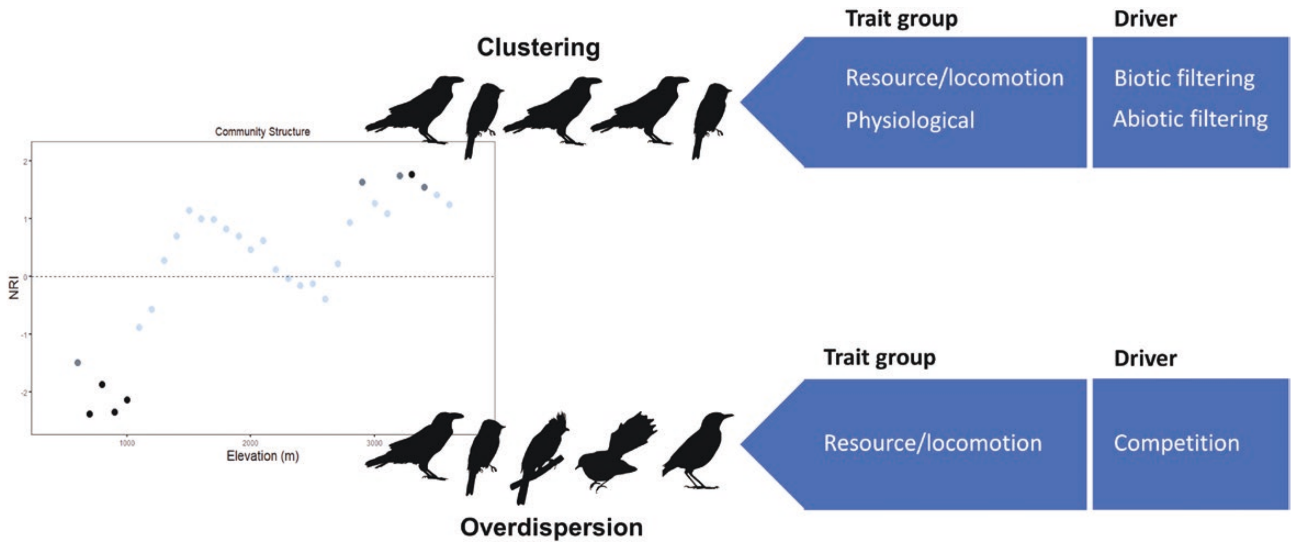

FIGURE 1. Conceptual figure showing expected community structure and trait structure patterns when communities are structured primarily by interspecific competition, abiotic filtering and biotic filtering. Silhouettes by Anthony Caravaggi and others (https://creativecommons.org/licenses/by-nc-sa/3.0/) and downloaded from phylopic.org.

MATERIALS AND METHODS

Study Site

We sampled bird communities on 2 mountains connected by a mid-elevation ridge within Kinabalu Park in Sabah, Malaysia (6°N): Mt. Kinabalu and Mt. Tambuyukon. Kinabalu Park is a large (754 km^2), continuous tract of intact tropical forest spanning lowland (450 m) dipterocarp forests in its northern and eastern sectors to stunted montane forest and bare rock at the summit of Mt. Kinabalu (4,100 m) near its southern border. In between are a large variety of elevationally defined forest types spanning a large climatic gradient (Kitayama 1992). Our sampling area covered 1,480–3,680 m on Mt. Kinabalu, and 600–2,579 m on Mt. Tambuyukon. Both sampling areas were bounded by the current extent of primary forest on the lower boundary. The upper boundary of our Tambuyukon transect was the summit, while our sampling area was truncated below the summit on Kinabalu to match the upper limit of vegetation.

Community Composition (Field Data)

We sampled bird communities using 10-min open-width point counts. Point count data were truncated at 100 m post-hoc to minimize bias towards detection of loud species and to eliminate the possibility of attributing a distant individual to the wrong elevational community in exceptionally steep topography. Point count stations were laid out along narrow and infrequently used forest trails such that stations were at least 250 m apart based on straight-line distance and each 200 m elevational band contained exactly 5 stations. Distances between stations and elevation were determined with a regularly calibrated handheld GPS unit (Garmin, Olathe, Kansas, USA). Birds were detected both visually and aurally, and distances were estimated for all detections. All point counts took place between February and June, 2012–2015, and were exclusively conducted by A.J.B. All points on Kinabalu were sampled 2–3 times per season, while Tambuyukon points were surveyed once per season. Point counts below 1,400 m on Tambuyukon, where species diversity is highest, were recorded so that any unknown vocalizations could be identified later. All bird species detected within a given 200 m elevational band were deemed to be present in that community. Additionally, birds were considered present in all elevational bands between their highest and lowest detection points on each gradient (McCain 2004). Despite the documented advantages of using abundance-weighted estimates in community structure analyses (Freilich and Connolly 2015), we did not attempt to do so here because of unequal sampling across sites and because estimating detection probability would have been problematic for a large number of rarely encountered species.

Community Composition (Literature Data)

We used elevational distribution data of Harris et al. (2012) for all species of birds known from Kinabalu Park. This dataset is based on multiple data sources including direct sampling by the authors, citizen science projects, the literature, and unpublished data from experienced observers. To improve the quality of the data, elevational ranges were broadened when direct observations from our field data fell outside of the published elevational range. Additionally, when elevational ranges included single observations that were >200 m either above or below all other known observations, we assumed these were misidentifications or represented temporary movements, and these records were discarded.

