

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:** β -diversity across elevational gradients

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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/). 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 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

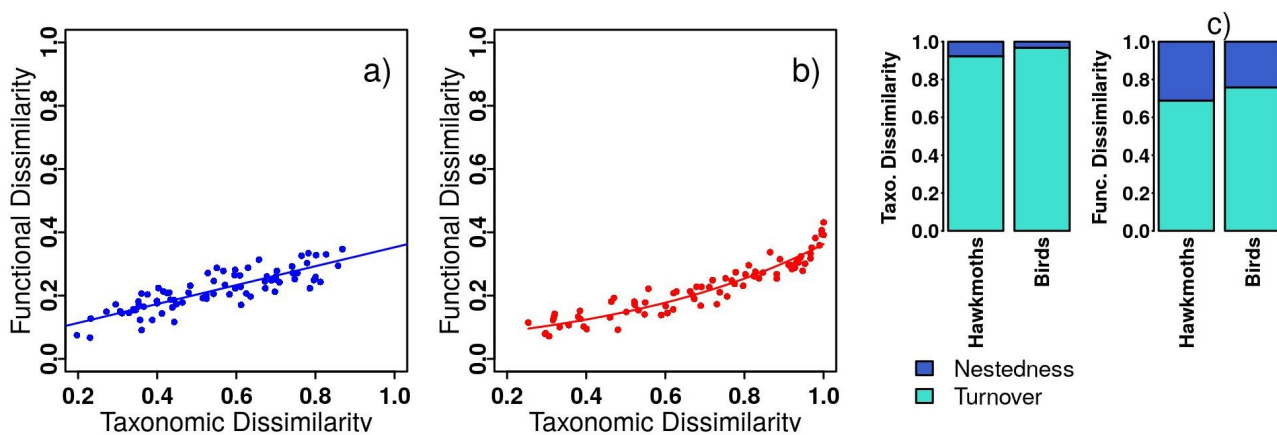


Figure 1. Relationship between functional and taxonomic dissimilarities for communities of a) Hawkmoths and b) Birds; c) The proportion of total dissimilarity attributable to the turnover and nestedness components for taxonomic (left) and functional (right) beta diversity for hawkmoths and birds.

