

1 **Title:** Functional randomness despite high taxonomic turnover across an elevational  
2 gradient in a global biodiversity hotspot: A case study of hawkmoths and birds

3  
4 **Running title:**  $\beta$ -diversity across elevational gradients

5  
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20 **Author contributions:** MM formulated the hypotheses, performed the analyses and  
21 drafted the manuscript. RA is the principal investigator of the larger on-going biodiversity  
22 project in the region. The collection and curation of field and trait data, were shared equally  
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33

34

35 **Conflict of Interest:** None.

36 **Abstract**

37 **Aim:** We examined the patterns and processes of taxonomic and functional dissimilarities  
38 for two disparate organismal groups (ectothermic hawkmoths and endothermic birds)  
39 across a broad tropical elevational gradient.

40

41 **Location:** Eaglenest Wildlife Sanctuary (northeast India), eastern Himalayan global  
42 biodiversity hotspot.

43

44 **Taxon:** 4,731 hawkmoths; 15,387 birds

45

46 **Methods:** Turnover and nestedness components for taxonomic and functional  
47 dissimilarities were obtained using the methods developed by Baselga (2013) and Leprieur  
48 et al., 2012. We used Generalized Dissimilarity Modeling (GDM) with geographic distance,  
49 contemporary and historic climatic variables to assess the relative importance of dispersal  
50 and environmental processes in determining the beta diversity. Functional redundancy  
51 (FRed) was calculated for both organismal groups using the Simpson's diversity indices.  
52 Null modeling was used to determine randomness in species and trait distributions.

53

54 **Results:** Turnover dominated taxonomic and functional dissimilarities, however the  
55 contribution of nestedness was considerably higher to the latter. Overall, the rate of  
56 dissimilarity with distance, for both facets of diversity, was significantly higher for birds,  
57 with stronger contributions of geographic distance and historic climate; whereas the  
58 hawkmoth dissimilarities were strongly correlated with only contemporary climate.  
59 Taxonomic dissimilarities deviated significantly from null, whereas functional dissimilarities  
60 exhibited high redundancy and randomness.

61

62 **Main Conclusions:** Overall, our results suggest that while the drivers of beta-diversity  
63 exhibit idiosyncrasy and taxon-specificity; for a given taxa, they are consistent across the  
64 two facets of dissimilarity. More importantly, regardless of the principal predictor, the net  
65 result was that of high taxonomic turnover, which is de-coupled to a high degree from  
66 functional turnover in these tropical ecosystems. The large redundancy in trait values,  
67 despite high species turnover, indicates functional resilience of these tropical communities.  
68 The consistency of this pattern, across two disparate organismal groups, is suggestive of a  
69 key mechanism in which tropical communities may retain functionality of ecosystems in a  
70 changing environment.

71

72 **Keywords:**

73 taxonomic beta diversity, functional beta diversity, elevational gradient, lepidoptera, birds,  
74 GDM, null model

75

## 76 **Introduction**

77 Beta diversity, or the compositional difference among communities, is a central concept in  
78 ecology and has received a renewed interest due to its pivotal role as a link between local  
79 (alpha) and regional (gamma) diversity (Buckley & Jetz, 2008). Especially within the  
80 context of tropical forests, where complete inventories on even local richness are seldom  
81 available for a wide variety of organisms, an understanding of the mechanisms generating  
82 the spatio-temporal variation in community composition, i.e. beta diversity, has provided  
83 valuable insights into the understanding of the mechanisms maintaining the high  
84 biodiversity in these regions (König et al., 2017). A common approach for investigating  
85 patterns in beta diversity across environmental gradients is by characterizing the Distance-  
86 Dissimilarity-Relationships (hereafter DDRs) i.e., the slope of the relationship between  
87 compositional (taxonomic/functional) dissimilarities and environmental/geographic  
88 distances (Nekola & White, 1999). Difference in slopes for different taxa has been  
89 explained by contrasting dispersal abilities, vagility and environmental tolerance/niche  
90 width (all three inversely related to the slope of DDRs; Soininen et al., 2007). Central to the  
91 analysis of DDRs are four major conceptual and methodological developments, each  
92 concerning itself with assessing the relative role of a mechanism from a pair of non-  
93 exclusive (complementary or antagonistic) processes responsible for generating and  
94 maintaining patterns in beta diversity.

95  
96 The first, and perhaps the most well documented, methodological advancement relates to  
97 partitioning the total observed dissimilarity into its two integral components – turnover and  
98 nestedness (Baselga, 2010, 2013). Compositional dissimilarity between any pair of  
99 communities can arise either due to turnover i.e. species replacement, or nestedness i.e.  
100 species loss. Different assembly processes are responsible for either type of change  
101 (environmental filtering versus extinction-colonization dynamics) and thus partitioning beta  
102 diversity into these two components can further the understanding of ecological drivers of  
103 dissimilarity (Soininen et al., 2018).

104  
105 The second methodological development concerning DDRs deals with a more pervasive  
106 statistical challenge – spatial auto-correlation of environmental variables. Community  
107 dissimilarity can arise either due to dispersal limitation (taxon-specific dispersal) or due to  
108 environmental filtering (selection imposed by abiotic conditions, taxon specific niche-  
109 width), and consequently disentangling the relative contribution of environment and  
110 geographic distances (Tilman, 1982; Hubbell, 2001) can provide important insights into  
111 patterns of beta diversity. However, since most environmental variables are strongly  
112 correlated with geographic distances, the relative influence of these two filters remains  
113 largely unresolved (Qian & Ricklefs, 2007).

114  
115 Globally, the Quaternary climatic changes have been shown to shape the current patterns  
116 of species distributions and diversity across a broad range of organisms (Araújo et al.,

117 2008, Hortal et al., 2011, Svenning et al., 2015), but it's relative contribution, in comparison  
118 with contemporary climate and spatially limited dispersal, especially across the Himalayas  
119 has been rarely investigated (Yang et al., 2008, Yu et al., 2015). The Himalayan glaciation  
120 was affected considerably during the Late Quaternary period (Owen, Derbyshire & Fort,  
121 1998, Owen, Finkel & Caffee, 2002). Geological evidences and Global Climatic Models  
122 (GCMs) reveal glaciation till up to 10 km further from contemporary ice boundaries during  
123 the Last Glacial Maximum (LGM), which reduced the monsoon precipitation in southeast  
124 Asia, and affected the distribution of many taxa (Owen et al., 2002). Thus, disentangling  
125 the relative contribution of historic and contemporary climate to observed patterns in  
126 composition is critical for predicting the fate of biodiversity in the light of emerging climate  
127 changes. The recent advancements in the assembly of historic climatologies have paved  
128 the way for this third important analytical advancement in the understanding of  
129 mechanisms generating beta diversity (Gent et al., 2011; Watanabe et al., 2011; Fitzpatrick  
130 et al., 2013; Giorgetta et al., 2013).