Phylogenetics

We constructed a phylogenetic tree of 255 individuals comprising 252 species representing most of the resident birds of Borneo (Supplementary Material Table S1). Of the 252 species, 28 were not sampled in the Borneo because we did not have Bornean specimens. DNA sequences of the following genes were collected for comparisons: 2 mitochondrial loci, NADH subunit 2 (ND2) and cytochrome-*b* (CYTB); and 2 nuclear loci, Transforming-Growth Factor Beta 2 (TGFB2) intron 5, and Muscle Skeletal Receptor Tyrosine-protein Kinase (MUSK) intron 13. When they were available, we downloaded sequences from GenBank. To fill gaps in the data, we generated 582 new sequences.

Total genomic DNA was extracted from frozen or alcohol-preserved tissue or blood samples using DNEasy Blood and Tissue Kit (Qiagen, Germantown, Maryland, USA) and manufacturer protocols. PCR amplifications were performed in 25 μL reactions using Taq DNA Polymerase (New England BioLabs, Ipswich, Massachusetts, USA). Various primers were used to amplify the corresponding regions of DNA (Supplementary Material Table S2). Amplification consisted of 34 cycles of denaturing at 95°C, annealing at temperatures varying according to the primer pair used, and extension at 72°C. An annealing temperature of 50°C was used for MUSK (primer pair 13F and 13R), 54°C for ND2 (primer pair L5215 and HTrpC), 55°C for CYTB (primer pair L14851 and H4A), and 58°C for TGFB2 (primer pair 5F and 6R). A new primer was developed for CYTB to amplify sequences of individuals in which the basic primer pair did not work. PCR products were visualized in 1% agarose gels stained with SYBR Safe DNA Gel Stain (Invitrogen, Carlsbad, California, USA). They were sequenced by Beckman Coulter Genomics (Danvers, Massachusetts, USA).

Sequence contigs were assembled in Geneious 8.1.9 (Biomatters, Aukland, New Zealand). Sequences were manually checked and trimmed to eliminate errors and to identify ambiguous sites. Sequences were aligned using MUSCLE (Edgar 2004) implemented in Geneious. The 4 loci were concatenated into sequences of 4,459 base pairs and placed in a single alignment containing all species. This dataset was divided into 8 partitions: mitochondrial genes with 3 partitions each based on codon position, and nuclear genes with 1 partition each. Bayesian Information Criterion, implemented in the program Partition Finder 1.1.1, was used to find the best substitution model for each partition.

Bayesian methods were used to construct trees from the concatenated sequences. A time-calibrated tree was generated using BEAST 2.3 (Drummond et al. 2002, 2006) with a relaxed clock, log normal distribution, and a birth-death speciation model. Default priors were used for all parameters. Two independent Markov chain Monte Carlo chains were run for 100 million generations. Tracer 1.6 (Rambaut et al. 2014) was used to check for convergence among runs, and TreeAnnotator was used to generate a maximum clade credibility tree after 25% of trees were discarded as burn-in.

Functional Traits

We used morphological measurements to describe species resource and substrate use (Miles and Ricklefs 1994). While many authors have applied categorical variables as functional traits to assign species to feeding or foraging guilds, such categorizations would be simplifications of actual resource use, especially for many of the rare or little-known species in our dataset. We compiled measurements of 5 morphological characters for species present in our communities: body mass, wing chord, tarsus, bill width, and exposed culmen length (Supplementary Material Table S3). These characters were chosen because they are easily measured on both live birds and specimens, and all are thought to be important in mediating biotic interactions via diet, foraging strategy, and foraging substrate (Hespenheide 1973, Miles and Ricklefs 1984, 1994, Pigot et al. 2016), or facilitating use of abiotically challenging environments. Specifically, greater body mass and large wings relative to body mass should be advantageous in cold, high elevation environments that favor lower surface to volume ratios to reduce rates of heat loss and increase flight power in thinner air, respectively (Altshuler and Dudley 2006, Graham et al. 2012, McNab 2016), while large bills, controlled for body mass, act as thermoregulatory organs and are important for dissipating heat in hot environments (Symonds and Tattersall 2010, Greenberg et al. 2012, Danner et al. 2017, Tattersall et al. 2017). Relative tarsus length, or tarsus length controlled for body mass, indicates foraging mode, with species showing longer tarsi associated with ground foraging and vice versa (Miles et al. 1987).

Data were primarily gathered from measurements of netted birds at a long-term field study at Kinabalu Park (T. E. Martin personal observation). When field data were absent, we measured specimens archived at the Sabah Parks Collection at Kinabalu Park headquarters and the Louisiana State University Museum of Natural Science. For species in which sex-specific trait values were available, we used the midpoint values of male and female trait means. For non-dimorphic species, all measurements were pooled, and population means were used. Only data from adult individuals were included in our analyses. Body mass data were obtained from the literature (Dunning 2007) in cases when they were unrecorded for museum specimens.

Statistical Analyses

Phylogenetic community structure. We calculated the net-relatedness index (NRI) and the nearest-taxon index (NTI) as metrics of phylogenetic community structure for each elevational community (200 m elevational bands for directly sampled point count data and 100 m bands for literature data). NRI describes the average pairwise phylogenetic distance among all species pairs in a sampled community, and NTI describes the average phylogenetic distance between each species and its closest relative within a community. These values are then compared with those from communities generated by a null-model algorithm from the regional species pool (Webb 2000) to determine if observed communities are more overdispersed or clustered than expected by chance alone. We employed both metrics because NRI outperforms NTI in detecting clustering, whereas NTI outperforms NRI in detecting overdispersion (Freilich and Connolly 2015).