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

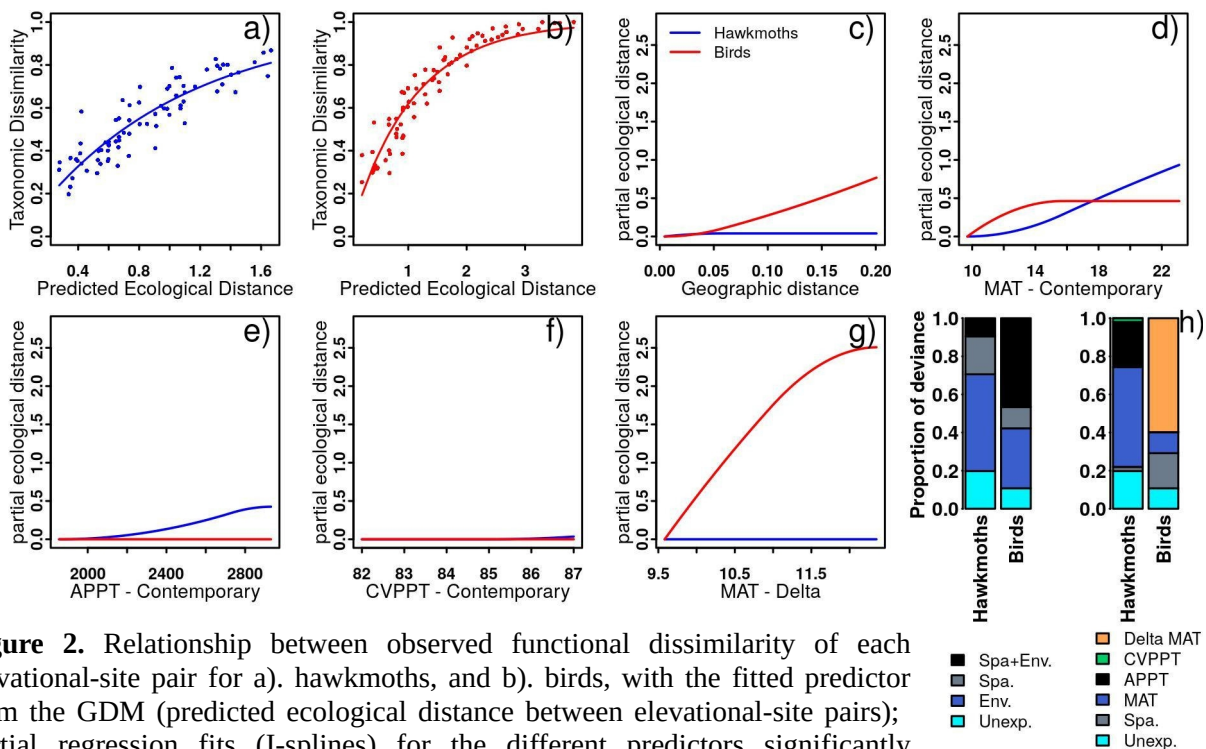


Figure 2. Relationship between observed functional dissimilarity of each elevational-site pair for a). hawkmoths, and b). birds, with the fitted predictor from the GDM (predicted ecological distance between elevational-site pairs); Partial regression fits (I-splines) for the different predictors significantly 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).

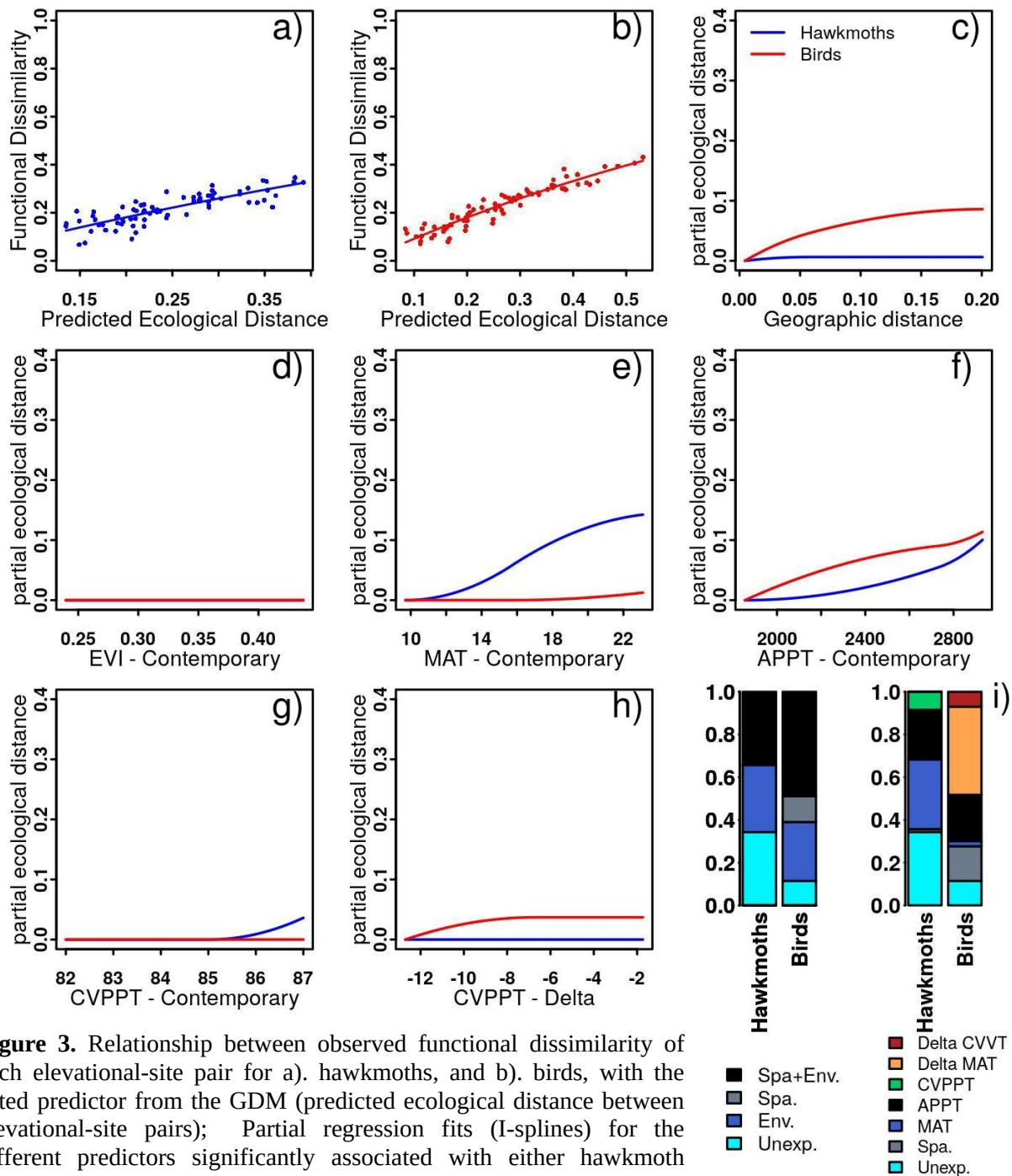


Figure 3. Relationship between observed functional dissimilarity of each elevational-site pair for a). hawkmoths, and b). birds, with the fitted predictor from the GDM (predicted ecological distance between elevational-site pairs); Partial regression fits (I-splines) for the different predictors significantly 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

