


RESEARCH ARTICLE

Abiotic and biotic drivers of functional diversity and functional composition of bird and bat assemblages along a tropical elevation gradient

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Abstract

Aim: The identification of the mechanisms determining spatial variation in biological diversity along elevational gradients is a central objective in ecology and biogeography. Here, we disentangle the direct and indirect effects of abiotic drivers (climatic conditions, and land use) and biotic drivers (vegetation structure and food resources) on functional diversity and composition of bird and bat assemblages along a tropical elevational gradient.

Location: Southern slopes of Mt. Kilimanjaro, Tanzania, East Africa.

Methods: We counted birds and recorded bat sonotypes on 58 plots distributed in near-natural and anthropogenically modified habitats from 700 to 4,600 m above sea level. For the recorded taxa, we compiled functional traits related to movement, foraging and body size from museum specimens and databases. Further, we recorded mean annual temperature, precipitation, vegetation complexity as well as the number of fruits, flowers, and insect biomass as measures of resource availability on each study site.

Results: Using path analyses, we found similar responses of bird and bat functional diversity to the variation in abiotic and biotic drivers along the elevational gradient. In contrast, the functional composition of both taxa showed distinct responses to abiotic and biotic drivers. For both groups, direct temperature effects were most important, followed by resource availability, precipitation and vegetation complexity.

Main Conclusions: Our findings indicate that physiological and metabolic constraints imposed by temperature and resource availability determine the functional diversity of bird and bat assemblages, whereas the composition of individual functional traits is driven by taxon-specific processes. Our study illustrates that distinct filtering mechanisms can result in similar patterns of functional diversity along broad environmental gradients. Such differences need to be taken into account when it comes to conserving the functional diversity of flying vertebrates on tropical mountains.

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KEYWORDS

biodiversity, climate, functional traits, land use, Mount Kilimanjaro

1 | INTRODUCTION

The identification of the mechanisms determining spatial variation in biological diversity along latitudinal or elevational gradients is a central objective in ecology and biogeography (Cardillo et al., 2005; Curran et al., 2012; Hawkins & Porter, 2001; Lomolino, 2001). The mechanisms behind this variation can be driven by abiotic or biotic factors (e.g. Ferger et al., 2014; Vollstädt et al., 2017). Three key ecological hypotheses attempting to explain variation in biodiversity in response to abiotic and biotic factors are the “physiological tolerance hypothesis,” the “vegetation structure hypothesis” and the “resource availability hypothesis” (Buckley et al., 2012; Currie et al., 2004; Davies et al., 2007; Hurlbert, 2004; Jetz et al., 2009; Tews et al., 2004). According to the “physiological tolerance hypothesis,” diversity is directly constrained by climate, and peaks in warm and wet environments as only a subset of species can tolerate and persist under extreme environmental conditions (Buckley et al., 2012; Currie et al., 2004; Ferger et al., 2014). In contrast, according to the “vegetation structure hypothesis” and the “resource availability hypothesis,” diversity is constrained by the structural complexity of habitats or resource availability, which both limit the number of species able to coexist in local communities via niche partitioning (Davies et al., 2007; Ferger et al., 2014; Hurlbert, 2004; Jetz et al., 2009; Tews et al., 2004). According to the latter two hypotheses, climate is mainly indirectly related to diversity via vegetation structure and resource availability. In addition to the effects of climate, diversity may also be indirectly affected by land use via changes in vegetation structure or resource availability (Vollstädt et al., 2017). Thus, for conserving biodiversity and ecosystem functioning, it is essential to understand which drivers are important and whether climate and land use have mainly direct or indirect effects on biological diversity.

To better understand the mechanisms that shape variation in biological diversity along environmental gradients, approaches based on functional traits are particularly useful (McGill et al., 2006; Violle et al., 2007). Functional traits are defined as morphological, behavioural, physiological or phenological attributes that impact individual performance under specific environmental conditions (McGill et al., 2006; Violle et al., 2007). As species often show functional adaptations to specific environments, for example through traits related to resource acquisition, energy requirements and movement ability (Hanz et al., 2019), functional traits are closely related to niche partitioning, species coexistence and community assembly (Mouchet et al., 2010; Pigot et al., 2016; Villéger et al., 2008). Community assembly processes, in turn, may control the community-level variation (functional diversity) and mean (functional composition) in the functional traits of co-occurring species (McGill et al., 2006). For instance, environmental filtering in harsh environments with limited resource availability may cause the directed loss of species with

particular trait values, which may entail a reduction of the functional diversity and shifts in the functional composition of ecological communities (Classen et al., 2017; Hanz et al., 2019). In addition, competition has been suggested to increase the dispersion of functional traits through competitive exclusion of functionally similar species (MacArthur & Levins, 1967; Montaña-Centellas et al., 2020).

Previous studies have assessed the effects of climate and land use on the functional diversity of single taxonomic groups along elevational gradients (e.g. Vollstädt et al., 2017, 2020) or have compared the effects on functional and phylogenetic diversity (e.g. Boyce et al., 2019; Hanz et al., 2019; Montaña-Centellas et al., 2020). However, it is still unclear whether patterns in functional diversity and composition can be generalized across disparate taxa with distinct evolutionary histories (Luck et al., 2012). In addition, a comparative analysis of functional diversity across taxa with different evolutionary histories can provide new insights into the possibility of generalizing relationships between environmental conditions and functional diversity across taxonomic groups. Birds and bats are suitable to address this question because they perform similar ecological functions (e.g. seed dispersal, pollination, biological control; García-Morales et al., 2016; Sekercioglu, 2012), but differ in their habitat requirements and ecology (Graham, 1990; Helbig-Bonitz et al., 2015). Moreover, both taxa possess analogous, but independently evolved functional traits related to physiology, energy requirements and movement capacity (e.g. body mass; Anderson & Jetz, 2005; Buckley et al., 2012; Currie et al., 2004), manoeuvrability and habitat use (e.g. wing shape; Aldridge & Rautenbach, 1987; Blakey et al., 2019; Sheard et al., 2020) and resource acquisition (e.g. bill or mouth shape; Arbour et al., 2019; Carnicer et al., 2008; Felice et al., 2019). We expected that the diversity and composition of these different types of functional traits were driven by different mechanisms. Climatic conditions should mainly influence body size (Anderson & Jetz, 2005; Buckley et al., 2012), vegetation structure should mainly be related to wing morphology (Aldridge & Rautenbach, 1987; Burney & Brumfield, 2009; Claramunt et al., 2012), and resource availability should primarily affect beak and mouth morphology as well as body size (Brown et al., 2004; Carnicer et al., 2008).