We used the "independent swap" algorithm (Gotelli 2000, Gotelli and Entsminger 2003) to generate 1,000 random communities while holding species richness and occupancy constant. This null model essentially treats elevational range breadth as "rarity", which may not be biologically accurate. However, using this method instead of a "richness" model, which allows occupancy to vary in null communities, should result in more conservative estimates of standardized effect sizes (NRI and NTI) by minimizing the likelihood of type 1 error (Gotelli 2000). We used all species present across elevations to populate the regional species pool as no geographic barriers exist along this gradient and all species sampled have distributions that extend beyond the study area (Sheldon et al. 2001), indicating that dispersal ability alone is not constraining elevational distributions. We used independent regional species pools for field and literature community datasets to eliminate the possibility of including species in the regional pool that were simply undetectable by the observer during field sampling. Analyses were done in R (R Core Team 2015) using the SES.MPD and SES.MNTD functions in the PICANTE package (Kembel et al. 2010).

Functional trait diversity. We used the same metrics (NRI, NTI) to describe the distribution of functional traits in elevational communities. Hereafter we denote the trait-based metrics as NRI_t and NTI_t. We used raw values to describe bill shape (bill width and culmen length) and residual values from regressions of log-transformed wing chord and tarsus on log-transformed body mass to describe relative wing size and relative tarsus length. Relative bill size values were residual values of a regression of bill surface area [(bill width × culmen length)/2] on log-transformed body mass. Log-transformed body mass was our final functional trait. We then calculated Gower's distance using the GOWDIS function in the FD package (Laliberte and Legendre 2010), a metric that integrates multiple traits into an index of dissimilarity for each pairwise combination of species (Gower 1971). These distances were used to populate a distance matrix, analogous to a distance matrix of phylogenetic relatedness. Because abiotic filtering and competition may be acting simultaneously and on different traits (Swenson and Enquist 2009, Graham et al. 2012), we also calculated NRI_t for each morphological trait individually using our literature dataset. NRI only detects the presence or absence of clustering, but not whether trait values in clustered communities are higher, lower, or intermediate compared with neutral or overdispersed communities. We also calculated mean ± SE trait values for each elevational community to test predictions on how abiotic filters may influence trait distributions at high elevations. As before, we used the SES.MPD and SES.MNTD functions in the PICANTE package.

Phylogenetic signal. We estimated Blomberg's *K* statistic as a measure of phylogenetic signal in 5 morphological functional traits thought to be important for either mediating competition or utilizing high elevation environments (see below). Blomberg's *K* is a measure of the trait variation among species compared with that expected based on a Brownian motion model of evolution, given shared evolutionary history determined from the phylogeny (Blomberg et al. 2003). When $K = 1$, trait similarity is proportional to that expected from a Brownian motion model (i.e. phylogenetic signal). When $K > 1$, traits are more similar than predicted by a Brownian motion null model. When *K* approaches zero, there is an absence of phylogenetic signal. *K* values were calculated in the PICANTE package using the function multiPhylosignal (Kembel et al. 2010).

Elevational patterns. To evaluate how phylogenetic and functional trait community structure varied across elevations, we used 2 methods. For field data we used the lme4 package to fit linear mixed-effect models with community structure metrics as response variables, elevation as a fixed effect, and site (Kinabalu, Tambuyukon) as a random effect. For literature data we used a simple linear model with community structure metrics as response variables and elevation as a fixed effect.

RESULTS

Phylogeny

Phylogenetic analysis of the DNA sequence data produced a tree (Supplementary Material Figure S1) that comprises 51 families of birds. Relationships among these families and their constituent species were mostly well supported (Supplementary Material Figure S1) and consistent with those observed in recent phylogenetic studies (Johansson et al. 2008, Moyle et al. 2016, Oliveros et al. 2019).

Sampling

Point count sampling resulted in the detection of 163 species of birds along the elevational transects. Our literature search, combined with directly sampled data, yielded elevational distribution data for 222 species. Phylogenetic data were not available for all species, so datasets for phylogenetic community structure analyses were restricted to 136 species (83% of sampled species) for our point-count data, and 180 (81%) species for our literature-based dataset. Trait data were also missing for some species, so functional community structure analyses based on field and literature data were restricted to 139 (85% of sampled species) and 189 (85%) species, respectively. The missing taxa included species of songbirds (Passeriformes), owls (Strigiformes), cuckoos (Cuculiformes), barbets (Piciformes), pheasants (Galliformes), hornbills (Bucerotiformes), pigeons (Columbiformes), and swifts (Apodiformes). The missing species are not expected to bias the trait or phylogenetic results because there was no systematic or elevational trend in species with missing morphological or genetic data, and no complete families were missing from analyses.