131  
132 Finally, ecological communities respond to the changing environment in not just the  
133 number, type and abundance of the constituent species, but also in their functional trait  
134 composition (Lamana et al., 2014). Taxonomic and functional dissimilarities are expected  
135 to be positively correlated due to the principles of limiting similarity, which predict a  
136 minimum permissible overlap across the niche space of two co-occurring species  
137 (MacArthur & Levins 1967). A redundancy in trait composition despite high taxonomic  
138 turnover may indicate ecosystem resilience to perturbations and environmental changes  
139 (Swenson et al., 2011). Similarly, a disproportionately higher loss in functional diversity, in  
140 comparison to taxonomic diversity may make communities more vulnerable to climate  
141 change (Robroek et al., 2017). Especially useful in this context have been the  
142 examinations of deviations between the expected and observed dissimilarities using null  
143 modeling approaches (Díaz et al., 2007; Cadotte et al., 2009; Swenson et al., 2011;  
144 Robroek et al., 2017). Studies examining the relative importance of deterministic vs  
145 stochastic processes using randomized species and trait diversities are a relatively recent,  
146 and crucial fourth analytical advancement in characterizing DDRs (Swenson et al., 2011;  
147 Matthews et al., 2015; Si et al., 2016; Almeida-Gomes et al., 2019).

148  
149 While there are a few studies that consider these concepts for taxonomic DDRs, there has  
150 been very little work that compares the relative contributions from turnover-vs-nestedness,  
151 environment-vs-geography, Quaternary-vs-contemporary climate and deterministic-vs-  
152 stochastic processes to both taxonomic and functional dissimilarity. Particularly lacking are  
153 studies that examine these multiple causative mechanisms within a comparative  
154 framework for different faunal taxa across a single elevational gradient. Majority of the  
155 studies on DDRs have investigated dissimilarities at large biogeographic scales, spanning  
156 multiple latitudes, using species presence / absence matrices (Poulin, 2003; Astorga et al.,  
157 2012; Wetzel et al., 2012; Fitzpatrick et al., 2013; but see Basset et al., 2015; Mori et al.,

158 2015; González-Reyes et al., 2017; Tonkin et al., 2017). At large biogeographic scales, the  
159 'true' environmental difference between communities is confounded by the added  
160 complexity of variation in historic climatic contingencies, which is seldom included in  
161 investigations (but see Fitzpatrick et al., 2013).

162

163 In this study we compare the patterns and processes for the taxonomic and functional  
164 dissimilarity of ectothermic hawkmoths and endothermic birds across a single 2600m  
165 elevational transect in the eastern Himalaya of Arunachal Pradesh, India. The concurrent  
166 sampling of the two taxa, along the same elevational transect, is expected to reduce the  
167 number of confounding factors due to the identical parameters associated with climate,  
168 vegetation and history. We investigate the relative contribution of turnover and nestedness  
169 to both these facets of diversity. To assess the relative contribution of environment and  
170 geographic distance, we use the recently proposed Generalized Dissimilarity Modeling  
171 (GDM, Ferrier et al., 2007), and incorporate Quaternary climatic variables in the model as  
172 additional, independent predictors. We further ask the question whether the functional  
173 turnover between communities of birds and hawkmoths is higher or lower than expected,  
174 given the observed taxonomic turnover, i.e. randomness in trait distributions.

175

176 More specifically, we test the following hypotheses: (i) Due to the broad environmental  
177 gradient across a small spatial extent, we expect turnover to dominate both taxonomic and  
178 functional dissimilarities and, (ii) a strong positive correlation between the two facets of  
179 diversity for both organismal groups. Due to the difference in life histories for the two taxa  
180 (ectothermic hawkmoths versus endothermic birds) and their high vagility, we expect (iii)  
181 higher rate of turnovers for hawkmoths due to the positive association between body size  
182 and dispersal ability (Gaston & Blackburn, 1996; Soininen et al., 2018), and (iv) a higher  
183 relative contribution of temperature parameters to the observed beta diversity patterns of  
184 hawkmoths, as compared to birds.

185

## 186 **Materials and Methods**

### 187 ***Study site and field sampling***

188 Light trapping for hawkmoths and transect counts for birds were carried out along the  
189 same transect in Eaglenest Wildlife Sanctuary (27.0–27.2°N, 92.3–92.6°E) in the state of  
190 Arunachal Pradesh, northeast India. The region, nested within the eastern Himalayan  
191 range, is one of the world's 8 '*hottest hotspot*' of biodiversity and endemism (Myers et al.,  
192 2000). Climate, vegetation and topography has been described elsewhere (Mungee &  
193 Athreya, 2019a).

194

195 Nocturnal phototropic Sphingidae were sampled at light screens at 13 elevations between  
196 200 and 2800m. Methodology, rarefaction curves and species richness has been  
197 discussed elsewhere (Mungee & Athreya, 2019a). For birds, line transect surveys were  
198 conducted at a finer scale of 50m elevational resolutions. The counts were pooled within

199 each 200m elevational band for comparisons with the elevational resolution of the  
200 hawkmoth data (see **Appendix S1**).

201

### 202 ***Trait data sets***

203 For hawkmoths, we used the morpho-functional traits of body mass, wing loading and wing  
204 aspect ratio (Mungee & Athreya, 2019a). Individual measurements for 3301 hawkmoths  
205 were obtained from field images after distortion-correction and size calibration (Mungee  
206 and Athreya, 2019b). For birds, we obtained species mean trait values for 227 (93%) out of  
207 the 245 birds in our sample from various sources (Dunning, 2008; Price et al., 2014; [http://](http://www.birdlife.org/)  
208 [www.birdlife.org/](http://www.birdlife.org/)). 6 quantitative and 3 categorical traits were used that have previously  
209 been linked to different avian functional strategies – body mass, wingspan, beak length,  
210 beak width, beak depth, tarsus length, primary substrate, foraging mode and diet  
211 (**Appendix S1**).