Here, we conduct a comparative analysis of the effects of abiotic and biotic factors on the functional diversity and composition of birds and bats across a tropical elevational gradient and aim to gain deeper insights into the mechanisms that shape the diversity of these two groups of flying vertebrates. Our study is based on a comprehensive data set of bird and bat assemblages and associated functional traits that has been collected along a 3.5 km elevational gradient of near-natural and anthropogenic habitats on the southern and south-eastern slopes of Mt. Kilimanjaro. Based on previous work, we hypothesized that functional diversity of birds and bats should increase with benign climatic conditions (“physiological tolerance hypothesis”), vegetation complexity (“vegetation structure

hypothesis”) and resource availability (“resource availability hypothesis”; Albrecht et al., 2018; Hanz et al., 2019; Vollstädt et al., 2017, 2020), and should decrease in response to land-use intensity (Farneda et al., 2020; Matuoka et al., 2020). Therefore, we expected direct effects of climatic conditions on functional diversity, but also indirect effects via vegetation structure and resource availability. With respect to the functional composition of bird and bat assemblages, we hypothesized that mean body size is primarily driven by climate, wing morphology by vegetation structure, and beak and mouth morphology by resource availability. However, owing to the differences in ecology and habitat requirements of birds and bats, we hypothesized that the functional composition of bird and bat assemblages may show distinct responses to abiotic and biotic factors along the elevational gradient (Graham, 1990; Helbig-Bonitz et al., 2015).

2 | METHODS

2.1 | Study area

The study was conducted on the southern slopes of Mt. Kilimanjaro, Tanzania, East Africa (2°45′–3°25′S, 37°00′–37°43′E). Mt.

Kilimanjaro is the highest free-standing mountain in the world (Hemp, 2006a, 2006b). Mt. Kilimanjaro rises from the savannah plains at an elevation of 700 m a. s. l. to a snow-capped summit at an elevation of 5,895 m a. s. l. Mean annual temperature decreases almost linearly with elevation and ranges from 23°C at the mountain base to –7°C at the mountain top. The Kilimanjaro region is characterized by two wet seasons, with short, heavy rains occurring in November, and long rains occurring from March until May. Along the elevational gradient, precipitation ranges from 600 mm per year to 2,700 mm per year, and peaks at an elevation of about 2,200 m a.s.l. (Hemp, 2006a, 2006b).

2.2 | Study design

We collected data on a total of 65 study sites (each with a size of 50 m × 50 m) along 5 transects on the southern slopes of Mt. Kilimanjaro (minimum pair-wise distance of 300 m; Figure 1a). The study sites cover six near-natural and seven disturbed habitat types: Near natural habitats were savanna (870–1150 m a.s.l.), lower montane forest (1560–2020 m a.s.l.), Ocotea forest (2120–2750 m a.s.l.), Podocarpus forest (2720–2970 m a.s.l.), Erica forest (3500–3880 m a.s.l.) and alpine Helichrysum vegetation

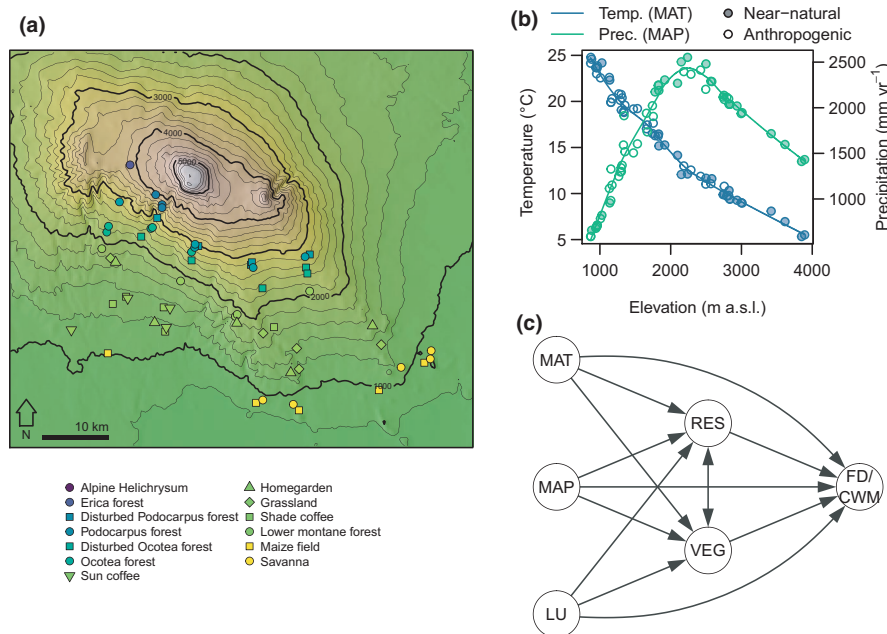


FIGURE 1 (a) Location of the study sites on Mt. Kilimanjaro, Tanzania. The symbols represent the 13 habitat types, in which the study sites are located ($n = 58$). The contour lines indicate elevation in m a.s.l. (b) Variation in mean annual temperature (MAT [°C], blue) and mean annual precipitation (MAP [mm/yr], green), as well as land use (LU; filled circles, near-natural habitats; open circles, anthropogenic habitats) along the elevational gradient of Mt. Kilimanjaro. The lines represent loess smooth functions (degree = 2, span = 0.5) fitted to the data across the elevational gradient. (c) Hypothesized a priori paths between exogenous variables (left circles) and endogenous variables (middle and right circles) based on the literature. Resource availability (RES), vegetation complexity (VEG) and measures of bird and bat functional diversity (FD) or composition (CWM) were treated as endogenous response variables. The models included all potential direct effects of mean annual temperature, mean annual precipitation and land use on resource availability and vegetation complexity, as well as on functional diversity and composition of birds and bats, respectively. Moreover, the models included the effects of resource availability and vegetation complexity on functional diversity and composition of birds and bats, respectively. A covariance term between vegetation complexity and resource availability was included to account for correlated errors due to common unmeasured sources of variance