Species richness declined with increasing elevation based on field-sampling ($\beta = -0.03$, $t = -11.96$, $P < 0.01$; Figure 2). Species richness was higher for a given elevation on Mt. Kinabalu than Mt. Tambuyukon ($\beta = -15.79$, $t = -4.14$, $P < 0.01$) with maximum species richness between 500 and 700 m on Tambuyukon (68 species) and between 1,650 and 1,850 m on Kinabalu (46 species), and minimum diversity between 2,500 and 2,700 m on Tambuyukon (3 species) and 3,650 and 3,850 m on Kinabalu (2 species). Species richness patterns were similar in our literature dataset for Kinabalu Park, with maximum diversity between 600 and 700 m (122 species) and minimum diversity between 3,800 and 3,900 m (1 species), with α diversity decreasing monotonically with elevation ($\beta = -0.04$, $t = -19.06$, $P < 0.01$; Figure 2).

Phylogenetic Signal in Functional Traits

All measured morphological traits showed strong, significant phylogenetic signal (Table 1), indicating that closely related species are more likely to possess similar morphology and thus similar ecological requirements. All 5 traits had *K* values >1, indicating that traits are even more similar among closely related species than expected if trait variation were proportional to phylogenetic distance.

Phylogenetic Community Structure

Bird communities exhibited a general pattern of neutral phylogenetic community structure over much of the elevational

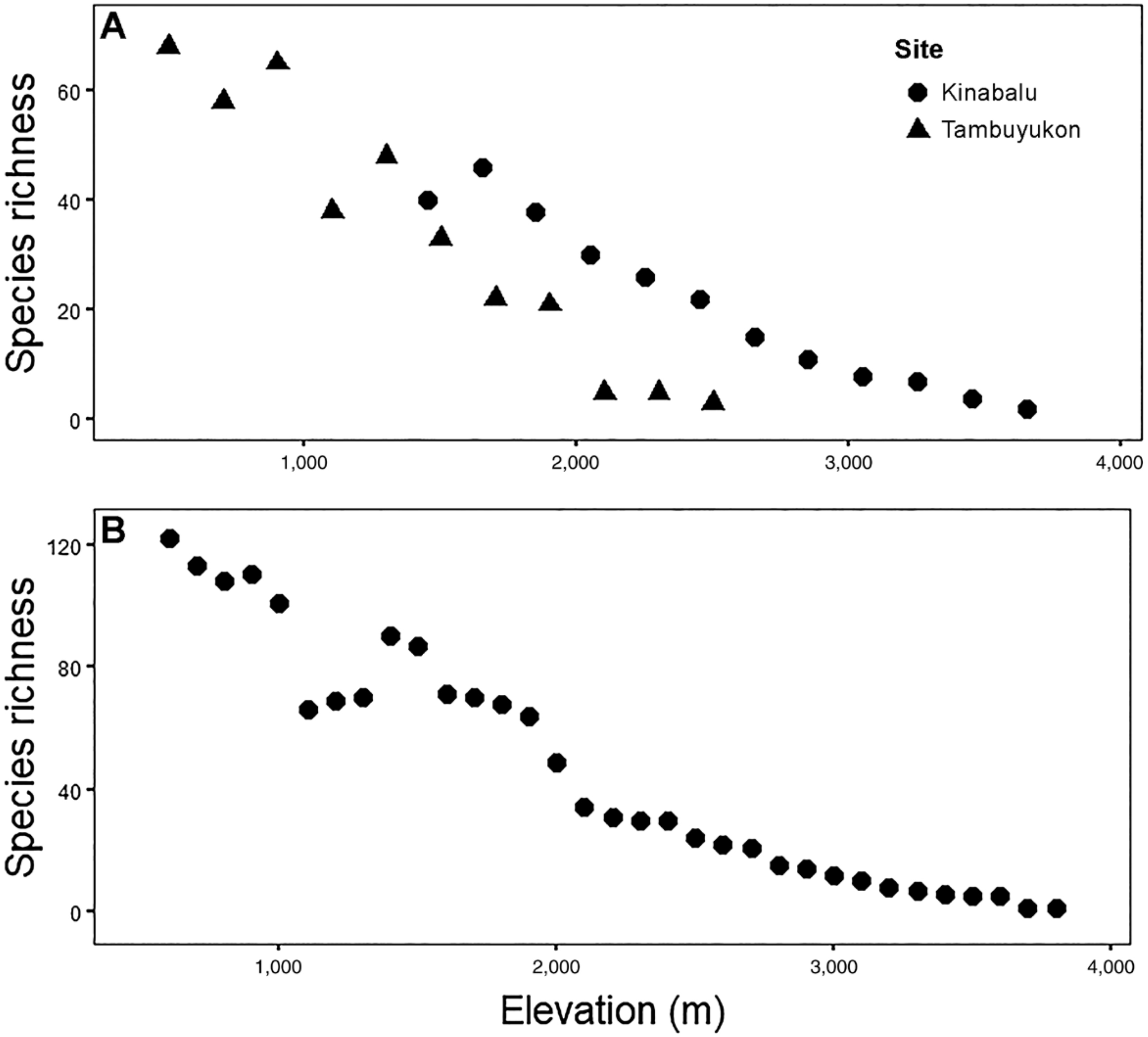

FIGURE 2. Changes in community species richness with elevation for (**A**) our directly-sampled datasets on Kinabalu and Tambuyukon and (**B**) our literature dataset spanning all of Kinabalu Park.