212

### 213 ***Environmental data sets***

214 Contemporary climate data was obtained from CHELSA climatologies ([http://chelsa-](http://chelsa-climate.org/bioclim/)  
215 [climate.org/bioclim/](http://chelsa-climate.org/bioclim/)), which is a recently assembled high resolution climatological data set  
216 that has been used in species distribution modeling with superior results (Karger et al.,  
217 2017). Rasters for mean annual temperature (MAT), maximum temperature of the warmest  
218 month (TMAX), minimum temperature of the coldest month (TMIN), annual precipitation  
219 (APPT) and precipitation seasonality (CVPPT) were downloaded at a 30m resolution and  
220 elevation specific mean values were obtained for the spatial coordinates of the sampling  
221 locations of hawkmoth light screens, which also correspond to the approximate mean  
222 elevations of each bird transect elevational band. The contemporary climatic data has  
223 been averaged from 1979 – 2013 (**Appendix S1**).

224

225 We assembled the same five bioclimatic variables (MAT, TMAX, TMIN, APPT and CVPPT)  
226 for the Last Glacial Maximum (~ 22,000 years ago) using three commonly used Global  
227 Climate Models (GCMs) – Community Climate System Model 4 (CCSM4; Gent et al.,  
228 2011), Model for Interdisciplinary Research on Climate – Earth System Model (MIROC-  
229 ESM; Watanabe et al., 2011) and the Max Planck Institute – Earth System Model running  
230 in low resolution grid and paleo mode (MPI-ESM-P; Giorgetta et al., 2013). The  
231 Quaternary climatic stability was defined as the change in the contemporary and historic  
232 variable (Jansson, 2003) and was averaged across the three GCMs. We used an  
233 uncorrelated subset ( $r < 0.75$ ) of contemporary climatic variables and Quaternary climatic  
234 stability to arrive at a final set of 5 environmental variables – TMAX-contemporary, APPT-  
235 contemporary, CVPPT-contemporary, Delta-MAT (change in MAT between LGM and  
236 present) and Delta-TMAX (change in TMAX between LGM and present). Only these five  
237 variables were used for all subsequent analyses.

238

239

240 **Statistical analyses**

241 *Taxonomic and functional dissimilarity*

242 Taxonomic dissimilarity was calculated using the abundance-based Bray-Curtis  
243 dissimilarity index (Baselga, 2013). For functional dissimilarities, the species-by-trait matrix  
244 was converted into a distance matrix using Podani's extension for ordinal traits (Podani  
245 1999). The distance matrix was used for cluster analysis (UPGMA method) to create a  
246 dendrogram (Petchey & Gaston 2002), which was subsequently converted to a functional  
247 tree. The abundance weighted Sørensen dissimilarity index was used to generate pair-  
248 wise dissimilarities across all sites. To quantify the relative importance of species turnover  
249 and nestedness to the overall dissimilarity, we used the procedures described by Baselga  
250 (2010, 2013) for abundance-based Bray-Curtis dissimilarity and extended for Sørensen  
251 (functional) dissimilarity by Leprieur et al. (2012). We also checked for correspondence  
252 between the taxonomic dissimilarities generated using Bray-Curtis index and Sørensen  
253 index using Mantel test.

254

255 *Generalized Dissimilarity Modeling*

256 To evaluate the relative contributions of environmental and geographic distances, we used  
257 Generalized Dissimilarity Modeling (GDM; Ferrier et al., 2007). GDM is a non-linear  
258 extension to matrix regression which can (i) account for the curvilinear relationships  
259 between community dissimilarity and environmental/geographic distances, (ii) assess the  
260 independent roles of multiple predictors, (iii) account for the variation in the strength of the  
261 relationship (between dissimilarity and individual predictor) along the gradient, and (iv) be  
262 used for model-deviance-partitioning (Borcard et al., 1992) to calculate the joint and  
263 independent contribution of geographic and environmental distances (Fitzpatrick et al.,  
264 2013).

265

266 For each predictor, GDM performs a transformation using a set of I-spline functions. The I-  
267 splines are essentially short stretches of polynomial functions, 'stitched' together with a  
268 high degree of smoothness. The coefficients for each I-spline are determined using  
269 maximum likelihood estimation and the model standardizes the different predictors to allow  
270 for a direct comparison. We used the default of three I-spline basis functions per predictor  
271 (Fitzpatrick et al., 2013). Each function gives two important pieces of information regarding  
272 the relationship between the predictor and the dissimilarity – (i) the maximum height of the  
273 I-spline function, i.e. the sum of the three coefficients, is an estimate of the proportion of  
274 turnover explained by that predictor, and (ii) the difference in the height of the function  
275 between any two points along the gradient, describes the variation in the relationship  
276 between the predictor and the dissimilarity. We fit the GDMs using both – the taxonomic  
277 and the functional dissimilarity matrix for hawkmoths and birds. We refer to these as  
278 taxonomic-GDM and functional-GDM below.

279



280 For both dissimilarities, taxonomic and functional, three separate GDMs were fitted to  
281 assess the relative contribution of environment and space - (i) full model – with both sets  
282 of predictors (environmental and geographic), (ii) only environmental predictors (both  
283 contemporary and historic), and (iii) only geographic distances. The full model deviance  
284 was partitioned into these three independent components using the variation partitioning  
285 method of Borcard et al. (1992). For significance testing of variables and model selection,  
286 we performed Monte Carlo sampling (999 permutations) and step-wise backward  
287 elimination. Relative importance of each predictor was obtained from the scaled values of  
288 the maximum height of the corresponding I-spline functions.

289

### 290 *Null Modeling Analysis*

291 A null distribution of functional beta diversity values was generated for each trait, and for  
292 overall functional dissimilarity using all traits, by randomizing (999 times) the names of the  
293 species across the tips of the trait dendrograms. Therefore, the randomization procedure  
294 maintains the species richness, relative abundance distributions and consequently  
295 taxonomic beta diversity at each elevational community (Swenson, 2011). A standardized  
296 effect size (SES) was calculated for functional beta diversity using the mean and standard  
297 deviation of the null distribution as follows:  $SES = \frac{X_{obs} - \mu(X_{null})}{s.d.(X_{null})}$ , where  $X_{obs}$  is the  
298 observed dissimilarity value between two communities,  $\mu(X_{null})$  the mean of the null  
299 distribution and  $s.d.(X_{null})$  the standard deviation of the null distribution. Values greater than  
300 1.96 indicate a higher than expected functional dissimilarity between the communities and  
301 *vice versa*.