(3880–4550 m a.s.l.). Anthropogenic habitats were maize field (870–1010 m a.s.l.), home garden (1150–1840 m a.s.l.), shade coffee plantation (1120–1660 m a.s.l.), sun coffee plantation (1150–1340 m a.s.l.), grassland (1300–1750 m a.s.l.), disturbed *Ocotea* forest (2220–2560 m a.s.l.) and disturbed *Podocarpus* forest (2770–3060 m a.s.l.) (Hemp, 2006a, 2006b). For measurements of vegetation structure, resources and bird counts (see below), we established eight subplots along the four margins of each study site, either as circles with a 20-m radius in densely vegetated habitats (savanna and all forest habitats) or as 35.5 m × 35.5 m squares on study sites in the more open habitats (maize, home gardens, coffee and *Helichrysum* vegetation) (Ferber et al., 2014). Hence, the sampled area on each study site approximated 1 ha. We had to exclude 7 study sites from the analyses as we only considered those study sites with at least one recorded bird and bat species, respectively. Thus, the final number of study sites included in the analysis was $n = 58$.

2.3 | Climatic factors, land use, vegetation complexity and resource availability

All study sites were equipped with temperature sensors that were installed ~2 m above the ground. Temperature sensors measured temperatures in 5-min intervals for a time period of ~2 years. We calculated the mean annual temperature (MAT, °C) as the average of all measurements per study site. Mean annual precipitation (MAP, mm/yr) was interpolated across the study area using a co-kriging approach based on a 15-year data set from a network of about 70 rain gauges on Mt. Kilimanjaro (Hemp, 2006a). Land use was classified as a binary variable. That is, we distinguished between anthropogenic and near-natural habitats. In our analyses, we also tested to what extent our conclusions were affected by the use of a binary instead of a quantitative land-use index. Analyses based on a quantitative land-use index, comprising measures of agricultural inputs, biomass removal, landscape composition and vegetation structure (Peters et al., 2019), yielded qualitatively identical results as presented in the main text (compare Figures 5 and S3).

We characterized the vegetation complexity on each subplot using an index consisting of three individual measures. First, we measured maximum canopy height above ground, using a laser range finder. Second, we measured canopy closure as the mean percentage of closed cells from four spherical canopy densitometer readings in the four cardinal directions. Third, we quantified vertical vegetation heterogeneity, by visually estimating the vegetation cover in layers at 0, 1, 2, 4, 8, 16, 32 and 64 m above ground and calculated the exponent of Shannon–Wiener diversity index across the strata (e^H), which is a measure of the effective number of vegetation layers (Bibby et al., 2000; Ferger et al., 2014). Each of the measurements was taken in a radius of 20 m around the centre of the eight subplots per study site (Ferber et al., 2014). We calculated the means of the three measures across the eight subplots per study site. We then calculated a vegetation complexity index for each study site as the resulting mean from the three measures (maximum canopy height,

canopy closure, vertical vegetation heterogeneity) after each individual measure had been scaled to zero mean and unit variance to account for the fact that they were measured on different scales. Thus, high values of the vegetation complexity index indicate a high vegetation complexity, whereas low values indicate low vegetation complexity (Hanz et al., 2019; Vollstädt et al., 2017).

We recorded food resources by estimating the number of ripe fleshy fruits and open flowers for every individual fruiting and flowering plant on all subplots on a logarithmic scale, considering woody plant species only (Ferber et al., 2014). In addition, we used 100 sweeps with a 30-cm-diameter sweep net along two parallel, permanently marked 50-m transects on the study sites to sample invertebrate biomass per study site in both seasons (Ferber et al., 2014). All invertebrates ≥1 mm were immediately weighed to obtain an estimate of fresh invertebrate biomass. For the analysis, we summed the estimates of fruit and flower availability and invertebrate biomass across the two seasons for each study site. Because birds included frugivores, nectarivores and insectivores, we calculated an estimate of the overall resource availability for birds by combining the three resource types into a single index (Hanz et al., 2019). To do so, we first log-transformed the amounts of fruits, flowers, and invertebrate biomass per study site. We then calculated a resource availability index for each study site as the resulting mean from these three measures after each individual measure had been scaled to zero mean and unit variance to account for the fact that they were measured on different scales (Hanz et al., 2019). High values of the resource availability index indicate a high resource availability, whereas low values indicate low resource availability. We used log-transformed fresh invertebrate biomass as an index of resource availability per study site for bats, because bats only included insectivorous species.

2.4 | Bird assemblages

Sampling of bird assemblages took place on 63 of the 65 study sites between March 2011 and October 2012, once during the warm dry season (December to March) and once during the cold dry season (July to October) using point counts (Ferber et al., 2014). All bird individuals heard or seen on each subplot were counted for 10 min and identified to species level. Point counts started 15 min before sunrise and were completed before 09:00 h. All 1,008 point counts (63 study sites × 8 subplots × 2 seasons) were conducted by the same observer (S.W.F.) to reduce inter-observer variability (Campbell & Francis, 2011). Individuals flying above the canopy were excluded, as these were assumed to not be part of the local bird assemblage. Sampling area per subplot (8 × 0.126 ha) was adequate for these structurally diverse, tropical ecosystems. Previous analyses using the same method showed that detectability is comparable across different habitat types (Mulwa et al., 2012; Santillán et al., 2018). For the further analyses, we summed all species' records over the 16 point counts per study site, yielding an overall measure of species' frequency on each study site (Ferber et al., 2017). Pooling the

data over the 16-point counts per study site (8 subplots \times 2 seasons) also ensured that we obtained almost complete records of bird assemblages with a sample coverage (Chao & Jost, 2012) of $97 \pm 2.5\%$ (mean \pm SD) across habitats (Table S1).

2.5 | Bat assemblages

Acoustic sampling of bat assemblages took place on 64 of the 65 study sites between December 2010 and March 2011, once during the warm dry season (December to March) and once during the cold dry season (July to October) (Helbig-Bonitz et al., 2015). Echolocation calls of flying insectivorous bats were recorded at the four corners of each study site following a point-stop method. Between sunset and 22:30 h, every point was visited for 5 min during one recording round, which was repeated four times in one night. All recordings were made using a real-time ultrasound bat recorder (D1000x, Pettersson Elektronik AB, Uppsala, Sweden) at a sampling frequency of 384 kHz. Bat calls were analysed using AviSoft-SASLab Pro (v. 5.1.05) software and classified into 20 sonotypes. For the classification, we used literature data and available reference calls to identify species. If it was not possible to assign calls to a particular species, calls were assigned to the respective genus or family. The bat abundance per study site was estimated based on detection frequencies as a proxy of abundance. Estimators of inventory completeness for bat sonotype richness indicated that we reached a sample coverage of $93\% \pm 7.0\%$ (mean \pm SD) with this sampling protocol across habitats (Table S1).