TABLE 1. Measures of phylogenetic niche conservatism as estimated by Blomberg's *K* for 5 morphological functional traits. *P*-values indicate the estimate is significantly different than zero, with larger numbers indicating stronger phylogenetic conservatism of a given trait

Trait	*K*	*P*
Mass	1.57	<0.001
Wing chord	1.71	<0.001
Tarsus length	1.27	<0.001
Bill width	1.23	<0.001
Culmen length	1.69	<0.001

range, but some overdispersion occurred at low elevations and phylogenetic clustering at high elevations (Figure 3A, Table 2). Clustering increased with elevation in our field-sampled dataset based on NRI, but no significant elevational pattern in community structure was detected using NTI (Table 2). In our literature dataset, clustering increased with elevation when using both NRI and NTI (Table 2). Both clustered and overdispersed communities were detected from the literature dataset using NRI, while only low elevation overdispersion was detected using NTI (Figure 3A).

Functional Trait Diversity

Elevational patterns of community structure based on functional traits (Figure 3B) were largely consistent with those based on phylogenetic relatedness (Figure 3A). This concurrence was not surprising given that our trait data

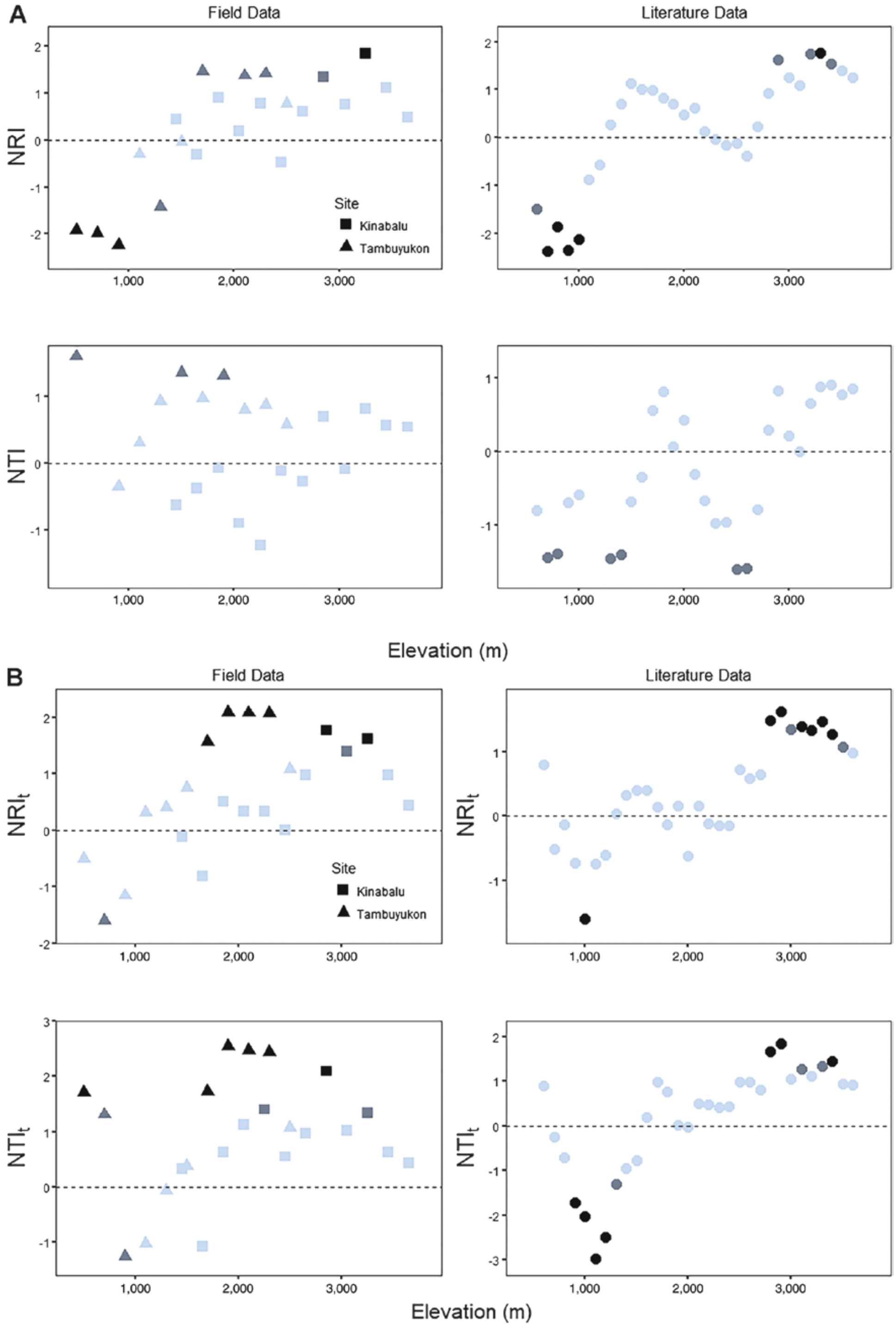

FIGURE 3. Plot of (**A**) phylogenetic-based community structure vs. elevation for directly sampled and literature datasets. Positive values of net-relatedness index (NRI) and nearest-taxon index (NTI) indicate clustering, while negative values indicate overdispersion. Point color denotes whether NRI and NTI values are statistically different from zero at thresholds of $P < 0.10$ (dark gray) or $P < 0.05$ (black). Plot of (**B**) trait-based community structure vs. elevation for directly sampled and literature datasets. Positive values of NRI and NTI indicate clustering, while negative values indicate overdispersion. Point color denotes whether NRI and NTI values are statistically different from zero at thresholds of $P < 0.10$ (dark gray) or $P < 0.05$ (black).

exhibited a strong phylogenetic signal (Table 1). Overall, functional traits were clustered at high elevations, neutral at middle elevations, and overdispersed at low elevations (Figure 3B). Based on NRI_t, the pattern of increased clustering with elevation was consistent for both our field-sampled gradients and our literature dataset (Table 2).

