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LETTER

Global functional and phylogenetic structure of avian assemblages across elevation and latitude

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Abstract

Mountain systems are exceptionally species rich, yet the associated elevational gradients in functional and phylogenetic diversity and their consistency across latitude remain little understood. Here, we document how avian functional and phylogenetic diversity and structure vary along all major elevational gradients worldwide and uncover strong latitudinal differences. Assemblages in warm tropical lowlands and cold temperate highlands are marked by high functional overdispersion and distinctiveness, whereas tropical highlands and temperate lowlands appear strongly functionally clustered and redundant. We additionally find strong geographic variation in the interplay of phylogenetic and functional structure, with strongest deviations between the two in temperate highlands. This latitudinal and elevational variation in assemblage functional structure is underpinned by nuanced shifts in the position, shape and composition of multivariate trait space. We find that, independent of latitude, high-elevation assemblages emerge as exceptionally susceptible to functional change.

Keywords

Biodiversity, birds, elevational gradient, functional diversity, latitudinal gradient, phylogenetic diversity, traits.

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INTRODUCTION

Species, and the communities they form, convey a range of functions to ecosystems and humans that are now under increasing threat from global change (Díaz *et al*., 2019). Mountain systems harbour exceptionally high biodiversity, but the lack of truly global characterisations of functional diversity along elevation for different taxonomic groups hinders understanding of potential ecosystem-level consequences of biodiversity loss for mountainous ecosystems. Spatially restricted transect-level studies (Graham *et al*., 2009; Machac *et al*., 2011; Pigot *et al*., 2016; He *et al*., 2018) suggest that lowlands tend to harbour more functional diversity than their species richness would suggest, resulting in functional overdispersion among community members. Correspondingly, functional diversity in the highlands has been suggested to decline below the levels suggested by species richness, resulting in trait similarity (i.e. functional clustering; Sydenham *et al*., 2015; Xu *et al*., 2017; He *et al*., 2018). Consensus about the generality of these patterns, however, remains elusive and variation among mountain ranges and hemispheres has been reported (Montaño-Centellas *et al*., 2020). With ca. extant 10 000 species, enormous ecological variation (Kissling *et al*., 2012; Pigot *et al*., 2020; Tobias *et al*., 2020), worldwide distribution across mountain systems (McCain, 2009; Quintero and Jetz, 2018) and available species-level phylogenetic and trait information (Jetz *et al*., 2012; Wilman *et al*., 2014), birds offer an excellent and unique system for a comprehensive assessment of elevational gradients in functional diversity.

Spatial non-stationarity in elevational gradients of functional diversity and structure is expected to emerge from diverse historical, ecological and evolutionary processes (Mittelbach *et al*., 2007), themselves spatially varying. For example, higher-temperature overlap along elevation in temperate regions is thought to select for species with wider thermal breaths (and thus elevational ranges), facilitating dispersal across mountain passes (Janzen, 1967) and contributing to strong spatial variation in elevational gradients of species richness. Evidence for the correlation of avian thermal limits with their habitat (Barnagaud *et al*., 2012) and dietary (Rapacciuolo *et al*., 2017) breadths further suggests that high-latitude mountain regions might be predominantly characterised by functional clustering in comparison with their tropical counterparts. Additionally, competition is thought to limit species' ranges at low elevations and low latitudes (e.g. Hargreaves *et al*., 2014; Louthan *et al*., 2015; Rohwer *et al*., 2015, but see Freeman, 2020), potentially resulting in least pronounced patterns of trait overdispersion in temperate and boreal highlands (but see Mayfield and Levine, 2010). Initial evidence from select elevational transects, however, suggests a weak impact

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of latitude on elevational gradients in avian functional structure, with tropical mountain systems seeing only slightly stronger transitions from functional overdispersion to clustering towards high elevations (Montaño-Centellas *et al*., 2020).

Assemblage functional structure is frequently assessed with multiple traits collapsed into a single metric of functional diversity (e.g. Petchey and Gaston, 2006; Villéger *et al*., 2008; Laliberté and Legendre, 2010; Blonder *et al*., 2014), which ignores the potential lack of uniformity in contributions of individual species to assemblage functional diversity. For example, rare species contribute disproportionately to assemblage functional structure (Mouillot *et al*., 2013; Leitão *et al*., 2016). Metrics designed to capture such uneven species influences can offer important nuances in global studies, particularly as, e.g. the contribution of rare species to bird diversity patterns is spatially non-stationary (Lennon *et al*., 2004), with low-latitude mountainous areas showing relatively high proportions of range-restricted species (Orme *et al*., 2006). A combination of metrics may, thus, be required to robustly illuminate functional variation along latitudinal and elevational gradients.

Under the assumption that species' traits result from their shared evolutionary history, patterns of phylogenetic structure have often served as a substitute for functional structure, particularly at large spatial and taxonomic scales (Devictor *et al*., 2010; Graham *et al*., 2012; Gerhold *et al*., 2015; Mazel *et al*., 2018). To date, however, the co-variation of these two biodiversity dimensions across elevations and the global latitudinal uniformity of this relationship has remained unelucidated. Deviations of functional from phylogenetic structure are likely to occur in birds because avian traits show pervasive convergent evolution (Pigot *et al*., 2020), with several morphological trait combinations (Pigot *et al*., 2020) and dietary characteristics (Kissling *et al*., 2012) having multiple origins within the clade. Dietary traits also show differential associations with phylogenetic structure (Barnagaud *et al*., 2019), with nectarivory, frugivory and insectivory being associated with phylogenetic overdispersion, while carnivory being phylogenetically clustered (Barnagaud *et al*., 2014), although it is unknown whether these traits show similar relationships with functional structure. Evaluating the association between functional and phylogenetic structure on a global scale, and potential factors in its variation, can help assess their surrogacy for basic and applied questions and hint at ecological and evolutionary causes of assemblage composition (Devictor *et al*., 2010; Graham *et al*., 2012; Gerhold *et al*., 2015; Mazel *et al*., 2018, but see Mayfield and Levine, 2010; Cadotte and Tucker, 2017).

Finally, we recognise a strong need to unpack how individual traits combine to generate patterns of functional diversity and structure. Any variation in assemblage functional structure is ultimately underpinned by how species and their traits are sorted along elevational and latitudinal gradients. Furthermore, individual traits often link to different ecological functions and opposing niche axes (Violle *et al*., 2007; Bernard-Verdier *et al*., 2012; Spasojevic and Suding, 2012) and can show disparate environmental associations (Weiher *et al*., 2011). Isolating the variation in single traits along gradients can help identify particularly relevant niche axes (Spasojevic and Suding, 2012), pinpoint those most strongly contributing to spatial variation in elevational gradients in functional diversity and identify traits underlying the strength of the surrogacy of phylogenetic for functional structure. Traits such as diet, foraging behaviour and body mass play a central role in resource acquisition and interspecific competition (Burin *et al*., 2016) and facilitate the diversification of clades (de Queiroz, 2002; Grant and Grant, 2006; Losos and Ricklefs, 2009), and are thus particularly crucial to understanding patterns of species co-existence.