2.6 | Bird and bat morphology and body mass

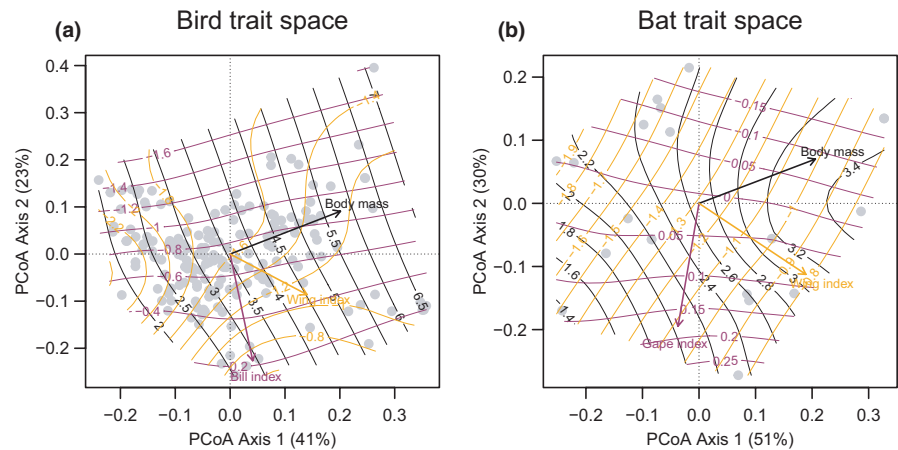
To compute functional diversity, we collected data on body mass and four morphological traits of birds and bats that are functionally related to movement ability and resource acquisition. We extracted information on body mass of birds and bats from the literature (Dunning, 2008; Wilman et al., 2014). Morphological traits of the respective bird and bat species were measured on museum specimens. For birds, we measured bill width, bill length, wing length and Kipp's distance (length from the tip of the first secondary to the tip of the longest primary) (Eck et al., 2011). For bats, we measured jaw width, rostrum length, and several wing characteristics (i.e. the lengths of upper arm, lower arm, third digit and fifth digit). In order to account for intraspecific variation, we aimed to measure at least two well-preserved specimens of each sex for each bird and bat species, and then calculated a species mean. For those bat sonotypes that were only identified to genus or family level, we took the means across the species in the respective genus or family occurring on Mt. Kilimanjaro. To account for size differences among species, we used two morphological indices for the traits related to movement and resource use, which were defined to depict ecological differences between feeding guilds and between species differing in foraging stratum. For the movement traits, we computed the

hand-wing index for birds as the Kipp's distance divided by wing length (Sheard et al., 2020). For bats, we calculated an analogue of the hand-wing index. To do so, we treated the difference between the length of the third and fifth digit of bats as analogous to the Kipp's distance of birds. Then, we calculated the hand-wing index for bats as the length of the difference between the length of the third and fifth digit divided by the length of the third digit. Both hand-wing indices are highly correlated with the aspect ratio of the wing, which is highly correlated with dispersal and movement ability in birds and bats (Aldridge & Rautenbach, 1987; Findley et al., 1972; Sheard et al., 2020). Low values of the hand-wing index indicate a short and rounded wing associated with low dispersal ability but high manoeuvrability, whereas high values indicate a long and pointed wing associated with high dispersal ability but low manoeuvrability (Aldridge & Rautenbach, 1987; Lockwood et al., 1998). For foraging traits, we used a bill index for birds (bill width divided by bill length), and a gape index for bats (jaw width divided by rostrum length; Table S2). Both indices are related to the type and diversity of resources used by birds and bats (Arbour et al., 2019; Carnicer et al., 2008; Felice et al., 2019). We log-transformed all traits before the analysis.

2.7 | Functional trait analysis

Based on the three traits of each taxonomic group, we computed measures of both functional diversity (i.e. trait variation) and functional composition (i.e. trait means) in bird and bat assemblages. To assess changes in functional diversity, we used multivariate functional dispersion of bird and bat assemblages. To do so, we first calculated distance matrices based on the Gower distances between species based on the combination of all three functional traits. The Gower distance equals the mean character difference across traits after standardization of the trait values by their ranges and has been recommended for calculation of functional diversity metrics based on multiple traits, because it is less sensitive to extreme trait values than the Euclidean distance (Botta-Dukát, 2005). Moreover, the standardization of the trait values by their ranges yields an empirical maximum value of the distance function that equals one (Botta-Dukát, 2005), which allows for a meaningful comparison among taxa with different sets of functional traits. Then, we projected species into a multi-dimensional functional trait space, using a principal coordinates analysis (PCoA, Figure 2). Based on this trait space, we calculated multivariate functional dispersion (functional diversity, hereafter) as the mean abundance-weighted distance of each species in a given community to the abundance-weighted centroid of all species in the respective community (Laliberté & Legendre, 2010). We chose functional dispersion because compared to other measures of functional diversity it is less influenced by extreme values and it is by definition unaffected by species richness (Laliberté & Legendre, 2010). In these calculations, we used the detection frequencies of the bird and bat species on the study sites as species weights.

FIGURE 2 First and second PCoA axes of (a) bird and (b) bat functional trait spaces on Mt. Kilimanjaro, Tanzania. The length and direction of the arrows indicates the correlation of individual traits with the first and second PCoA axes, respectively. The trend surfaces depict the two-dimensional variation of the individual traits across the first two axes of the trait space



To assess changes in the functional composition of the assemblages in relation to biotic and abiotic factors, we calculated community weighted means based on the species scores of the first or second PCoA axes ($CWM_{axis\ 1}$ and $CWM_{axis\ 2}$) of the trait spaces of birds and bats, respectively. By using the species scores on the first and second PCoA axes instead of individual traits, we avoided spurious conclusions due to correlations between traits, because PCoA axes are uncorrelated by definition. In addition, using the first and second PCoA axes in the analyses allowed us to reduce the dimensionality of the data and, consequently, the number of structural equation models in our statistical analyses.