302

303 We additionally calculate functional redundancy (FRed) metric as a measure of resilience  
304 of hawkmoth and bird communities to environmental change across the elevational  
305 gradient. FRed was defined as the difference between Simpson's species diversity and  
306 functional diversity, and ranges from 0 to 1, indicating complete divergence or  
307 convergence between the two facets, respectively (Robroek et al., 2017). Observed FRed  
308 for the hawkmoth and bird communities was compared with those obtained from 999  
309 randomly assembled matrices, using SES values as previously. We also compared  
310 Simpson's and Sørensen's functional dissimilarities using ordinary least squares  
311 regression.

312

313 Finally, to compare the results from GDM with an analogous non-parametric linear  
314 regression approach, we used partial mantel tests and its more commonly used extension  
315 – distance based multiple matrix regressions with randomizations (MMRR; Wang 2013).  
316 Correlation between taxonomic dissimilarities (or functional dissimilarities) and  
317 environmental distances was obtained while accounting for geographic distances, and  
318 *vice versa*. The significance of the statistics was assessed with 999 permutations.

319

320 All analyses were performed in R 3.4.4 on a Ubuntu (linux-gnu) 18.04.1 platform (R Core  
321 Development Team 2013). Individual functions and packages used for various analyses  
322 have been provided as **Appendix S2**.

323

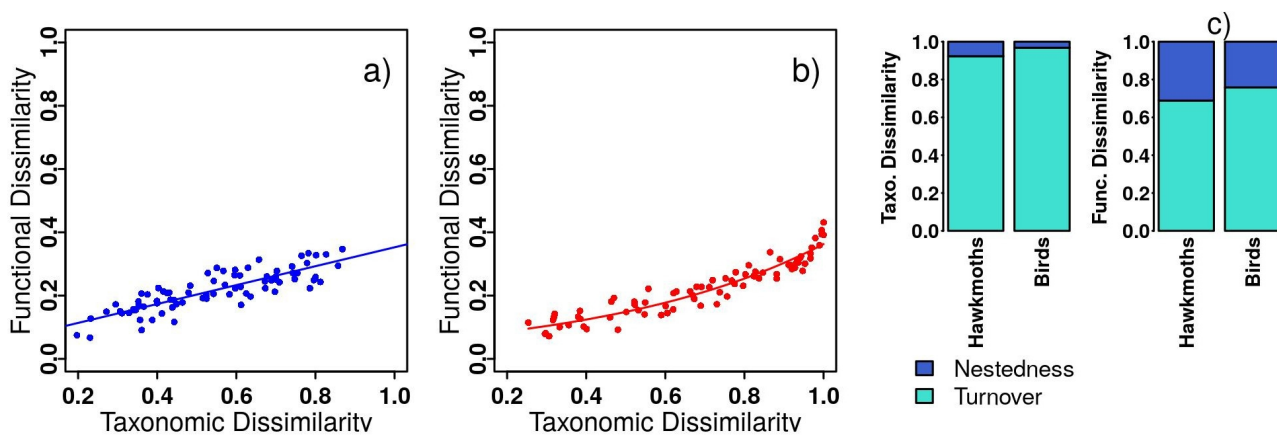
## 324 Results

### 325 Taxonomic and functional dissimilarity

326 We recorded a total of 4,731 hawkmoth individuals spanning 80 morphospecies, 30  
327 genera and 3 subfamilies. We reliably measured morpho-functional traits of body mass,  
328 wing loading and wing aspect ratio for 3,301 individuals and arrived a species mean trait  
329 values for all species (Mungee & Athreya 2019a, 2019b). 15,387 individual birds, spanning  
330 235 species, 150 genera and 50 families were recorded and species mean traits were  
331 obtained from various published sources for a subset of 227 (93%) of the species  
332 (Dunning, 2008; Price et al., 2014; <http://www.birdlife.org/>) (**Appendix S1**).

333

334 Functional and taxonomic dissimilarities were strongly correlated (*hawkmoths* – Mantel's  $r$   
335 = 0.84,  $p < 0.005$ ; *birds* – Mantel's  $r = 0.93$ ,  $p < 0.005$ ; **Figure 1**). The relationship was  
336 linear for hawkmoths ( $\beta_{\text{func}} \sim 0.30\beta_{\text{taxo}} + 0.05$ ,  $r^2 = 0.70$ ,  $p < 0.005$ ) but the quadratic  
337 relationship was a superior fit for birds;  $\Delta\text{AIC} > 20$  ( $\beta_{\text{func}} \sim e^{(-2.8 + 1.8\beta_{\text{taxo}})}$ ,  $p < 0.001$ ). Bray-  
338 Curtis and Sørensen taxonomic dissimilarities were highly correlated (*hawkmoths* –  
339 Mantel's  $r = 0.92$ ,  $p < 0.001$ ; *birds* – Mantel's  $r = 0.96$ ,  $p < 0.001$ ; **Appendix S2**). The  
340 taxonomic beta diversity was dominated by species turnover (92 % for hawkmoths and 97  
341 % for birds), while nestedness component had a considerable contribution to the functional  
342 beta diversity (31 % for hawkmoths and 24 % for birds) (**Figure 1**). Overall, bird  
343 communities exhibited a greater slope for both taxonomic and functional DDRs than  
344 hawkmoth communities (taxonomic dissimilarity Fisher's  $z = 8.68$ ,  $p$ .value  $< 0.001$ ;  
345 functional dissimilarity Fisher's  $z = 6.03$ ,  $p$ .value  $< 0.001$ ; **Appendix S2**). The taxonomic



**Figure 1.** Relationship between functional and taxonomic dissimilarities for communities of a) Hawkmoths and b) Birds; c) The proportion of total dissimilarity attributable to the turnover and nestedness components for taxonomic (left) and functional (right) beta diversity for hawkmoths and birds.

346 dissimilarities for birds using the subset of 227 species (for which functional dissimilarities  
 347 were calculated) exhibited similar slopes (**Appendix S2**).