Here, we provide a comprehensive evaluation of global variation in both functional and phylogenetic diversity of extant birds. This is enabled by extensive trait data (Wilman *et al*., 2014), a time-calibrated phylogeny (Jetz *et al*., 2012) and elevational distributions (Quintero and Jetz, 2018) addressing nearly all extant bird species across all of the world's main mountain regions replicated along latitude. We consider 8410 bird assemblages spanning the globe and an elevational range from sea level to 7340m, measured at 110km lateral and 500m elevational spatial grain. We use this unique coverage to test how elevational gradients in functional and phylogenetic structure vary along latitude, from warm and stable to cold and highly seasonal conditions. We predict strong latitudinal variation in elevational gradients in avian functional structure, with temperate and boreal mountain systems seeing weaker transitions from functional overdispersion to clustering towards high elevations. Our study does not suffer from biases often associated with local, transect-based elevational studies such as variation in sampling effort or sample size (Quintero and Jetz, 2018), and offers, to our knowledge, the first, truly comparative and global characterisation of the functional and phylogenetic assemblage structure along the world's most defining geographic gradients.

MATERIALS AND METHODS

Mountain systems, geographic and elevational distributions and biodiversity sampling

We used 46 broad-scale mountain regions delineated by the Global Mountain Biodiversity Assessment (GMBA, http://www.mountainbiodiversity.org). Data on breeding distributions for 9993 species were compiled from the best available sources for a given broad geographical region or taxonomic group (for individual expert range maps, see Map of Life at https://mol.org). The database of bird elevational ranges was compiled by Quintero and Jetz (2018) at 500 m elevational grain (data available at https://mol.org/downloads/). We used a total of 8410 assemblages (point locations) containing 8470 species within our delimited mountain systems (median = 71 assemblages/mountain region), sampled by Quintero and Jetz (2018) (https://mol.org/downloads/). The assumed accuracy of our species range data was 110-km lateral and 500-m elevational. While admittedly coarse-scale and solely presence-absence, the combination of distributional and elevational data used here comprises the best current understanding of bird distributions at the global scale. For details on biodiversity data and sampling procedure, see Supplementary Materials.

Avian phylogenetic and functional diversity, and trait space

For each assemblage, we calculated avian dendrogram-based functional diversity (FD; Petchey and Gaston, 2006). We based estimates of FD on a compilation of function-relevant (i.e. reflecting species' functional role in an ecosystem; Kissling *et al.*, 2012; Junker *et al.*, 2019) traits in Wilman *et al.* (2014), with four trait categories: body mass, nocturnality, diet and foraging niche. Diet and foraging niche categories included seven axes each: proportions of invertebrates, vertebrates, carrion, fruits, nectar and pollen, seeds and other plant materials in species' diet (diet); proportional use of water below surface, water around surface, terrestrial ground level, understory, mid canopy, upper canopy and aerial (foraging niche). Following existing practice (Pavoine *et al.*, 2009; Jarzyna and Jetz, 2017), we calculated multivariate trait dissimilarity using Gower's distance for each pairwise combination of all 9,993 species in the dataset. Equal weights were given to each of the trait categories and to each axis within trait categories (i.e. each diet and foraging niche axis was given a 1/7 weight for a total weight of 1 for diet and foraging niche categories, body mass and nocturnality were given a weight of 1). Gower's distance can handle quantitative, semi-quantitative and qualitative variables and assign different weights to individual traits (Pavoine *et al.*, 2009). The functional dendrogram was built using UPGMA clustering, which ensures most faithful preservation of the original distances in the dissimilarity matrix (Mérigot *et al.*, 2010). For each point location, the functional dendrogram was pruned of the branches for species absent at that location and FD was calculated as a sum of branch lengths of such local functional dendrogram. Because using a dendrogram-based approach might in some cases artificially increase the functional distance between species that have similar trait values, we quantified the mean squared deviation (mSD) to assess the congruence between the functional distance as given by Gower's metric and the cophenetic distance on the functional dendrogram (Maire *et al.*, 2015; Villéger et al. 2017). mSD equalled to 0.001, suggesting the average absolute deviation between Gower's and the dendrogram-based distances of approximately 1%. The correlation between Gower's distance matrix and the distance matrix based on functional dendrogram equalled to 0.92, further indicating minimal loss of information. To ensure that our choice of the clustering algorithm did not significantly alter the inferences (Villéger *et al.*, 2008), we further quantified functional diversity as the assemblage trait volume (FD_H), using the expectation hypervolume corresponding to a convex hull metric quantified with *expectation_convex* function in the *hypervolume* package v2.0.11 (see Supplementary Material for details; Blonder *et al.*, 2014).

We used the same local functional dendrogram to quantify the assemblage mean (FDI_{avg}) and skewness (FDI_{skew}) of species' local functional distinctiveness (FDI). FDI was calculated as the fair proportion branch length of the branches in a local functional dendrogram leading to a species tip. FDI measures the distinctiveness of a species functional characteristics in the context of all species of that assemblage and, as such, decomposes overall FD into individual species contributions. FDI is equivalent to species evolutionary distinctiveness as calculated for a local tree (Redding and Mooers, 2006). FDI_{avg} measures the average functional distinctiveness of a species in an assemblage; high FDI_{avg} indicates an assemblage comprised of on average functionally distinct species. Skewness of species' local functional distinctiveness values, FDI_{skew}, is a measure of symmetry of the distribution of FDI values and measures whether individual species contribute uniformly or unevenly to overall FD (low and high FDI_{skew} respectively). The three metrics of functional diversity—FD, FDI_{avg} and FDI_{skew}—provide complementary information on avian community composition: FD measures overall functional diversity of an assemblage, FDI_{avg} measures species average contributions to FD and FDI_{skew} measures whether species contributions are uniformly (all species are equally distinct) or unevenly (some species are more distinct than others) distributed. We used R package *moments* (https://cran.r-project.org/web/packages/moments/index.html) to calculate skewness. We did not find strong deviations between FDI_{avg} and other commonly used metric of functional distinctiveness—i.e. mean pair-wise distance (MPD; Violle *et al.*, 2017)—for a subset of mountain ranges (Fig. S1).

To calculate dendrogram-based phylogenetic diversity (PD; Faith, 1992), we used 20 trees sampled from full pseudo-posterior distribution of phylogenetic trees assembled by Jetz *et al.* (2012). PD was calculated as the total branch length of the phylogenetic tree averaged over 20 phylogenetic trees. 20 trees provide a sufficiently strong estimate (Schipper *et al.*, 2016).