2.8 | Statistical analysis

To test for direct and indirect effects of climate and land use on bird and bat functional diversity and functional composition via vegetation complexity and resource availability, we performed path analyses using structural equation modelling (Rosseel, 2012). To do so, we fitted separate structural equation models for FD, as well as for $CWM_{axis\ 1}$ and $CWM_{axis\ 2}$ of birds and bats, respectively. Our analysis followed a two-step approach (Grace, 2020): First, we defined an a priori conceptual model based on the specific hypothesized causal relationships among variables (Grace, 2020). Then, we used a stepwise model simplification to identify the most parsimonious model that is plausible given the hypothesized causal structure. In the a priori model, we treated mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm/yr) and land use (LU, binary variable) as exogenous predictor variables (Figure 1c). We treated vegetation complexity and resource availability, as well as measures of bird and bat functional diversity (FD) and functional composition ($CWM_{axis\ 1}$ and $CWM_{axis\ 2}$) as endogenous response variables. The model included all potential direct effects of MAT, MAP and LU on vegetation complexity and resource availability, as well as on FD, $CWM_{axis\ 1}$ and $CWM_{axis\ 2}$ of birds and bats, respectively. Moreover, the models included the effects of vegetation complexity and resource availability on FD, $CWM_{axis\ 1}$ and $CWM_{axis\ 2}$ of birds and bats, respectively. We also included a covariance term between vegetation complexity and

resource availability to account for correlated errors due to common unmeasured sources of variance.

We first assessed whether the a priori models were in agreement with the observed covariance structure in the data using the χ^2 -statistic, SRMR, GFI and CFI indices (a model was accepted if the χ^2 -test was non-significant; if GFI and CFI had values greater than 0.90; and if SRMR had a value of less than 0.08) (Grace, 2020; Rosseel, 2012). Then, we simplified the models using a backward stepwise selection procedure (Grace, 2020). At each step of the backward selection, we removed one path at a time, assessed the change in Bayesian Information Criterion (ΔBIC) and deleted the path that led to the greatest improvement in BIC. We continued the backward procedure until the deletion of paths caused no further improvement in BIC. We also assessed whether the simplified path models were still in agreement with the covariance structure in the data using the χ^2 -statistic (Grace, 2020). Because for most response variables there was no single best model, we calculated the BIC weights for all models considered during the stepwise simplification and calculated average path coefficients and unconditional 95% confidence intervals across those models in the 95% confidence set (those models that together accounted for at least 95% of the BIC weight) (Lukacs et al., 2010). We present path models based on the model-averaged path coefficients (Table S2). We used the model-averaged path coefficients to quantify the total effects of the biotic and abiotic factors (i.e. the sum of direct and indirect effects), to compare the direction and magnitude of effect sizes between predictors and between the two taxa.

All analyses were performed in R version 4.0.3 (R Development Core Team, 2020), using the packages *FD* version 1.0-12 (Laliberté & Legendre, 2010; Laliberté et al., 2014), *vegan* version 2.5-7 (Oksanen et al., 2020), *ade4* version 1.7-16 (Thioulouse et al., 2018), *lavaan* version 0.6-7 (Rosseel, 2012) and *qgraph* version 1.6.5 (Epskamp et al., 2012).

3 | RESULTS

The study plots with at least one detected bird or bat species covered an elevational gradient of 869–3892 m a.s.l., a temperature gradient

of 5.3–24.8°C and a precipitation gradient of 588–2552 mm/year (Figure 1b). Mean annual temperature decreases quasi-linearly with elevation, whereas mean annual precipitation shows a hump-shaped pattern with a peak at about 2,200 m a.s.l. (Figure 1b). Likewise, vegetation complexity and resource availability showed hump-shaped patterns along the elevational gradient with peaks between 2000 and 2,500 m a.s.l. (Fig. S1).

A total of 185 species of birds were recorded, and echolocation calls of bats were categorized into 20 distinct sonotypes. The multivariate trait spaces of both taxa revealed very similar structures (Table 1; Figure 2). For birds, the first axis explained 41% of the variation and was mainly related to variation in body mass ($r^2 = 0.83$, $p < .001$) and wing shape ($r^2 = 0.42$, $p < .001$), whereas the second axis explained 23% and was mainly related to variation in bill shape ($r^2 = 0.83$, $p < .001$; Figure 2a). Similarly, for bats, the first axis explained 51% of the variation and was mainly related to variation in body mass ($r^2 = 0.78$, $p < .001$) and wing shape ($r^2 = 0.72$, $p < .001$), whereas the second axis explained 30% and was mainly related to variation in mouth shape ($r^2 = 0.89$, $p < .001$; Figure 2b). While

functional diversity of both birds and bats declined with increasing elevation, functional composition in body mass and wing shape ($CWM_{axis\ 1}$), as well as in bill and mouth shape ($CWM_{axis\ 2}$), showed distinct elevational patterns in the two taxonomic groups (Fig. S2).

The structural equation models revealed that the functional diversity of birds and bats was strongly positively and directly related to mean annual temperature and resource availability (Figure 3). In addition, mean annual temperature and precipitation increased the functional diversity of both groups indirectly via their effects on resource availability (Figure 3). This indicates that the functional diversity of bird and bat assemblages was higher in warmer and wetter environments with higher resource availability than in cold and arid environments with low resource availability.