348

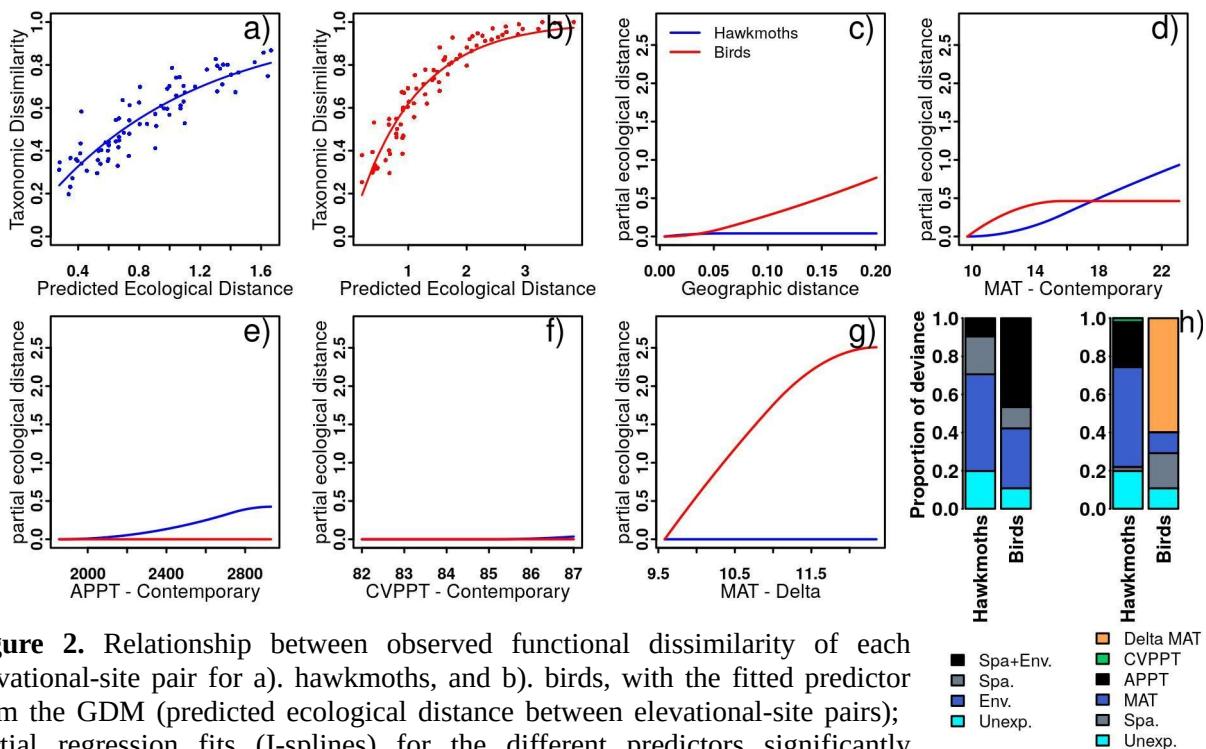
349

### 350 *Generalized Dissimilarity Modeling*

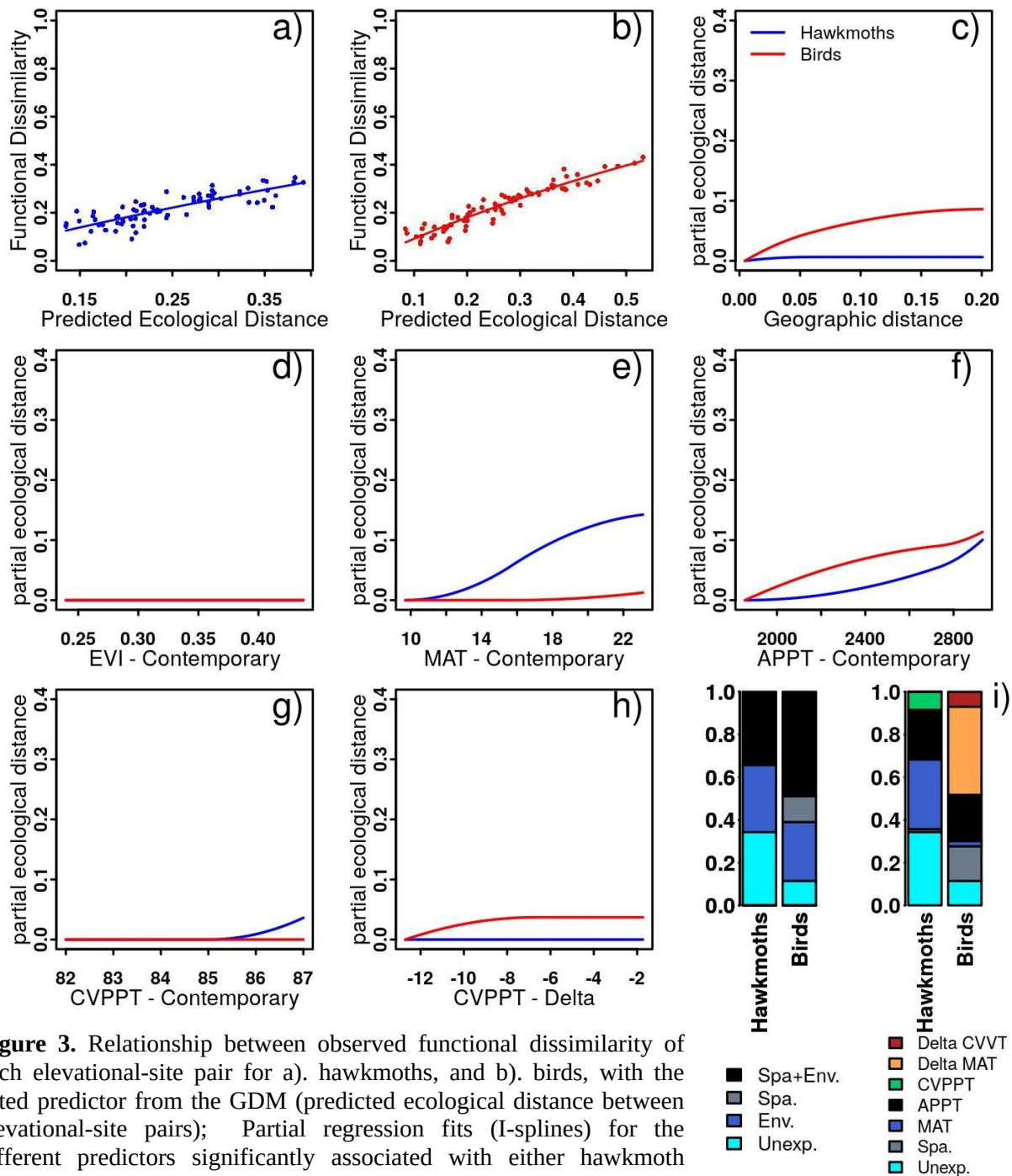
351 For taxonomic-GDM, 90% deviance could be explained by using the full model  
 352 (environmental and geographic distances both) for birds, whereas deviance explained for  
 353 hawkmoths was slightly lower (80%). Joint and independent effects of geographic distance  
 354 and environment varied between hawkmoths and birds with over 50% contribution  
 355 attributed to purely environment for hawkmoths as compare to 31% for birds, whereas the  
 356 joint contribution of environment and geographic distance was much higher for birds (47%)  
 357 than hawkmoths (10%). Geographic distance alone explained very little deviance for  
 358 hawkmoths and birds (19% and 11%, respectively). The relative importance of individual  
 359 predictors differed strongly for taxonomic dissimilarities of the two organismal groups.  
 360 Hawkmoth communities were more strongly correlated with contemporary climate,  
 361 especially MAT (52%) and APPT (24%), whereas bird communities exhibited strongest  
 362 correlations with Quaternary climatic changes, especially Delta-MAT (60%) (**Figures 2 &**  
 363 **3; Table 1**).