TABLE 2. Summary of models describing elevational patterns of phylogenetic and functional community structure based on literature and field-based datasets. Negative β-coefficients indicate increasing clustering with increasing elevation. R^2 values are presented for simple linear models but are not presented for field-based models which included a random effect for site

Dataset	Metric	β elevation (m)	*t*-value	*P*	R^2
Literature	NRI	−0.001	−6.50	<0.001	0.59
	NTI	−0.001	−4.38	<0.001	0.40
	NRI_t	−0.001	−6.15	<0.001	0.57
	NTI_t	−0.001	−5.77	<0.001	0.54
Field	NRI	−0.001	−3.83	0.012	–
	NTI	−2.00E-04	−1.23	0.231	–
	NRI_t	−0.001	−4.89	<0.001	–
	NTI_t	−5.00E-04	−1.82	0.086	–

NRI, net-relatedness index; NRI_t, trait-based NRI; NTI, nearest-taxon index; NTI_t, trait-based NTI.

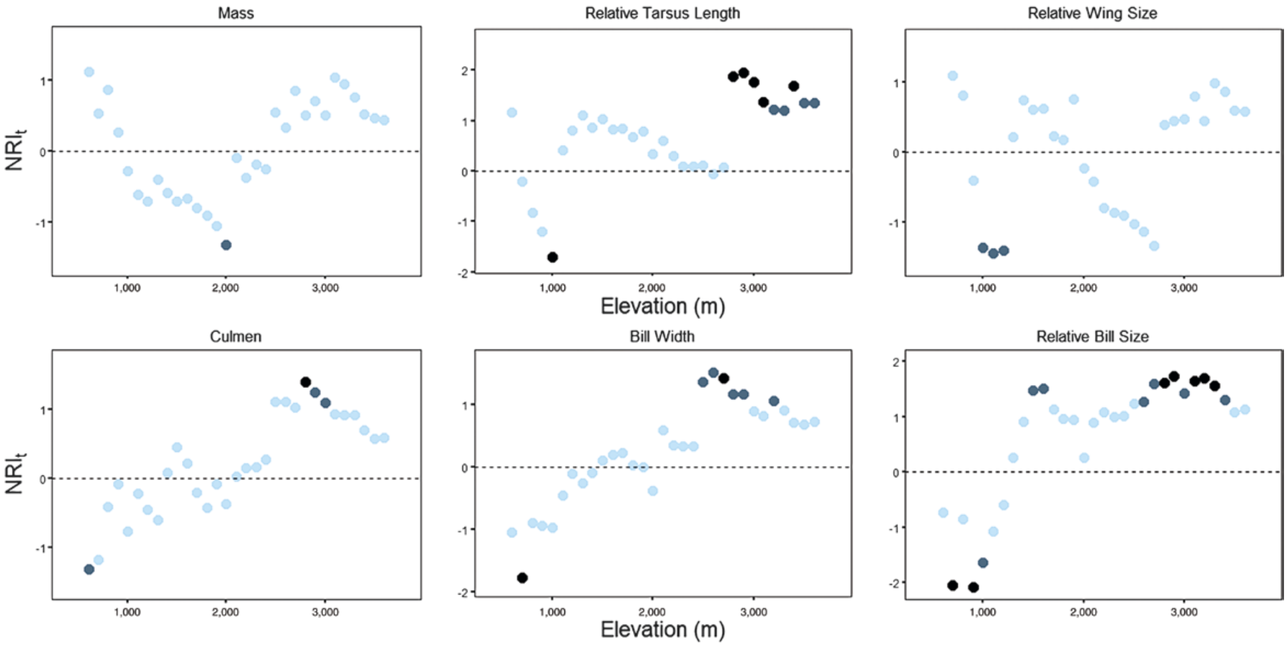

FIGURE 4. Community structure patterns for morphological functional traits across elevations based on our literature dataset. Positive values indicate that traits are more clustered than expected under a null-model distribution. Point color denotes whether net-relatedness index (NRI) values are statistically different from zero at thresholds of $P < 0.10$ (black) or $P < 0.05$ (dark gray).

Based on NTI_t, there was no elevational pattern in clustering based on the field data but a highly significant increase in clustering with elevation for our and literature dataset (Table 2). In contrast to other analyses, our field data showed 2 clustered communities at low elevations based on NTI_t.

Analysis of community structure patterns based on individual traits revealed informative patterns. Relative tarsus length, bill width, culmen length, and relative bill size showed strong patterns of overdispersion at low elevations and clustering at high elevations (Figure 4). All morphological measures that were clustered at high elevations also showed significant changes in mean trait values across elevations (Figure 5, Table 3). High elevation communities contained species with lower body mass and longer relative tarsus length, as well as narrower and shorter bills, and bills that were of a smaller relative bill size compared with low elevation bird communities (Figure 5, Table 3). On the other hand, relative wing size exhibited no elevational pattern in community structure (Figure 4), and body mass showed greater clustering at high elevations ($P = 0.04$), but the pattern was weak compared with other traits (Figure 4). Initially, we were concerned that the absence of hornbills (Bucerotidae, 4 species) at high elevations, combined with their massive size compared with other bird species, was driving the results presented above. However, removing hornbills from trait-based datasets had no qualitative effect on any of our results. The data presented here are those with hornbills excluded and are thus conservative.