To further evaluate how assemblage trait volume changes with elevation, we quantified an overlap in trait volume (FD_O) among the point locations falling along the elevational gradient using *hypervolume_overlap_statistics* function in the *hypervolume* package (Blonder *et al.*, 2014). FD_O statistics was quantified using trait volumes, FD_H. For each point at elevation a, we selected the geographically closest point that lies within (a + 500m, za + 1000m) elevational region. Because we wanted to evaluate changes in trait volume along elevation rather than changes that might arise from geographic distance, we excluded all pairs of points that were geographically farther apart than 500km. For each pair of points, we quantified trait volume overlap using Sørensen (FD_O) and Simpson's (FD_T) similarity and unique fractions of trait volume for points at lower (FD_{Ul}) and higher (FD_{Uh}) elevation (Blonder *et al.*, 2014). FD_T measures the component of FD_O that results from true species turnover, rather than changes in species richness (i.e. nestedness *sensu* Baselga, 2010). FD_T was derived from FD_{Ul} and FD_{Uh} and equalled to the intersection of FD_{Ul} and FD_{Uh} divided by trait volume of the assemblages with a smaller unique fraction (Baselga, 2010). FD_O, FD_T, FD_{Ul} and FD_{Uh} are beta-diversity metrics which provide information on among-site variation and are, thus, complementary to the alpha-level metrics of FD, FD_H, FDI_{avg} and FDI_{skew}. We conducted sensitivity analysis by repeating the above steps for points falling within (a + 250m, a + 750m) and (a + 750m, a + 1250m), and for pairs of points located geographically not farther than 100 km and 250 km (Fig. S2).

We also assessed assemblage mean of individual components of avian trait volume: dietary and foraging niche, nocturnality and body mass. For each assemblage, we quantified

mean relative proportion (i.e. prevalence) of each axis within the diet and foraging trait categories. Assemblage mean nocturnality was simply the number of nocturnal species per species richness of the local assemblage. To account for the effect of separate mountain ranges, we first assessed individual components of avian trait volume for each mountain range and then averaged those values to obtain a global estimate.

Richness-controlled avian phylogenetic and functional diversity, and trait space

Interpretations of assemblage functional and phylogenetic structure benefit from statistically controlling for the association with species richness (SR). To control for SR, we generated null models for PD, FD, FDI_{avg}, FDI_{skew}, FD_H and individual components of assemblage trait space. Even though FDI values provide estimates of individual species contributions to FD, their assemblage-level means (FDI_{avg}) and skewness (FDI_{skew}) are often closely associated with SR (Jarzyna and Jetz, 2016) and their species richness-controlled equivalents allow more in-depth interpretations of assemblage structure.

We developed the expected values of all metrics by randomly selecting (100 times) species from a regional species pool (i.e. a mountain region), keeping point-level SR constant (Swenson, 2011). We calculated the standardised effect sizes (SES) as the difference between observed values and those expected from the null model, expressed in units standard deviation. SES were considered species richness-controlled equivalents of biodiversity metrics and denoted as cPD, cFD, $cFDI_{avg}$, $cFDI_{skew}$ and cFD_H. Negative and positive values of SES indicated that an observed value was lower and higher, respectively, than the average expected value. Negative and positive values of cPD, cFD, $cFDI_{avg}$ and cFD_H suggested clustering and overdispersion respectively. Negative and positive values of $cFDI_{skew}$ suggested less and more, respectively, even distribution of species functional distinctiveness values.

We futher calculated quantile scores for the observed values of PD, FD, FDI_{avg}, FDI_{skew} and FD_H, and estimated their associated p-values (two-tailed test, $\alpha = 0.05$). The observed values falling outside the 2.5% and 97.5% quantiles of the null distribution were considered statistically significantly lower (clustering) and higher (overdispersion), respectively, than expected given SR. While the quantile scores and the associated p-values remove some of the potential biases resulting from the shape of the null distribution, they also remove information regarding the effect size itself (Swenson, 2011). We, thus, report both the SES and quantile scores with associated *P*-values.

We evaluated how well assemblage functional structure can be predicted by its phylogenetic structure in two ways. First, we tested the relationship between cFD and cPD by using a linear model (eqn 3). To explore influences of latitudinal position on the relationship between cFD and cPD, we included the average absolute latitude of the mountain system as a random effect on the intercept and slope (eqn 5). Second, we assessed the predictive ability of the phylogeny by quantifying the probability (Pr) with which phylogenetic structure predicted functional structure of an assemblage following Bayes theorem,

$$\Pr(\mathrm{cFD}|\mathrm{cPD}) = \frac{\Pr(\mathrm{cPD}|\mathrm{cFD}) \cdot \Pr(\mathrm{cFD})}{\Pr(\mathrm{cPD})} \quad (1)$$

where cFD and cPD indicate functional and phylogenetic structure of an assemblage. We quantified Pr for both designations of overdispersion and clustering: based on SES and based on quantile scores. For example, to assess the SES-based probability of predicting functional clustering given phylogenetic clustering, we followed

$$\Pr(\mathrm{cFD}<0|\mathrm{cPD}<0) = \frac{\Pr(\mathrm{cPD}<0|\mathrm{cFD}<0) \cdot \Pr(\mathrm{cFD}<0)}{\Pr(\mathrm{cPD}<0)} \quad (2)$$

To account for the effect of separate mountain ranges, Pr was averaged per mountain region, and mountain region's central latitude was used to evaluate the latitudinal gradient in Pr.

Global elevational gradients of avian functional, phylogenetic and trait diversity

To explore how all metrics vary with elevation x_i, we used two different models: following a linear relationship,

$$\mu_i = \beta_0 + \beta_1 x_i \quad (3)$$

and a quadratic relationship,

$$\mu_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 \quad (4)$$

To estimate a global pattern, we used two-level generalised hierarchical model, in which the parameters for each mountain system came from a multivariate normal distribution (for model details, see Quintero and Jetz, 2018). Log-transformed PD, FD, $FDist_{avg}$, and $FDist_{skew}$, FD_H, as well as cPD, cFD, $cFDI_{avg}$, $cFDI_{skew}$, cFD_H followed a Gaussian distribution $N(\mu_i, \sigma_i^2)$. FD_O, FD_T, FD_{Ul}, FD_{Uh} and individual traits are all bounded by (0,1) and thus followed a beta-distribution $beta(\alpha_i, \beta_i)$; with exception of log-transformed body mass, which followed a Gaussian distribution. All predictors were standardised to have mean of 0 and standard deviation of 1. Each model was fitted in a Bayesian framework using INLA (Rue *et al.*, 2009) through the *R-INLA* package for R v3.4.3 (https://www.r-project.org/). Watanabe–Akaike information criterion (WAIC) was used to select the best fitting model (quadratic or linear). WAIC is preferable to similar alternatives because it averages over the posterior distribution rather than using only point estimates (Gelman *et al.*, 2014). We did not use the coefficient of determination, R^2, to evaluate goodness-of-fit of each model because R^2 does not integrate across the full posterior probability and, thus, ignores uncertainty in parameter estimates.