364

365



**Figure 2.** Relationship between observed functional dissimilarity of each elevational-site pair for a). hawkmoths, and b). birds, with the fitted predictor from the GDM (predicted ecological distance between elevational-site pairs); Partial regression fits (I-splines) for the different predictors significantly associated with either hawkmoth (blue) or bird (red) functional dissimilarities are shown in plots c) through g). The maximum height and shape of each function provides an indication of the independent contribution of the predictor and variation in it's strength along the environmental gradient. Relative importance of each predictor, obtained from the scaled values of the maximum height of the corresponding I-spline functions is shown in h).



**Figure 3.** Relationship between observed functional dissimilarity of each elevational-site pair for a). hawkmoths, and b). birds, with the fitted predictor from the GDM (predicted ecological distance between elevational-site pairs); Partial regression fits (I-splines) for the different predictors significantly associated with either hawkmoth (blue) or bird (red) functional dissimilarities are shown in plots c) through h). The maximum height and shape of each function provides an indication of the independent contribution of the predictor and variation in its strength along the environmental gradient. Relative importance of each predictor, obtained from the scaled values of the maximum height of the corresponding I-spline functions is shown in i).

367

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371

Similar to taxonomic-GDM, the functional-GDM for hawkmoth communities was more strongly correlated with contemporary climate, especially MAT (33%) and APPT (23%), whereas bird communities exhibited strong correlations with Quaternary climate, especially Delta-MAT (41%). Only 64% deviance could be explained by using the full model

**Table 1.** The proportion of total explained deviance attributable purely to space, purely to environment, jointly to both variables (shared), and not explained by the fitted GDM for the taxonomic and functional dissimilarities of hawkmoths and birds across the elevational gradient. The independent, relative contributions from the individual predictors, while keeping all others constant, are also shown.

		Unexplained	Spatial + Env.	Spatial	Environmental
Taxonomic	Hawkmoths	0.20	0.10	0.20	0.51
	Birds	0.11	0.47	0.11	0.31
Functional	Hawkmoths	0.34	0.34	0.00	0.31
	Birds	0.11	0.50	0.12	0.28

373

		Unexplained	Spatial	MAT - contemporary	APPT - contemporary	CVPPT - contemporary	Delta - MAT	Delta - CVPPT
Taxonomic	Hawkmoths	0.20	0.02	0.52	0.24	0.02	0.00	0.00
	Birds	0.11	0.18	0.11	0.00	0.00	0.60	0.00
Functional	Hawkmoths	0.34	0.01	0.33	0.23	0.08	0.00	0.00
	Birds	0.11	0.16	0.02	0.22	0.00	0.41	0.07

374

375

376

377 (environmental and geographic distances both) for hawkmoths, whereas deviance  
 378 explained for birds was close to 90% for functional dissimilarities. Variance partitioning  
 379 showed that the relative contribution by the environment alone was similar for hawkmoths  
 380 (31%) and birds (28%), whereas the contribution of spatially limited dispersal was higher  
 381 for birds (12%) than hawkmoths (0%) (**Figures 2 & 3; Table 1**).