The community weighted means of the first dimension of the trait space related to body mass and wing shape ($CWM_{axis\ 1}$) increased with mean annual temperature in birds, but decreased with mean annual temperature in bats (Figure 4a,b). These results indicate that the functional composition of bird assemblages shifted towards larger species with more pointed wings in warm environments, whereas the opposite was the case for bats. In addition, bat

| Trait | PCoA Axis 1 | | PCoA Axis 2 | | PCoA Axes 1 & 2 | |
|-----------------|-------------|-------|-------------|-------|-----------------|-------|
| | r^2 | p | r^2 | p | r^2 | p |
| (a) Birds | 0.41 | | 0.23 | | 0.64 | |
| Body mass | 0.83 | 0.001 | 0.084 | 0.001 | 0.91 | 0.001 |
| Bill index | 0.055 | 0.003 | 0.83 | 0.001 | 0.89 | 0.001 |
| Hand-wing index | 0.42 | 0.001 | 0.079 | 0.001 | 0.50 | 0.001 |
| (b) Bats | 0.51 | | 0.30 | | 0.81 | |
| Body mass | 0.78 | 0.001 | 0.072 | 0.25 | 0.85 | 0.001 |
| Gape index | 0.041 | 0.38 | 0.89 | 0.001 | 0.93 | 0.001 |
| Hand-wing index | 0.72 | 0.001 | 0.20 | 0.042 | 0.92 | 0.001 |

TABLE 1 Correlations of functional traits with the first and second PCoA axes of the (a) bird and (b) bat trait spaces. The strength of the associations is given as r^2 . p -values are based on $n = 999$ permutations of the trait data. The uppermost r^2 -values in each column for birds and bats indicate the percentage of variation in the trait space that is associated with each of the PCoA axes

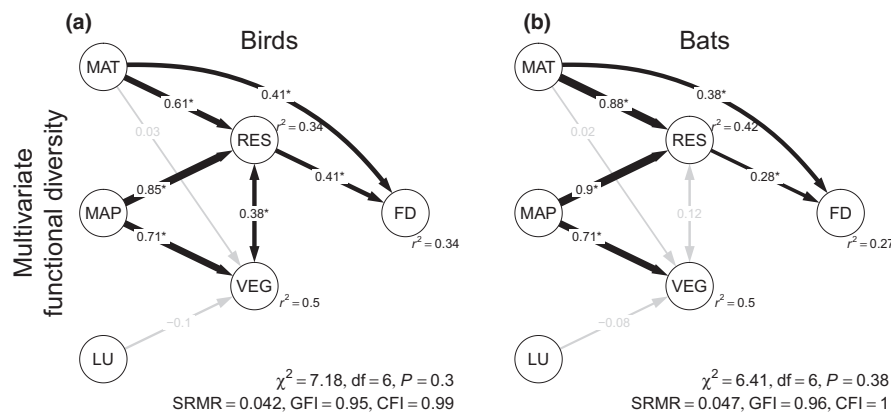


FIGURE 3 Model-averaged path models for multivariate FD of (a) birds and (b) bats. Presented are standardized and model-averaged path coefficients, r^2 -values for endogenous variables, and fit indices, summarizing the fit of the path models to the observed variance–covariance matrix. Paths for which the 95% confidence interval of the path coefficient did not include zero are shown in black and coefficients highlighted with an asterisk, whereas paths for which the 95% confidence interval included zero are shown in grey. Abbreviations for variables are MAT, mean annual temperature; MAP, mean annual precipitation; LU, land use; RES, resource availability; VEG, vegetation complexity; FD, functional diversity. Abbreviations for fit indices are SRMR, Standardized Root Mean Square Residual; GFI, Goodness of Fit Index; CFI, Comparative Fit Index. Note that both models fit the observed variance–covariance matrix

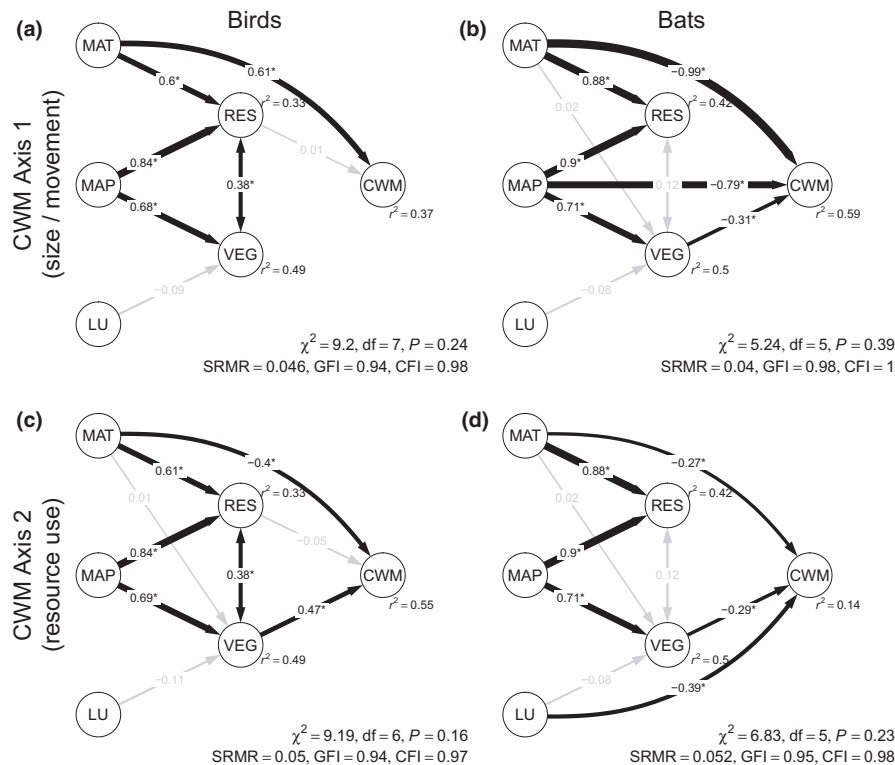


FIGURE 4 Model-averaged path models for (a,b) CWM based on PCoA axis 1 and (c,d) CWM based on PCoA axis 2 of the (a,c) bird and (b,d) bat trait spaces, respectively. Presented are standardized and model-averaged path coefficients, r^2 -values for endogenous variables, and fit indices, summarizing the fit of the path models to the observed variance-covariance matrix. Paths for which the 95% confidence interval of the path coefficient did not include zero are shown in black and coefficients highlighted with an asterisk, whereas paths for which the 95% confidence interval included zero are shown in grey. Abbreviations for variables are MAT, mean annual temperature; MAP, mean annual precipitation; LU, land use; RES, resource availability; VEG, vegetation complexity; FD, functional diversity; CWM, community weighted mean. Abbreviations for fit indices are SRMR, Standardized Root Mean Square Residual; GFI, Goodness of Fit Index; CFI, Comparative Fit Index. Note that all models fit the observed variance-covariance matrix

assemblages in environments with high precipitation and vegetation complexity were composed of smaller species with more rounded wings (Figure 4b).