Latitudinal influences on elevational gradients of avian functional, phylogenetic and trait diversity

To explore influences of latitudinal position on the elevational gradients in all biodiversity metrics, we expanded the global hierarchical model to include average absolute latitude of the mountain system following Quintero and Jetz (2018). Average

latitude y_i was fitted as interaction terms with linear effects of elevation,

$$\mu_i = \beta_0 + \beta_1 x_i + \beta_2 y_i + \beta_3 x_i y_i \quad (5)$$

and with quadratic effects of elevation,

$$\mu_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + \beta_3 y_i + \beta_4 x_i y_i + \beta_5 x_i^2 y_i \quad (6)$$

Lastly, we used the expanded best fitting global model (i.e. one including average latitude as the interaction term) to predict the latitudinal gradients in PD, cPD, FD, cFD, FDI_{avg}, $cFDI_{avg}$, FDI_{skew}, $cFDI_{skew}$, FD_H and cFD_H at different elevational bands. R code is available on GitHub (https://github.com/Jarzyna-Lab/Global-Avian-Assemblage-Structure-Elevation-Latitude).

RESULTS

Functional structure

Globally, absolute dendrogram-based (FD) and hypervolume-based (FD_H) functional diversity peak at ca. 1500–2000 m (Fig. 1a, Figs. S2 and S3, Table S1). Both low and high elevations exhibit functional overdispersion with higher levels of FD and assemblage mean of species' local functional distinctiveness (FDI_{avg}) than their species richness would suggest, as quantified by richness-controlled values—cFD, cFD_H and $cFDI_{avg}$ (Fig. 1b and e, Fig. S4). In contrast, mid elevations are generally more functionally clustered (Fig. 1b and e, Fig. S4). But a strong latitudinal variation in this pattern is evident (Fig. 1, Fig. S3–S5, Table S1). The richness-controlled metrics, cFD, cFD_H and $cFDI_{avg}$, all decline along elevation in the tropics (<23.5°) and sub-tropics (23.5-35°), but increase towards high elevations in temperate regions (>35°; Fig. 1b and e, Figs. S3–S4, Table S1). Accordingly, cFD, cFD_H and $cFDI_{avg}$ decrease with latitude in low-to-mid elevations, but this trend reverses for high elevations (Fig. 1c and f, Figs. S3-S4, Table S1). The distribution of species' local functional contribution, measured by $cFDI_{skew}$, is highly uneven along elevation and latitude, with a small number of species contributing much more functional distinctiveness than the rest in cooler and more seasonal regions (Fig. 1g–i, Figs S3–S4, Table S1). While $cFDI_{skew}$ increases towards higher elevations in the tropics and sub-tropics, the opposite applies to temperate regions (Fig. 1h, Figs S3-S4, Table S1). Consequently, $cFDI_{skew}$ increases from the tropics to the boreal region at low-to-mid elevations (Fig. 1i, Figs. S3–S4, Table S1), but declines at high elevations.

Interaction and surrogacy of phylogenetic and functional structure

Absolute (PD) and richness-controlled (cPD) phylogenetic diversity follow elevational and latitudinal trends broadly similar to those of function (Fig. 1j–l, Fig. S3, Table S1). However, the relationship between cFD and cPD is strongly dependent on latitude (Fig. 2c). In low-latitude regions, strongly phylogenetically clustered or overdispersed assemblages do not always show equally strong functional structuring (Fig. 2c). Towards higher latitudes, functional clustering becomes closely associated with phylogenetic clustering, but this positive relationship does not hold for functional overdispersion (Fig. 2c).

We find that phylogeny provides only a limited proxy for functional structure (Fig. 2c and d, Table S2). In the tropics, phylogenetic structure offers some, but not strong, surrogacy for functionally overdispersed (probability, Pr, of predicting $cFD > 0$ given $cPD > 0$; $Pr = 0.63$) and weak surrogacy for functionally clustered (probability of predicting $cFD < 0$ given $cPD < 0$; $Pr = 0.48$) assemblages (Fig. 2d, Table S2). The predictive power of phylogenetic structure diverges strongly with latitude (Fig. 2d, Table S2), reaching, respectively, $Pr = 0.21$ and $Pr = 0.81$ for functionally overdispersed and clustered assemblages in temperate and boreal regions. This general latitudinal pattern of the predictive ability of the phylogeny is upheld by quantile scores and associated estimated p-values (Fig. S7, Table S3).

Turnover and decomposition of the multivariate trait volume

Globally, the orientation and centroid location of assemblage trait volume vary little up to ca. 3500m elevation, but both shift drastically above that (Fig. 3a and b), suggesting strong among-assemblage trait redundancy from low to mid elevations and increasing distinctiveness above. This is confirmed by the global pattern of overlap in assemblage trait volume, FD_O, whose rapid decline towards high elevations (Fig. 3c) coincides with the global peak in functional clustering (at *c.* 2000 m; Fig. 1). This pattern applies to tropical mountain systems, but is different in temperate and boreal regions where FD_O slightly increases towards higher elevations (Fig. 3c). Simpson's similarity, FD_T, remains high and relatively constant along elevation both globally and in the tropics, but increases slightly in temperate regions (Fig. 3d). Fraction of trait volume unique to lower elevation assemblages, FD_{Ul}, increases strongly with elevation globally and in the tropics, but this increase is less pronounced for temperate and boreal regions (Fig. 3e). Fraction of trait volume unique to higher elevations, FD_{Uh}, declines slightly with elevation globally and in high-latitude regions, but shows a slight humped pattern in the tropics (Fig. 3f).

The elevational and latitudinal variation in avian functional structure and trait volume we uncover is underpinned by an expected variation (Fig. S7) in the prevalence of select traits (Fig. 4, Figs S9 and S10). Certain functional components—e.g. mid- and upper-canopy and open-water foragers—generally decline drastically with increasing elevation (Fig. 4b, Figs. S9 and S10), although this decline is less drastic in temperate regions (Fig. S11). Nocturnal species mostly disappear towards higher elevations (Fig. 4e), with exception of select mountain ranges in highly seasonal environments (Fig. S11), likely as a result of harsher night-time temperatures and decreased daytime competition. The prevalence of birds of prey and granivorous birds holds relatively steady and that of ground foraging birds increases linearly with elevation in temperate and boreal regions, but closer to the equator shows a mid-elevation peak and a steep decline thereafter (Fig. 4d, Figs. S9–S11). The proportion of insectivorous species increases with elevation for some mountain regions in the