382

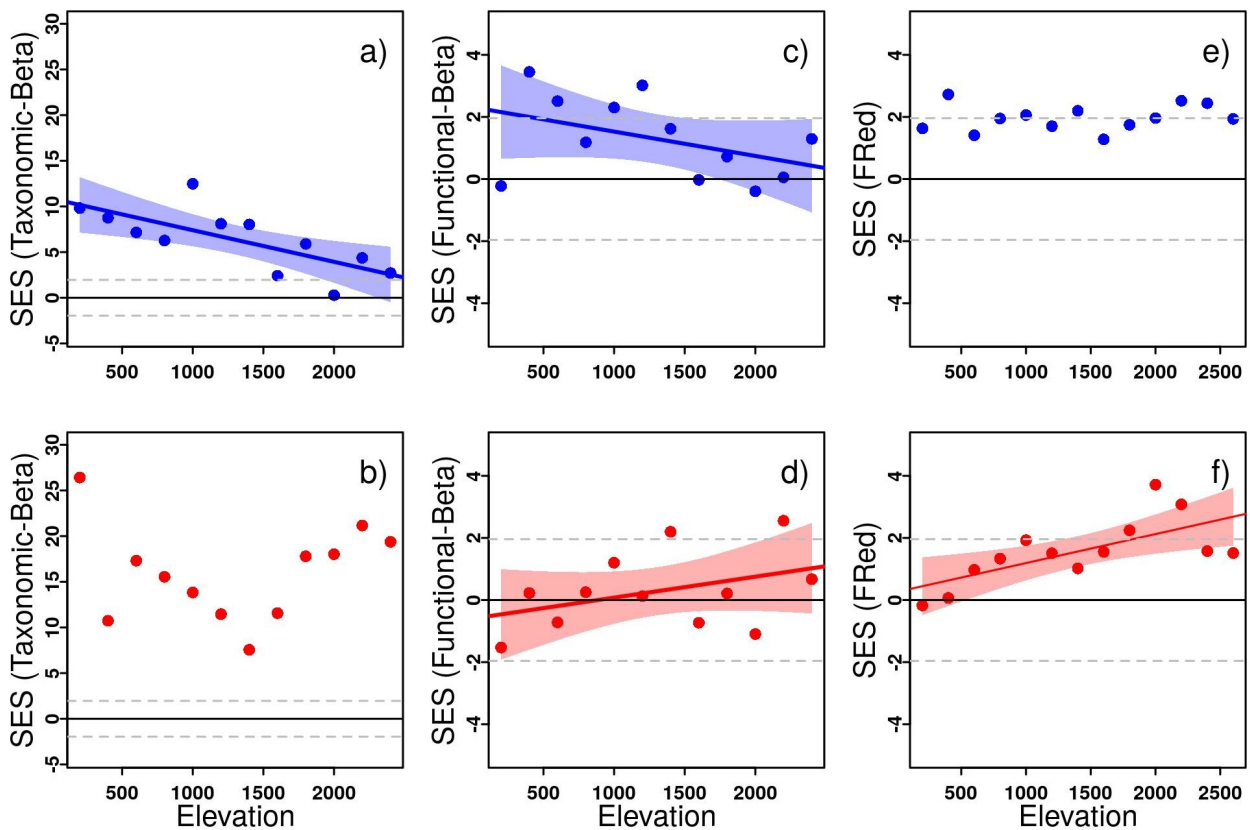
### 383 *Null Modeling Analysis*

384 SES values for the taxonomic beta diversity were significantly greater than null for both  
 385 hawkmoths and birds (except one high elevation community for hawkmoths; **Figure 4**).  
 386 Additionally, the SES values exhibited a significant negative slope with elevation for  
 387 hawkmoth taxonomic dissimilarity. Interestingly, the overall functional beta dissimilarity  
 388 across all traits was not significantly different from null for majority of the communities of  
 389 hawkmoths and birds. The patterns were very similar using individual traits for hawkmoths  
 390 and birds, and are presented in **Appendix S2**. The observed functional redundancy values  
 391 were high for both organismal groups (Hawkmoths –  $FRed_{\mu} = 0.55$ ,  $FRed_{\sigma} = 0.02$ ; Birds –  
 392  $FRed_{\mu} = 0.51$ ,  $FRed_{\sigma} = 0.02$  **Appendix S2**). The values were not significantly different from  
 393 null at most elevations, except the highest elevations for birds (**Figure 4**).

394

395 Partial Mantel tests showed similar results for birds, with a higher contribution of  
 396 geographic distances to taxonomic and functional dissimilarities (Mantel's  $R_{\text{taxonomic}} = 0.61$ ,  
 397  $p.\text{value} < 0.005$ ; Mantel's  $R_{\text{functional}} = 0.66$ ,  $p.\text{value} < 0.005$ ) as compared to the independent  
 398 contribution from environment alone (Mantel's  $R_{\text{taxonomic}} = 0.20$ ,  $p.\text{value} = 0.06$ ; Mantel's  
 399  $R_{\text{functional}} = 0.14$ ,  $p.\text{value} = 0.17$ ). However, for hawkmoths results were different from GDM,  
 400 indicating little contribution of environment (Mantel's  $R_{\text{taxonomic}} = 0.11$ ,  $p.\text{value} = 0.18$ ; **Figure**

401



**Figure 4.** SES values for the deviation of observed metrics of taxonomic beta-diversity (a & b), functional beta-diversity (c & d) and Functional redundancy (e & f) along the elevational gradient, presented for hawkmoths (blue; top row) and birds (red; bottom row). SES values greater than 1.96, or less than -1.96 (the dashed grey lines) indicate that the observed values of the respective metrics are higher or lower than the values obtained under randomized assembly (see text for details).

403

404 Mantel's  $R_{\text{functional}} = 0.12$ ,  $p.\text{value} = 0.18$ ) as compared to geographic distance (Mantel's  
 405  $R_{\text{taxonomic}} = 0.48$ ,  $p.\text{value} < 0.005$ ; Mantel's  $R_{\text{functional}} = 0.29$ ,  $p.\text{value} < 0.05$ ). Results were  
 406 similar with MMRR; environmental distance did not show significant correlation with either  
 407 of the diversity facets for the two taxa, whereas geographical distances were strongly  
 408 correlated with both facets of dissimilarity and with both taxa. Similar to GDM, the  
 409 coefficients for the overall MMRR model (including geographic distance and environmental  
 410 distance matrices) were higher for birds ( $R^2_{\text{taxonomic}} = 0.60$ ,  $p.\text{value} < 0.05$ ;  $R^2_{\text{functional}} = 0.63$ ,  
 411  $p.\text{value} < 0.05$ ) than hawkmoths ( $R^2_{\text{taxonomic}} = 0.41$ ,  $p.\text{value} < 0.05$ ;  $R^2_{\text{functional}} = 0.21$ ,  $p.\text{value}$   
 412  $< 0.05$ ) (**Appendix S2**).

413

414

## 415 Discussion

416 We compared the patterns and processes for taxonomic and functional dissimilarities of  
 417 hawkmoths and birds across a broad elevational gradient in the east Himalayan global  
 418 biodiversity hotspot. The two facets of diversity exhibit strong correlation, however, despite  
 419 high species turnover, the functional composition of the communities exhibited high

420 redundancy and higher nestedness. The high randomness in the distribution of traits  
421 across communities may be indicative of community resilience to changing environment  
422 with the overall community-level functional roles remaining constant. Overall, the two  
423 facets of diversity had very similar relative contributions from the abiotic predictors for a  
424 given organismal group, but there was significant variation across taxa.

425

### 426 **Taxonomic and functional dissimilarities**

427 Our results show that the further apart two sampling sites are, along an elevational  
428 gradient, the more dissimilar they are in terms of both species and functional composition,  
429 however the contributions of turnover-versus-nestedness varied considerably across the  
430 two facets of diversity. There was higher functional nestedness across both taxa, as  
431 compared to taxonomic nestedness, indicating that the functionality of local communities  
432 are increasingly nested subsets of the total suite of available functionalities in the regional  
433 pool, in spite of a high species turnover. Contrary to our predictions, we observed a  
434 significantly higher rate of turnover for birds as compared to hawkmoths, which gives  
435 valuable taxon-specific signatures (slope of the DDR; **Appendix S3**).