368

369

370

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

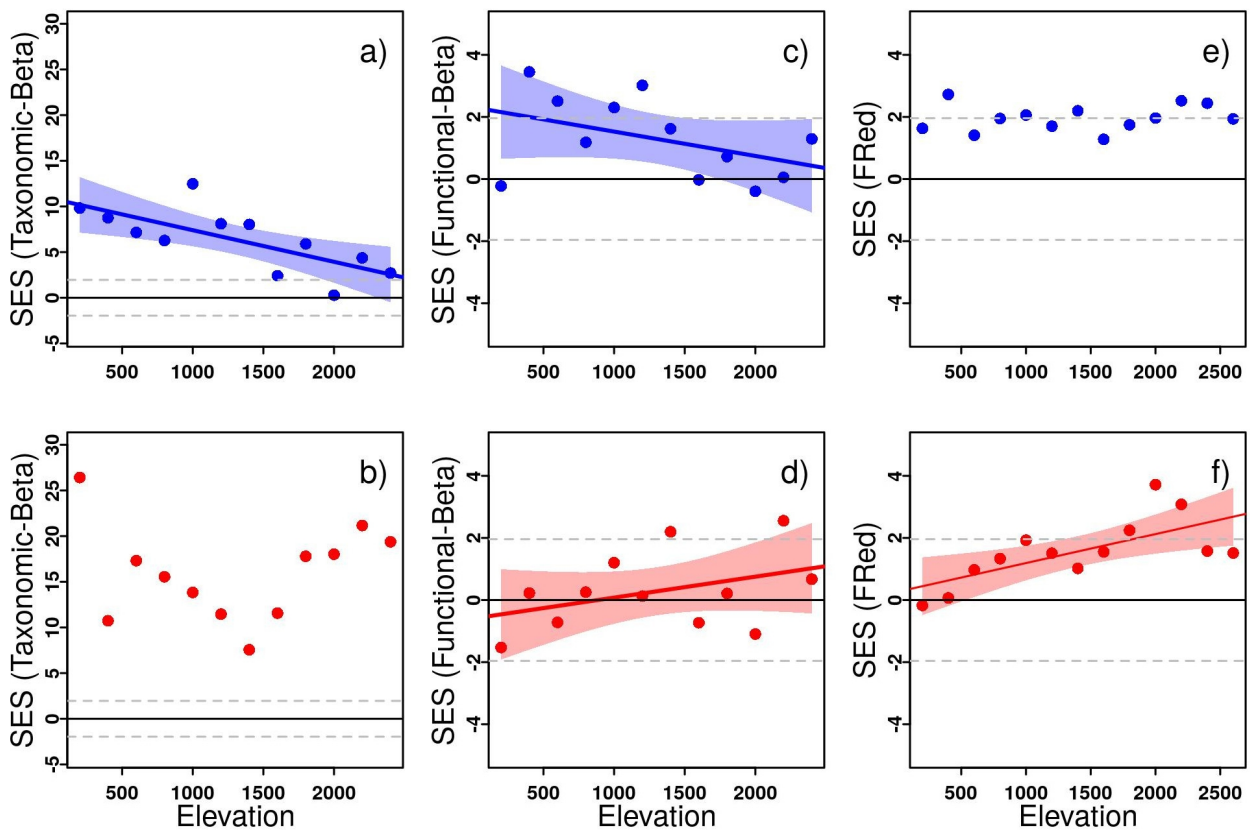


Figure 4. SES values for the deviation of observed metrics of taxonomic beta-diversity (a & b), functional beta-diversity (c & d) and Functional redundancy (e & f) along the elevational gradient, presented for hawkmoths (blue; top row) and birds (red; bottom row). SES values greater than 1.96, or less 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.value = 0.18) as compared to geographic distance (Mantel's
 405 $R_{\text{taxonomic}} = 0.48$, p.value < 0.005; Mantel's $R_{\text{functional}} = 0.29$, p.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.value < 0.05; $R^2_{\text{functional}} = 0.63$,
 411 p.value < 0.05) than hawkmoths ($R^2_{\text{taxonomic}} = 0.41$, p.value < 0.05; $R^2_{\text{functional}} = 0.21$, p.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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528

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709 **Biosketch**

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