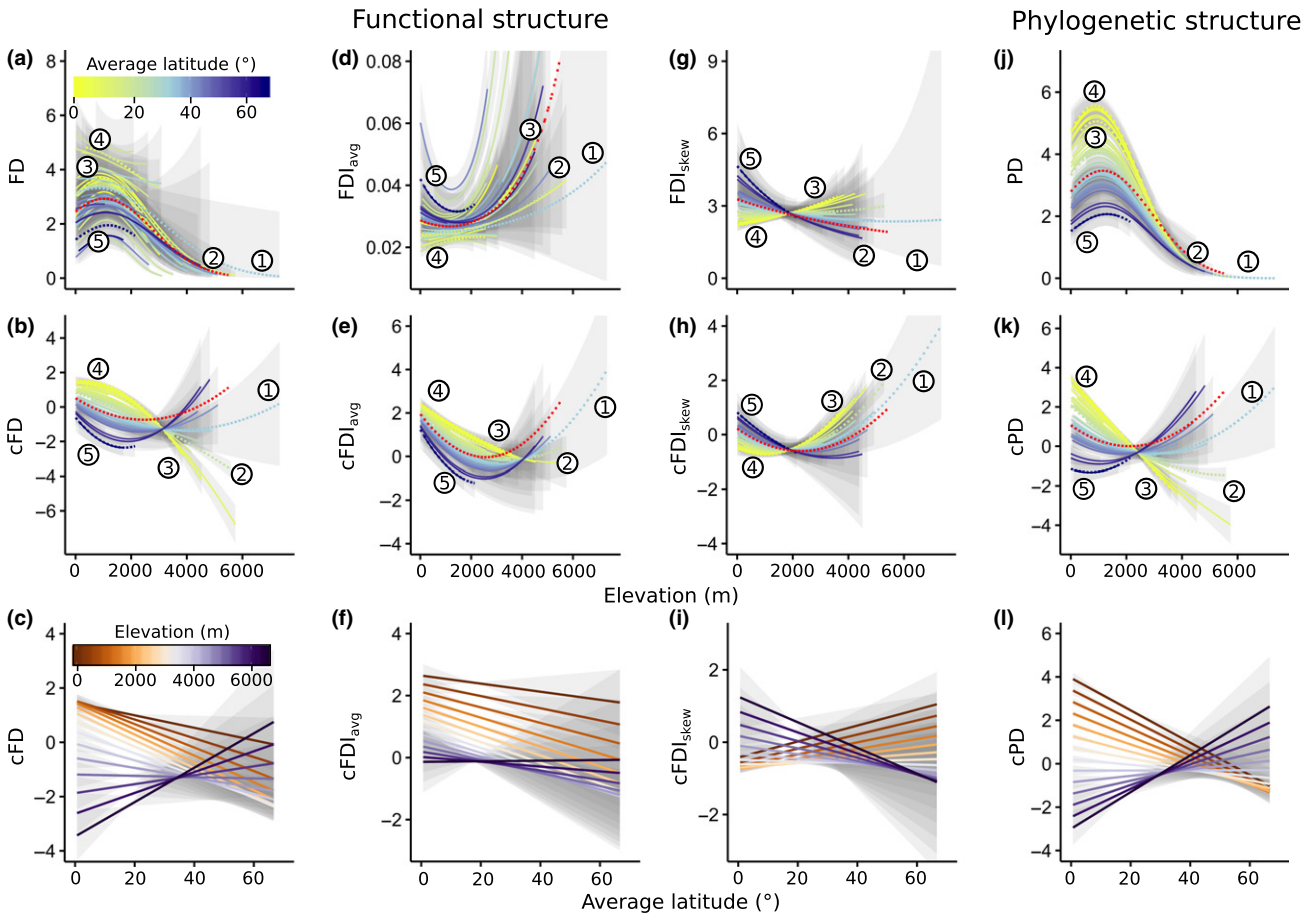

Figure 1 The interaction of central latitude of mountain regions with elevational gradients of avian functional and phylogenetic assemblage structure. Top: Fitted elevational trends for dendrogram-based assemblage functional diversity (FD; a), mean (FDI$_{avg}$; d) and skewness (FDI$_{skew}$; g) of species' local functional distinctiveness, and dendrogram-based assemblage phylogenetic diversity (PD; j). Middle: fitted elevational trends for the species richness-controlled FD (cFD; b), FDI$_{avg}$ (cFDI$_{avg}$; e), FDI$_{skew}$ (cFDI$_{skew}$; h) and PD (cPD; k), measured using standardised effect sizes. Bottom: latitudinal trends for cFD (c), cFDI$_{avg}$ (f), cFDI$_{skew}$ (i) and cPD (l), given by predictions from models in b, e, h and k. Fitted global patterns, with mountain ranges included as random effects in the model, are shown in dashed red line. cFD, cFDI$_{avg}$ and cPD values > 0 and < 0 indicate overdispersion and clustering respectively; cFDI$_{skew}$ values > 0 and < 0 indicate more and less even distribution of species FDI than expected by chance. Values of PD (in MYA) were scaled by 1/1000. Five highlighted in dashed line regions are the Hindukush-Himalaya (1), the Andes (2), the Sumatran Islands (3), the Cameroon Mountains (4) and the Scandinavian Mountains (5) ranges. Grey areas are 95% credible intervals. For details on multi-level models, see Materials and Methods.

tropics, but not in highly seasonal regions, suggestive of lower insect abundance at high elevations there (Fig. 4c). Average assemblage body mass declines from lower to mid elevations and then, at least in higher latitudes, strongly increases towards high elevations (Fig. 4f), consistent with Bergmann's rule type pattern (Blackburn *et al.*, 1999).

DISCUSSION

Our results confirm our expectation of strong latitudinal variation in elevational gradients in functional diversity and structure. Consistent with previous findings (Graham *et al.*, 2009; Machac *et al.*, 2011; He *et al.*, 2018), we find a prominence of functional overdispersion and high functional distinctiveness in more productive and stable environments (i.e. tropical low elevations). Correspondingly, we find that functional clustering dominates in tropical highlands (>1500–2000 m) as well as across most of the elevational gradient in regions characterised by stronger seasonality and freezing temperatures, which mirrors earlier findings (Sydenham *et al.*, 2015; Xu *et al.*, 2017; He *et al.*, 2018). Contrary to our predictions, however, we find increasing functional overdispersion and high functional distinctiveness in temperate and boreal highlands (> *c.* 2000 m), which is consistent with findings of functional overdispersion at both ends of the resource availability spectrum (Bernard-Verdier *et al.*, 2012; Spasojevic and Suding, 2012), assuming that environmental harshness correlates with resource availability. Temperate highlands, thus, emerge as functionally rich and distinctive ecosystems, despite their overall low species richness (Quintero and Jetz, 2018).