The community weighted mean of the second dimension of the trait space related to bill shape ($CWM_{axis\ 2}$) decreased with increasing temperature and increased with vegetation complexity in birds (Figure 4c). This indicates that the functional composition of bird assemblages shifted towards species with long and narrow bills in cold environments and in closed vegetation. For bats, the community weighted mean in the second dimension related to mouth shape decreased with increasing temperature and vegetation complexity (Figure 4d). This indicates that bat assemblages in cold environments and open vegetation were composed of species with long jaws and narrow gapes. In addition, for bats we detected a direct negative effect of land use on the community weighted mean in the second dimension (Figure 4d), indicating that bat assemblages in anthropogenic habitats were composed of species with shorter jaws and wider gapes than those in near-natural habitats.

Overall, the structural equation models indicated that mean annual temperature had the strongest effects on the functional diversity and composition of bird and bat assemblages, followed by resource availability, mean annual precipitation and vegetation

complexity (Figure 5). Thereby, mean annual temperature was directly related to the functional diversity of bird and bat assemblages, and together with mean annual precipitation affected functional diversity indirectly via resource availability. Among biotic drivers, resource availability was more strongly related to functional diversity than to functional composition, whereas vegetation complexity was more strongly related to functional composition than to functional diversity (Figure 5). Strikingly, the directions of the effects of biotic and abiotic factors on functional diversity were highly consistent between birds and bats (Figure 5a), whereas the directions of the effects on functional composition differed between both taxonomic groups (Figure 5b,c).

4 | DISCUSSION

Our study provides a comparative cross-taxon analysis of functional diversity and functional composition of bird and bat assemblages along a tropical elevational gradient. Our results reveal strikingly similar responses of the functional diversity of bird and bat assemblages to abiotic and biotic factors on Mt. Kilimanjaro, whereas the functional composition of bird and bat assemblages

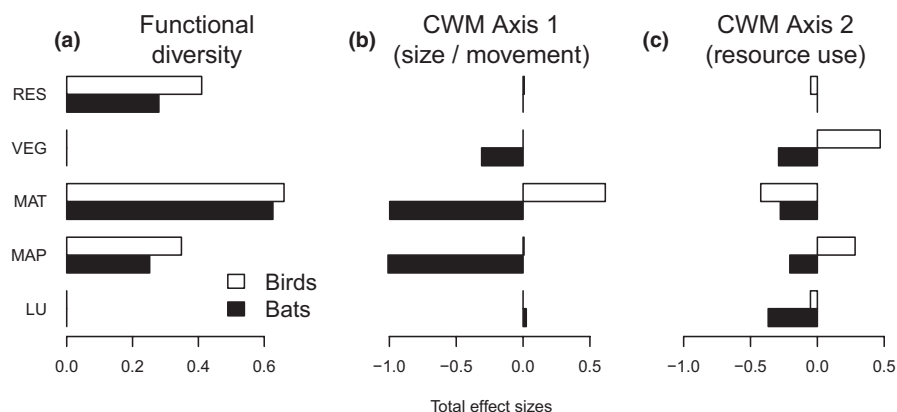


FIGURE 5 Direction and magnitude of total effects size of each predictor variable in explaining the functional diversity (a) and CWMs based on PCoA axis 1 (b) and 2 (c) of the bird and bat trait spaces, respectively. The total effect is measured as the sum of the direct and indirect effects of a given predictor variable. Abbreviations for variables are MAT, mean annual temperature; MAP, mean annual precipitation; LU, land use; RES, resource availability; VEG, vegetation complexity

showed contrasting responses. For both groups, direct temperature effects were most important in shaping functional diversity and composition, followed by resource availability, precipitation and vegetation complexity. Thus, our analysis shows how trait-based approaches can be used to identify generalities and idiosyncrasies in the drivers of functional diversity for taxa with distinct evolutionary histories.

We found that the functional diversity of bird and bat assemblages increased with mean annual temperature. The temperature gradient covered by the study sites ranged from 24.8°C at the base of the mountain to 5.3°C at the highest elevations. The direct effect of temperature on functional diversity can at least partly be explained as a consequence of the effects of environmental filtering due to low temperatures at high elevations (Currie et al., 2004; McCain, 2007, 2009; Montaña-Centellas et al., 2020). Accordingly, lower functional diversity at high elevations might result from a loss of species due to environmental filtering preventing species that cannot persist in or colonize these thermally extreme environments (Hoiss et al., 2012; Montaña-Centellas et al., 2020). Direct effects of ambient temperature on diversity have been hypothesized to be more important for plants and ectothermic animals than for endothermic animals like birds and mammals (Buckley et al., 2012; McCain, 2007, 2009). However, previous work has also shown that energy expenditure in endotherms is strongly linked to ambient temperature and increases in colder environments because the energetic costs for maintaining basal metabolism increase (Anderson & Jetz, 2005). Higher temperatures at lower elevations may therefore release animal communities from energetic constraints and might allow for a wider range of metabolic and morphological niches (e.g. in terms of body mass; Anderson & Jetz, 2005). This might particularly apply to endotherms in tropical lowland ecosystems that are adapted to warm temperatures (Fristoe et al., 2015; Londoño et al., 2017). This idea is supported by the fact that functional and phylogenetic diversity of bird assemblages decline more strongly with increasing elevation in tropical than in temperate elevational gradients (Montaña-Centellas et al., 2020). Overall, our results support the “physiological tolerance hypothesis” for birds and bats and indicate a key role of temperature in filtering trait variation in flying vertebrate assemblages along broad climatic gradients.

We also found consistent indirect effects of mean annual temperature and precipitation on the functional diversity of bird and bat assemblages that were mediated by increased resource availability in more favourable climatic conditions (i.e. warm and wet environments). In particular, we found a consistent increase in the functional diversity of bird and bat assemblages with resource availability along the elevational gradient. The increase in functional diversity with resource availability is in line with previous work on different facets of bird diversity on Mt. Kilimanjaro and in the Ecuadorian Andes (Ferber et al., 2014; Hanz et al., 2019). Our findings generalize the results of these previous studies by including a broader range of ecosystems and by increasing the taxonomic scope. The effect of resource availability suggests that, apart from the direct effects of ambient temperature, differences in resource availability constrain the functional diversity along the elevational gradient. Therefore, our findings support the “resource availability hypothesis” (Davies et al., 2007; Jetz et al., 2009), which assumes that the diversity of a specific trophic level is limited by the amount of energy provided by lower trophic levels (i.e. availability of fruits, nectar and invertebrates for birds and availability of invertebrates for insectivorous bats). Overall, our findings suggest that the interplay of climatic conditions and resource availability play a key role in shaping the functional diversity of birds and bats along broad elevational gradients. The increase of functional diversity with ambient temperature and resource availability suggests that the niche space (i.e. variation in body size, bill shape and wing shape) within the assemblages of both taxa expands and the abundance of functionally distinct species increases under favourable conditions that allow for a wider range of functional strategies.