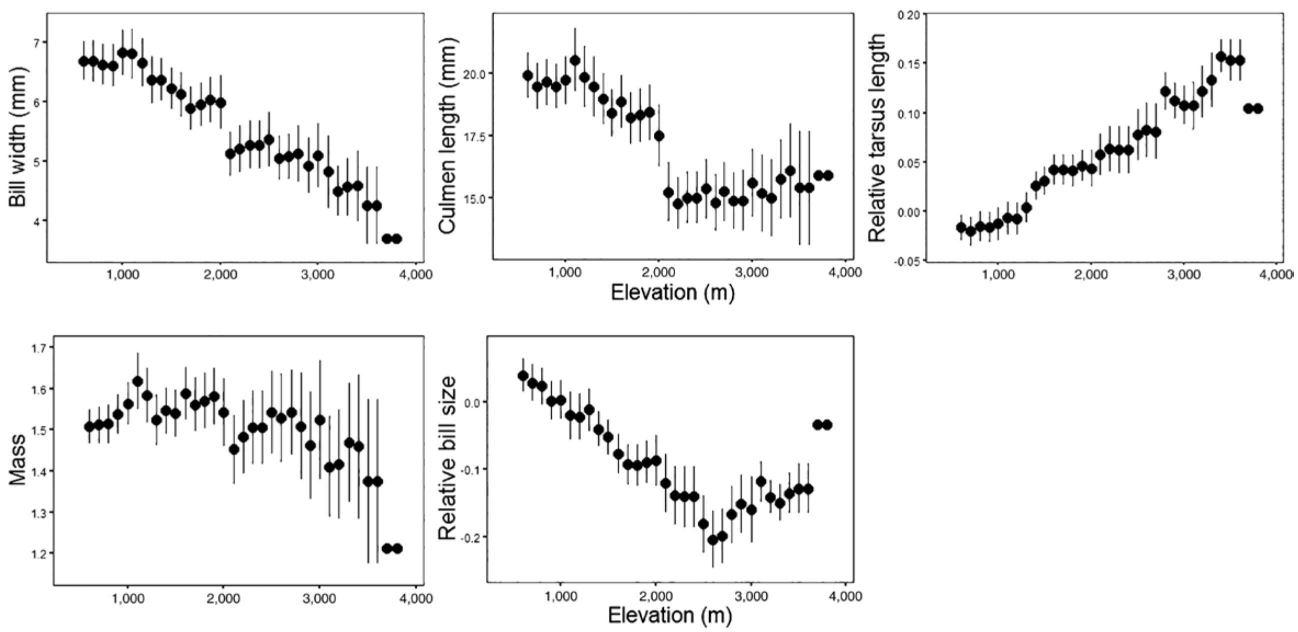

FIGURE 5. Changes in mean ± SD trait values for bill width, culmen length, and residual tarsus length for avian communities across an elevational gradient based on our literature dataset. Bill width and culmen length are presented as raw values, residual tarsus length is calculated as the residual value from a regression of tarsus length on log-transformed body mass, and body mass is log-transformed.

TABLE 3. Summary of models describing elevational patterns of mean functional trait values with elevation. Negative β-coefficients indicate decreasing trait values with increasing elevation

Trait	β elevation (m)	*t*-value	*P*	R^2
Mass (g)	−6.83E-05	−5.61	<0.001	0.49
Relative tarsus length (mm)	5.47E-05	19.49	<0.001	0.92
Culmen length (mm)	−1.78E-03	−8.98	<0.001	0.71
Bill width (mm)	−9.32E-04	−24.06	<0.001	0.95
Relative bill size (mm^2 g^{-1})	4.89E-05	−5.23	<0.001	0.45

DISCUSSION

Several studies have found overdispersed communities of disparate kinds of organisms at low elevations (Machac et al. 2011, Graham et al. 2014) and clustered communities at high elevations (Bryant et al. 2008, Graham et al. 2009, Machac et al. 2011, Wang et al. 2012, Smith et al. 2014). In respect to high elevation, we also found clustering, but an in-depth look revealed that it was associated primarily with traits related to locomotion (especially in respect to leg length) and resource acquisition (bill size and shape), and not abiotic tolerance (mass and relative wing size), as would normally be expected (Hanz et al. 2018). These trait patterns suggest that constrained niche space plays a principal role in driving avian community structure at high elevations. At low elevation, there was some support for overdispersion. We found that metrics of bill size and shape were overdispersed in a few low elevation communities (Figure 4), providing some evidence for resource competition given the role of bill size in food acquisition (Schoener 1971, Hespenheide 1973). However, relative bill size was generally larger at low elevations (Figure 5). Large bills relative to body size may act as thermoregulatory organs in hot, humid environments (Symonds and Tattersall 2010, Tattersall et al. 2017), suggesting that abiotic conditions may play a role in structuring communities at all elevations.

Overall, across the entire elevational gradient, we found far more clustered than overdispersed communities (Figure 3), matching results in hummingbirds (Graham et al. 2009). This leads to the conclusion that interspecific competition is not the dominant force in avian community assembly in our Bornean mountain system and, given the hummingbird finding, perhaps it is not as important as long believed in all tropical systems (Terborgh 1971, Terborgh and Weske 1975, Jankowski et al. 2010, Freeman 2015). Yet this does not discount the possibility that interspecific competition is important at finer spatial or taxonomic scales.