We provide a much needed joint evaluation of the interplay of phylogenetic and functional structure. We find strong elevational and latitudinal differences in their covariation, affirming that a complex interplay of ecological and evolutionary processes contribute to diversity of avian assemblages (Mittelbach *et al.*, 2007; Quintero and Jetz, 2018; Tobias

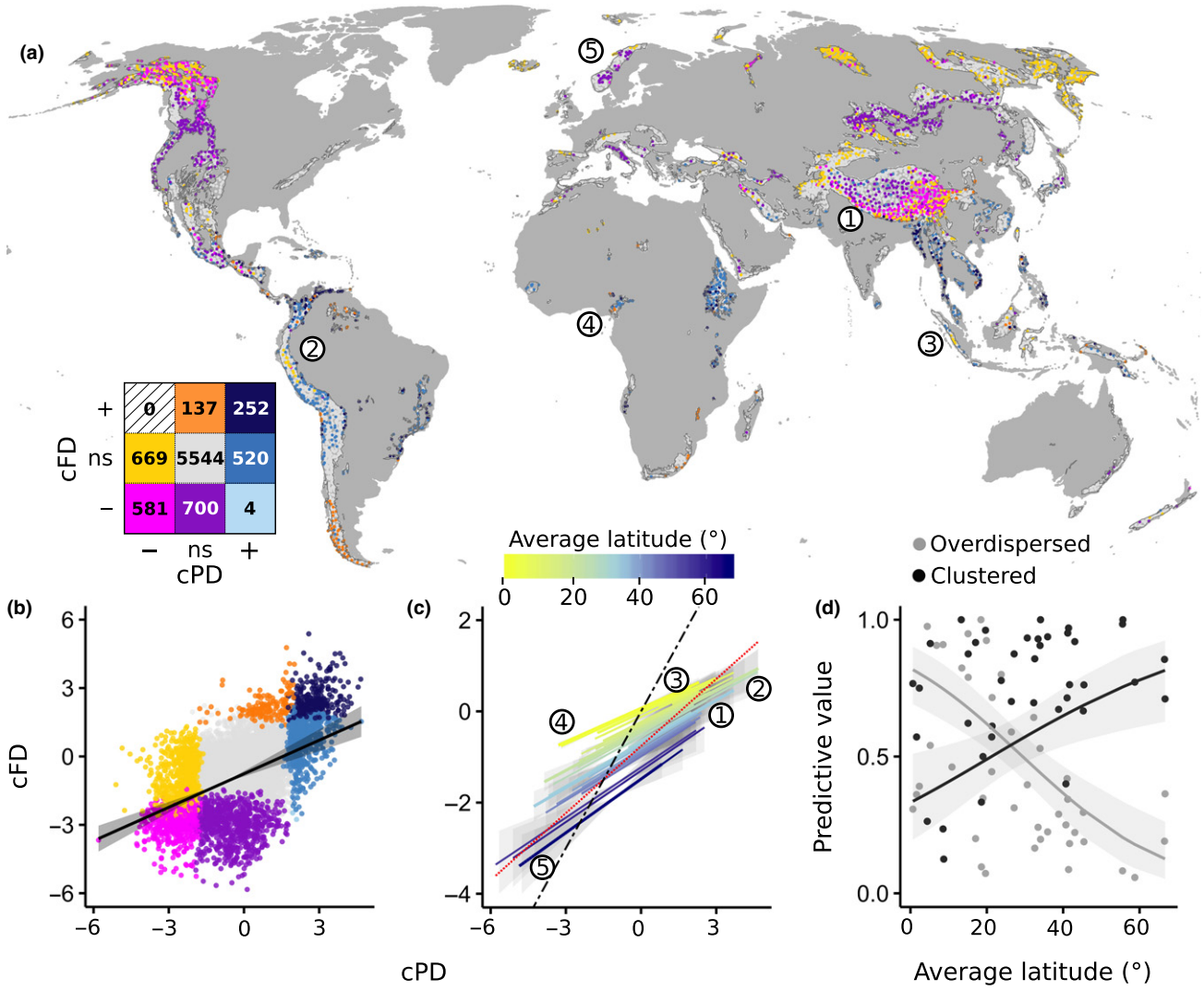

Figure 2 Interaction of phylogenetic and functional structure of all 8410 analysed assemblages in mountain regions worldwide across the latitude. Structure is given as species richness-controlled phylogenetic (cPD) and functional (cFD) diversity (standardised effect sizes). Statistically significant deviations in (a) and (b) are denoted by + (overdispersion), - (clustering); ns denotes non-significance; numbers in the contingency table show the number of sites with a statistically significant deviation. (c) Illustrates the interaction of central latitude of mountain regions with the relationship between cPD and cFD, with fitted aggregate global pattern shown in dashed red line and (0, 1) line shown in dashed black. (d) Illustrates the latitudinal gradient of the predictive value of the phylogeny, quantified using the probability (Pr) with which phylogenetic structure predicts functional structure of an assemblage. For highlighted regions, see Fig. 1.

et al., 2020) and that the imprint of phylogenetic structure is overridden by universal convergent evolution of avian traits (Pigot *et al.*, 2020). In tropical lowlands, where overdispersion is more common, most, but not all, distantly related species also show significant trait dissimilarities. As elevation in the tropics increases, functional and phylogenetic structure become more decoupled suggesting that only some close relatives share similar trait combinations. As clustering becomes more dominant towards higher latitude, the congruence of phylogenetic and functional structure increases sharply and most closely related species display similar trait characteristics. In contrast, functionally dissimilar species in temperate and boreal highlands tend not to be distantly related. Such disparities in phylogenetic and functional structure in temperate highlands are not necessarily unexpected. Traits such as dietary and foraging characteristics have evolved multiple times within clades (Kissling *et al.*, 2012; Burin *et al.*, 2016), and it is plausible that a restricted pool of clades that inhabit cold and highly seasonal temperate regions displays large variation in its trait characteristics.

Our results provide important evidence that phylogeny is an unreliable proxy for assemblage functional composition, corroborating previous work (Mazel *et al.*, 2017, 2018). Phylogenetic structure tends to be a poor substitute for functional structure in functionally diverse tropical and sub-tropical regions, consistent with previous findings on decreasing surrogacy value of phylogenetic diversity with increasing species pool richness (Mazel *et al.*, 2018). We also find, however, that phylogenetic structure is a weak proxy for functional structure in species poor but strongly ecologically divergent