The path analyses revealed distinct responses of birds and bats with respect to changes in functional composition along the elevational gradient. In birds, warmer temperatures were associated with a compositional shift towards larger species with more pointed wings. The decrease in bird body mass in response to decreasing temperature is consistent with previous work on Bornean bird assemblages (Boyce et al., 2019). Similar patterns have also been observed in ectotherms (e.g. bees; Classen et al., 2017), and have been attributed to energy-based community assembly rules, which predict declines of large-bodied species with high metabolic demands in

energy-limited cold environments, such as at high elevations (Brown et al., 2004; Damuth, 1981). This might be especially true for tropical birds, which are adapted to warm temperatures (Fristoe et al., 2015). An alternative explanation might be reduced flight performance due to lower air pressure at higher elevations, which would favour smaller bird species with a lower wing load (Altshuler, 2006; Segre et al., 2016). Yet, these explanations seem to not be applicable to bats, which showed more complex relationships with their environment. In bats, warmer temperatures, higher precipitation and increased vegetation complexity were associated with a compositional shift towards smaller species with more rounded wings. Consistent with these results, previous work has shown that forest dwelling bats are smaller and have more rounded wings (Blakey et al., 2019; Findley et al., 1972). Moreover, small bats may have advantages in environments with high precipitation, because rain imposes additional energetic costs on bat flight due to higher thermoregulatory costs and lowered aerodynamic properties, especially for large species (Voigt et al., 2011). The differences in the responses of birds and bats to temperature might further be related to differences in their reproductive biology, because breeding birds are typically more exposed to variation in ambient temperature than cavity-roosting bats (Carroll et al., 2018; Du et al., 2019; Rodriguez-Durán & Soto-Centeno, 2003; Wang et al., 2020). Together, our results reveal that multiple factors related to abiotic conditions and habitat structure affect the functional composition of bat assemblages in terms of body size and wing shape, whereas in birds these traits seem to be mainly constrained by temperature.

The path analyses also showed differential responses of birds and bats with respect to changes in the functional composition of foraging related traits. The composition of bird assemblages shifted towards species with long and narrow bills in colder environments and more closed vegetation at mid and high elevations. This suggests a shift towards more insectivorous and nectarivorous species (Carnicer et al., 2008; Felice et al., 2019) and may at least partly be explained by shifts in the abundance of invertebrates as well as flowering and fruiting plants along the elevational gradient (e.g. Ferger et al., 2014). The composition of bat assemblages shifted towards species with long jaws and narrow gapes in colder environments and in habitats characterized by more open vegetation. These changes in the composition of bat assemblages are most likely related to different foraging behaviour and echolocation strategies in bats associated with open and closed vegetation, respectively (Aldridge & Rautenbach, 1987; Arbour et al., 2019). Therefore, distinct mechanisms drive changes in the functional composition of these traits related to differences in resources use of bird and bat assemblages along broad elevational gradients.

In contrast to previous meta-analyses (Farneda et al., 2020; Matuoka et al., 2020), we found no consistent direct or indirect effects of land-use intensity on the functional diversity of bird and bat assemblages. Nonetheless, our results are consistent with previous studies on Mt. Kilimanjaro, which found only weak or no effects of land use on the functional diversity of different taxonomic groups including birds, plants and insects (Albrecht et al., 2018;

Classen et al., 2015; Schellenberger Costa et al., 2017). The lack of land-use effects might be explained by the fact that human disturbance of ecosystems on Mt. Kilimanjaro is moderate, because agriculture mainly consists of small-scale subsistence farming with high levels of semi-natural habitats on or around crop fields. The small field sizes and the diversity of different cropping systems result in a mosaic-like heterogeneous landscape in the study area. Yet, particular feeding guilds appear to be more sensitive to land use than others (e.g. frugivorous birds; Vollstädt et al., 2017). Such differences could explain the direct effect of land use on the second trait axis related to resource use in bats. The observed functional shift in skull morphology between natural and anthropogenic habitats might be driven by changes in the species composition of available prey, because skull morphology is related to diet and foraging behaviour in bats (Arbour et al., 2019; Dumont, 2007). In general, small-scale farming seems to currently support a high functional diversity of birds and bats on Mt. Kilimanjaro. However, given the relatively low levels of land-use intensity, it is difficult to anticipate the potential effects of future land-use intensification on the functional diversity and composition of bird and bat assemblages on Mt. Kilimanjaro.

In conclusion, our results show that climate and resource availability shape the functional diversity of bird and bat assemblages in similar ways, even though the functional composition of both taxonomic groups is shaped by distinct abiotic and biotic factors and mechanisms. Therefore, our study illustrates that distinct filtering mechanisms can result in similar patterns of functional diversity of different animal taxa along broad environmental gradients. In the context of global change, our results imply that climate warming and land-use driven changes in resource availability and vegetation structure are likely to alter patterns of functional diversity and composition of flying vertebrates on tropical mountains. Our results highlight that conservation strategies need to account for taxon-specific responses to climate and habitat structure, even in taxa that fulfil similar functional roles in ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.


PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13403>.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available in *figshare* (Byamungu et al., 2021) with the identifier <https://doi.org/10.6084/m9.figshare.14958312>.

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BIOSKETCH

Robert M. Byamungu is a scholar with a comprehensive teaching and research experience in the fields of ornithology and biodiversity conservation. Recently, he has a growing interest in the conservation of vertebrate pollinators and seed dispersers, particularly on investigating the effects of climate and land use on functional diversity of birds and bats.

Author Contributions: RMB, MS, MT and JA conceived the study. RMB measured bat specimen, AN measured bird specimen. MHB collected acoustic data on bats, SWF collected bird, vegetation and resource data. RMB and JA performed data analysis, in consultation with MS. RMB wrote the first draft of the manuscript with contributions from JA, MS and MT. All authors made inputs on the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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