436

437 Hawkmoths and birds are both active dispersers, and their range size may be expected to  
438 increase with body size (Gaston & Blackburn, 1996). Contrary to this expectation, we  
439 observed a significantly higher rate of turnover for birds. This result supports the most  
440 recent meta-analysis on the subject – body size & beta-diversity relationships do not follow  
441 a universal trend and may be context dependent (Soininen et al., 2018). Many tropical  
442 bird species are highly specialized, exhibit high endemism, narrow niche widths and  
443 extreme dispersal limitation (Moore et al., 2008 and references therein). Unlike the tropical  
444 bird species, hawkmoth species are found throughout the Indo-Australian archipelago and  
445 have demonstrated a very broad resource utilization spectrum (Beck et al., 2006; Beck et  
446 al., 2007).

447

448 As with any functional diversity related analysis, a comment of the implications of the traits  
449 used is warranted. The hawkmoth morphological traits used here exhibit a strong response  
450 to the environmental gradient in the study region (Mungee & Athreya 2019a) and have  
451 previously been implicated in resource requirements, thermoregulation and dispersal  
452 ability (Heinrich 1996, Hassal 2015, Vágási et al. 2016). However larval diet breadth is an  
453 important strategy that has shown to correlate strongly with the distribution of Sphingidae  
454 across the Indo-Malayan Archipelago (Beck et al., 2006; Beck & Kitching, 2007). The traits  
455 used for bird assemblages on the other hand, encompass broader categories of  
456 functionality across resource use, thermoregulation, dispersal ability, feeding guild or the  
457 impacts of species on other trophic levels (Petchey et al., 2007; Flynn et al., 2009; Ding et  
458 al., 2013; Price et al., 2014; Pigot et al., 2016), and thus may better encapsulate the  
459 functional dissimilarities across large distances where communities exhibit largely non-  
460 overlapping taxonomic compositions (Bray-Curtis dissimilarities > 0.97). Due to a lack of

461 information on the hawkmoth host plants and their distribution in the study region, currently  
462 we do not have the means to account for their resource niches.

463

464 There are only a few analyses of changes in functional composition of animal communities  
465 along tropical altitudinal gradients, and there are still large gaps in knowledge regarding  
466 the role of functional beta diversity in maintaining ecosystem resilience of tropical  
467 assemblages (Villéger et al., 2013; Dehling et al., 2014; Nunes et al., 2016). Our findings  
468 indicate high redundancy in traits, which may be an important mechanism for tropical  
469 ecosystems to retain a fundamental, base-line functionality despite the high rate of species  
470 turnover (Mori et al., 2015).

471

### 472 **Generalized Dissimilarity Modeling**

473 The ecological literature is replete with several predictions for the variation in distance  
474 dissimilarity relationships across regions and across taxa (Nekola & White, 1999; Palmer,  
475 2005; Soininen et al., 2007; Soininen et al., 2018). On the contrary, there are very few  
476 general hypotheses for determining the relative role of geographic and environmental  
477 distances and most meta-analyses indicate idiosyncratic, taxon-specific contributions of  
478 these two non-mutually exclusive predictors (Fitzpatrick et al., 2013; Glassman et al.,  
479 2017; KÖnig et al., 2017). Using Generalized Dissimilarity Modeling, we demonstrated that  
480 rates of compositional dissimilarity vary substantially as a function of the predictor  
481 considered and with position along gradients, thus enabling the identification of regions of  
482 high vulnerability associated with different predictors in isolation and in quantifying the  
483 sensitivity of different ecological communities to future perturbations. Beyond indicating  
484 greater overall turnover for the birds of tropical Himalaya than the hawkmoths, the  
485 functions from GDM suggested that the historic environmental gradients, especially mean  
486 temperature, and spatially limited dispersal, most strongly associated with the beta  
487 diversity of birds, whereas the hawkmoths distribution was shaped by contemporary  
488 climate (mean temperature and annual precipitation). Thus, while MAT was the single best  
489 predictor for beta diversity patterns of both hawkmoths and birds, the relative importance  
490 of contemporary and historic temperatures was widely disparate.

491

492 A primary result from the GDM analysis was the similarity in the relative contributions of  
493 different predictors across the two facets of diversity for the same organismal group. This  
494 is interesting and indicates that while there is a large difference in the rate of response of  
495 taxonomic and functional turnover of a taxa, to the same environmental gradient, their  
496 relationship with individual predictors is similar. Apart from the higher unexplained variance  
497 in functional-GDM of hawkmoths, contemporary mean annual temperature had the highest  
498 relative contribution to both facets of dissimilarity, followed by contemporary precipitation.  
499 Historic climate did not contribute at all to the observed taxonomic and functional  
500 dissimilarities of hawkmoths of eastern Himalaya. Delta-MAT, i.e. the change in the mean  
501 annual temperature between the Last Glacial Maximum and present, was the most



502 important correlate for both – taxonomic and functional dissimilarity of birds. The joint and  
503 independent contributions of environmental and geographic distance was remarkably  
504 similar across the two facets of dissimilarities for birds (Joint > Env. > Spatial), whereas it  
505 was slightly more variable for hawkmoths. The discrepancy between the relative  
506 contributions of individual predictors was however magnified when comparing across taxa,  
507 even for the same facet of dissimilarity.

508

509 Overall, our results suggest that variation in the relative role of environmental and  
510 geographic filters in determining beta-diversity patterns is persistent across organismal  
511 groups even along the same, identical elevational transect. While the drivers of beta-  
512 diversity exhibit idiosyncrasy and taxon-specificity; for a given taxa, they are consistent  
513 across the two facets of dissimilarity. The consistency of this pattern, across two disparate  
514 organismal groups, is suggestive of a key mechanism in which tropical communities may  
515 retain functionality of ecosystems in a changing environment. More importantly, regardless  
516 of the principal predictor, the net result was that of high taxonomic turnover, which is de-  
517 coupled from functional turnover for two contrasting taxa. The large redundancy in trait  
518 values, despite high species turnover, indicates functional resilience of these tropical  
519 communities. Such comparative studies on the relationship of different environmental  
520 predictors, across multiple facets of diversity will help improve our understanding of the  
521 processes generating beta-diversity in the species rich tropical systems.

522

### 523 **Data availability Statement**

524 The data has been provided as Online Supporting Information.

525

526

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#### 709 **Biosketch**

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