Study of functional traits, as opposed to phylogenetic metrics, was particularly important to our investigation of community structure and assembly. Trait-based metrics detected significantly overdispersed or clustered communities with similar or higher frequency than phylogenetic metrics regardless of the metric applied (NRI, NTI) or the dataset (our observations or from the literature; Figures 3 and 4). Our ability to detect drivers of clustering at high elevations was only possible with trait-specific analyses, and our results suggest methods assessing phylogenetic or multi-trait functional community structure alone are insufficient for gaining inference on forces producing the community structure they describe.

Our investigation offers an interesting contrast to the hummingbird study of Graham et al. (2012). In hummingbirds, large relative wing size and large mass were significantly clustered at high, cool locations in the Ecuadorean Andes, where Graham and colleagues gathered their data (2009, 2012). On Borneo, however, relative wing size showed no pattern of increased clustering at high elevations (Figure 4). Hummingbirds also increased in mass with elevation, whereas Bornean birds decreased in mass with elevation. These alternative patterns may be explained in terms of geography (differences between mountain systems) and phylogeny (differences between clades). Mt. Kinabalu is an isolated massif with a summit elevation of 4,095 m, 1,500–2,000 m higher than any other mountains on Borneo. The Ecuadorean Andes, on the other hand, are part of an extensive mountain range in which peaks commonly reach 5,000–6,000 m. The more abiotic conditions in the high Andes would exert a stronger abiotic filter than the highest elevations at our study site. Body size and wings are especially important in hummingbirds, which are small and thus subject to rapid heat loss in cold environments, and which use flight maneuvers that are particularly aerodynamically demanding at low atmospheric pressures (Segre et al. 2016). In tropical South America and Africa, bird functional and phylogenetic diversity decline with increasing elevation, and are associated primarily with resource availability and vegetation structure, respectively (Hanz et al. 2018). Our findings from tropical Asia concur, and suggest that patterns of avian community structure on tropical mountains are primarily driven by reductions in resources and habitat complexity with increasing elevation, and less so by competition or the direct effects of climate.

Based on an analysis of morphological traits we found no evidence that abiotic factors such as cold temperatures or low atmospheric pressure directly drove clustering in the high elevation bird communities of Kinabalu and Tambuyukon. This finding agrees with evidence that Bergmann's rule does not apply to birds on tropical mountains (Freeman 2017) and upper elevational limits do not appear directly related to cold tolerance in some tropical birds (Freeman 2016). Instead, clustered traits were those related to food acquisition and foraging mode. Specifically, species at high elevations are smaller and have short and narrow bills (Figures 4 and 5). Avian body size and bill shape are correlated with prey size (Schoener 1971, Sam et al. 2017) and insect body size declines with increasing elevation (Janzen 1973, Sam et al. 2017). Thus, a possible cause for the smaller bills of high elevation species is an absence of large prey. The argument that insect size distributions may drive patterns of avian diversity has been made in the context of latitudinal gradients (Schoener 1971), but our results suggest it may apply to elevational gradients as well. Further, relative tarsus length is clustered in high elevation communities, where species have long tarsi relative to body size (Figures 4 and 5). Long relative tarsus length is typically associated with ground-foraging species (Miles et al. 1987). High elevation forests have lower canopy height and simplified structure compared with low elevation forests, suggesting that this simplified habitat structure may be driving morphological clustering. Overall, our results suggest that abiotic factors may not be directly influencing avian community structure, but are doing so indirectly by influencing community structure of prey organisms and vegetation.

Despite increased clustering at high elevations, estimates of community structure at the highest elevations often approached neutral values (Figure 3). This result may reflect issues related to low species richness in these communities. While habitat filtering may be less intense at high elevations, simulations show that the power to detect environmental filtering decreases sharply when species richness is small relative to the regional species pool (Freilich and Connolly 2015). The decrease in clustering at high elevations was most evident in directly sampled datasets (Figure 3), which depended on communities with especially low species richness (Figure 2). Additionally, summit communities experience the coldest temperatures and lowest atmospheric air pressures, conditions thought to be physiologically challenging for birds (Altshuler and Dudley 2006, Graham et al. 2009, Cheviron and Brumfield 2012). These factors strengthen the likelihood that the neutral-tending values of community structure at the highest elevations are a statistical artifact and not ecologically meaningful.

Studies of community structure suggest that the forces governing community assembly are complex and vary across geographic gradients and among clades (Cavender-Bares et al. 2006, Bryant et al. 2008, Graham et al. 2012). We show that tropical bird communities along a large elevational gradient exhibit clustered structure due to a lack of resource and habitat complexity at high elevations and, to a lesser extent, appear to be simultaneously influenced by interspecific competition and warm temperatures at low elevations. These results generally agree with recent work in tropical Africa and South America (Hanz et al. 2018), suggesting that this is a globally consistent pattern.

Furthermore, the rarity of overdispersed communities in this study and others (Graham et al. 2009, 2012) provides evidence that interspecific competition may not be the primary driver of avian community structure as once believed.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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Author contributions: A.J.B. and T.E.M. formulated the idea. A.J.B. performed fieldwork, analyses, and wrote the original manuscript. F.H.S., S.S., and R.G.M. reconstructed the phylogeny and provided morphological data. All authors contributed to editing and improving several versions of the manuscript.

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