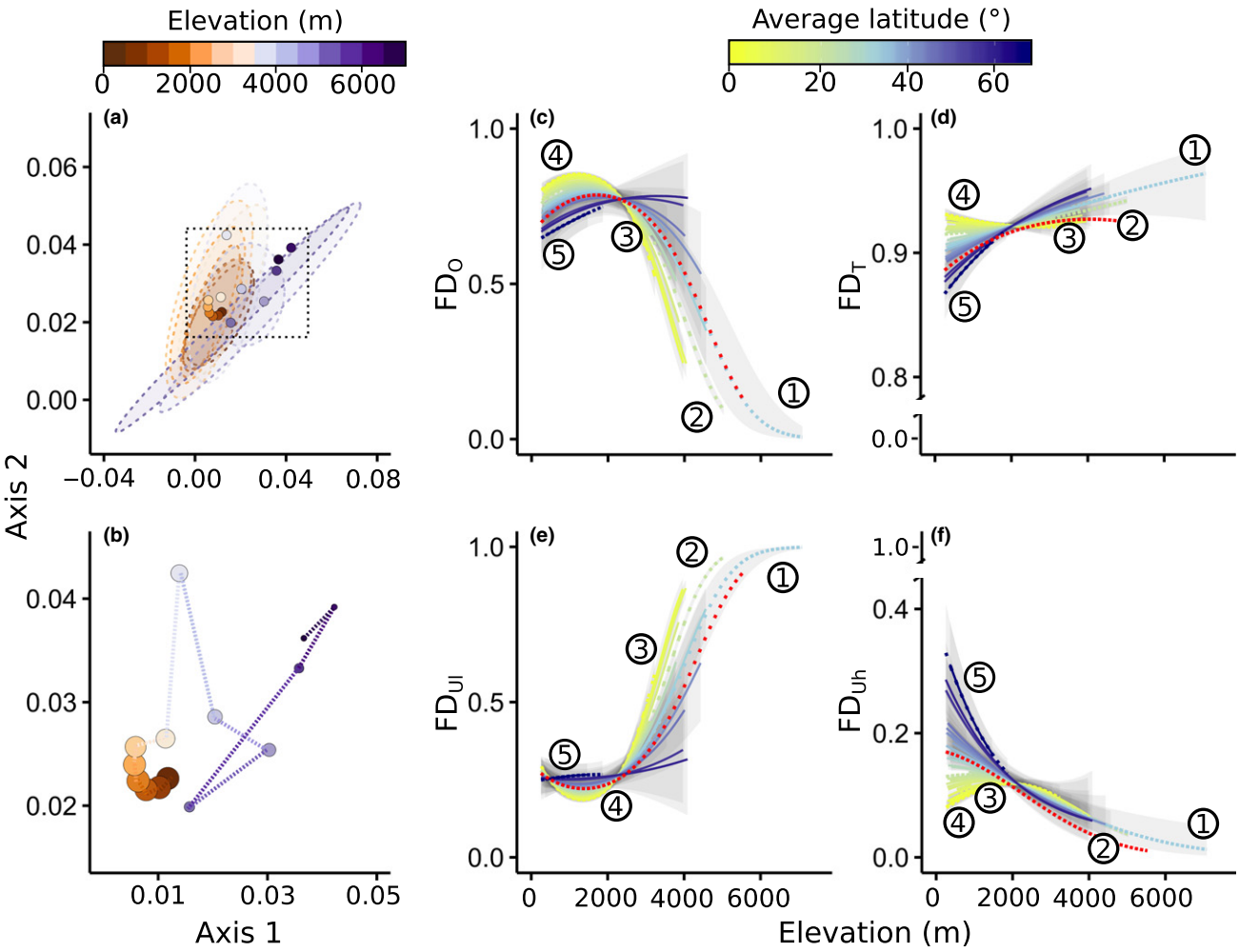

Figure 3 Elevational gradients of assemblage trait space. (a and b) Provide the two-dimensional global trait space resulting from Principal Coordinate Analysis (PCoA); points are the centroids of the trait space specific to each consecutive elevational band of 500m intervals averaged over all mountain regions, with 75% confidence ellipses encompassing assemblages at each elevational band (a) and their trajectory towards higher elevations (b). Size of points in (b) illustrates the number of mountain regions informing each elevational band, decreasing with elevation from 42 at 500m to 19 at 4000m to 1 at 6000m. (c–f) Show the interaction of central latitude of mountain regions with elevational gradients of the overlap in trait volume (FD_O, Sørensen similarity; c), turnover (FD_T, Simpson's similarity; d) and fractions of trait volume unique to assemblages located at lower (FD_{Ul}; e) and higher (FD_{Uh}; f) elevations. In (c–f), fitted aggregate global patterns are shown in dashed red line. For highlighted regions, see Fig. 1.

assemblages, suggesting that factors other than species richness (Mazel *et al.*, 2018; Tucker *et al.*, 2018) drive the surrogacy value of phylogeny. We conclude that, at presented scale of analysis, phylogeny alone is ill-suited for recognising regions with particularly distinct ecosystem-relevant functions.

Our results for a globally encompassing dataset confirm recent indications of among-regional variation in elevational gradients in functional diversity for a survey data from a subset of mountain areas (Montaño-Centellas *et al.*, 2020), thus, highlighting the importance of scale (extent) in the search for generalities. In contrast to this recent work, however, we find strong generalities in elevational gradients in functional diversity, their variation along latitude and in the latitudinal gradient in the congruence of assemblage phylogenetic and functional structure. We attribute this to the larger geographic extent, coarser spatial grain and broader taxonomic scope of our study which provide a more encompassing and representative characterisation of avian trait, phylogenetic and spatial variation. Potential biases associated with scale and detection that affect elevational survey data may further contribute to limited power or biased inferences for global-scale analyses (Nogués-Bravo *et al.*, 2008; Jarzyna and Jetz, 2016; Quintero and Jetz, 2018).

We shed a light on the complexity of spatial patterns in assemblage structure along elevational gradient by providing an assessment of assemblage functional composition and turnover, down to the level of single traits (Kraft *et al.*, 2015; Carmona *et al.*, 2016). Globally, we find a strong among-assemblage trait redundancy from low to mid elevations and increasing uniqueness above. We attribute the escalating dissimilarity in traits along elevation to decreases in species richness and its associated functional diversity (i.e. nestedness *sensu* Baselga, 2010) rather than turnover in species functions and, possibly, their identities. Globally, as elevation increases, species holding functions reflecting elevational, treeline or terrain, dependencies of associated habitats drop out from

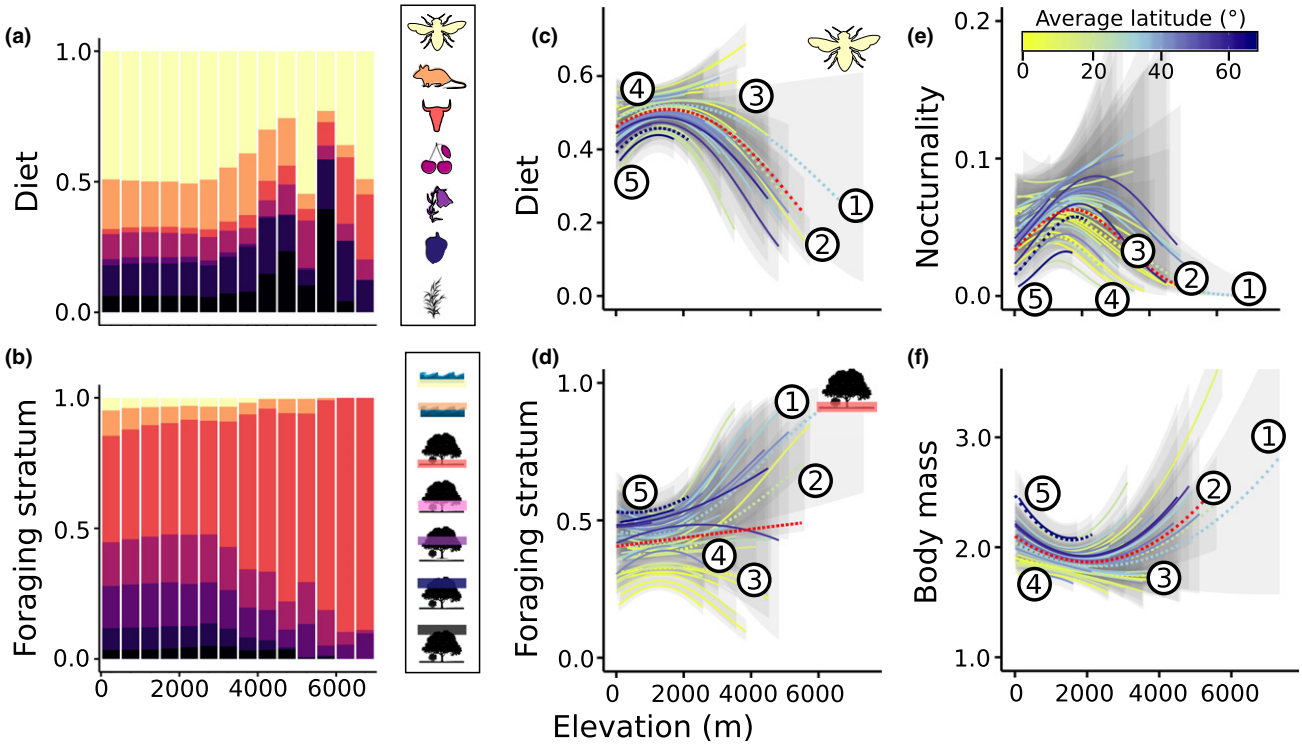

Figure 4 Elevational gradients in the specific aspects of trait space. Shown are all components of the (a) dietary and (b) foraging stratum axes, (c–f) selected individual traits—proportions of insectivorous diet (c), ground foragers (d), nocturnality (e), and average body mass (f). (c–f) Illustrate the interaction of central latitude of mountain regions with elevational gradients of the given functional attribute. In (c–f), fitted aggregate global patterns are shown in dashed red line. For highlighted regions, see Fig. 1.

assemblages. However, strong latitudinal variation in functional dissimilarity patterns and select underlying traits exists. In the tropics and sub-tropics, increasingly depauperate assemblages are strongly functionally dissimilar along elevation. This is consistent with the fact that tropical mountain ranges see higher turnover in climates over elevational gradients, leading to increased variation in ecological properties and resource heterogeneity, which in turn promote elevated dissimilarity in biodiversity along elevation (Janzen, 1967; Rahbek *et al.*, 2019). We find that, in the tropics, the components of the foraging stratum trait as well as nocturnality undergo significant reductions towards the highlands, underpinning the pattern of increasing functional clustering. In temperate and boreal regions, among-assemblage functional similarity is more stable along elevation, although slightly increasing functional turnover is evident. In those high-latitude regions, the components of the foraging stratum and nocturnality traits undergo lower reductions along elevation than those closer to the equator, suggesting that these trait axes might contribute particularly strongly to the non-stationarity of biodiversity patterns investigated here.

While many species in high-latitude systems occupy territories only during the breeding season, we anticipate that the general patterns of assemblage structure revealed here are broadly robust with regards to the migratory behaviour. During the northern hemisphere winter months, species richness in sub-tropical and tropical regions increases due to migration, likely leading to increases in overall functional diversity, although how this translates to patterns of assemblage functional distinctiveness and structure remains unexplored. At the same time, temperate regions experience a decline in species richness wherein, presumably, the remaining species have traits conferring tolerance to freezing conditions (e.g. granivorous and scavenging birds; Carnicer and Díaz-Delgado, 2008), resulting in functional clustering. Despite these predictions, it remains to be explored how migratory species, while overall being the minority (ca. 18% of all bird species), affect patterns of assemblage functional and phylogenetic structure, particularly in high-latitude regions (>60°) where the percentage of migratory birds often exceeds 80%.

Functional and phylogenetic overdispersion and clustering have routinely been interpreted as evidence for biotic and environmental constraints, respectively, in assembly of communities (Webb *et al.*, 2002; Kraft *et al.*, 2007; Graham *et al.*, 2009; Machac *et al.*, 2011). Recent work has begun to further qualify the ability to infer community assembly processes from observational data without further experimental manipulation (Mayfield and Levine, 2010; Cadotte, 2017; Cadotte and Tucker, 2017) or more evolutionary process-based models (Drury *et al.*, 2016; Quintero and Landis, 2019). For example, functional clustering may be a result of large fitness differences and competitive exclusion rather than environmental filtering (Mayfield and Levine, 2010). Additionally, while it is recognised that multiple processes operating at different spatial and temporal scales often combine to structure communities (Cavender-Bares *et al.*, 2006), process-based models that

integrate biogeographic history and trait evolution to discern assembly processes are only beginning to emerge and are computationally restricted to only a few hundred species and a few areas (Quintero and Landis, 2019). While further interpretation of our results regarding elevational community assembly is outside scope, the uncovered non-stationarity of elevational patterns of assemblage structure suggests a complex interaction of historical, environmental, biotic and evolutionary constraints acting together on community assembly.

Overall, our results suggest that, at small scales, temperate highlands are disproportionately susceptible to the loss of critical ecological functions because they harbour high assemblage functional distinctiveness and low species richness. At larger scales, sustaining the regional multi-functionality of ecosystems requires high dissimilarity among assemblages (Hector and Bagchi, 2007; Mori *et al*., 2016) because no single, local assemblage can support all ecosystem processes (Hillebrand and Matthiessen, 2009). We uncover such high levels of among-assemblage functional uniqueness in tropical and sub-tropical highland ecosystems, and identify them as particularly susceptible to disruption of their functioning. Globally, high-elevation ecosystems emerge as exceptionally prone to future ecological perturbations and loss of functions.

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AUTHORSHIP STATEMENT

M.A.J., W.J. and I.Q. conceived the manuscript idea. M.A.J. performed all analyses and I.Q. assembled data. M.A.J. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

The authors confirm that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad, Figshare or Hal) and the data DOI will be included at the end of the article.

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SUPPORTING INFORMATION

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

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