

1 **Title: Tropical montane gradients elucidate the contributions of functional traits to**
2 **competitive and environmental fitness**

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1 MM and RA conceived the ideas and designed methodology; RP collected the data; MM analyzed the data; MM wrote the original draft of the manuscript; MM and RA led the editing and review of the manuscript. All authors gave final approval for publication. We declare that the work presented here is our original research and has not been published elsewhere

13 **Abstract**

14 Functional traits can be classified as alpha or beta, based on their relative importance in
15 determining a species' competitive and environmental fitness, respectively. However, the link
16 between a trait and its contribution to a particular aspect of fitness is not always straight-
17 forward. We investigated phylogenetic and functional diversity for bird communities along a
18 200-2800 m elevational transect in the eastern Himalayas. We hypothesized that beta traits,
19 associated with environmental tolerances, would exhibit a directional change in mean values,
20 while alpha traits, linked to competitive strategies, would show a decrease in dispersion with
21 elevation. Our findings showed that most functional traits exhibited a decrease in dispersion
22 with elevation. However, surprisingly, the mean values of these traits also exhibited a
23 significant relationship with elevation, suggesting their involvement in both competitive and
24 environmental fitness. Furthermore, we observed that morphological traits, traditionally
25 considered beta traits associated with environmental tolerance, were influenced more strongly
26 by resource availability and habitat structure rather than aspects of temperature or air density.
27 These results challenge the simplistic classification of traits as either alpha or beta. We
28 suggest that future studies should carefully analyze the variation in mean values and
29 dispersion of individual traits before assigning them solely to a particular category of fitness.
30 The results contribute to a broader understanding of the complex interactions between
31 functional traits, fitness, and environmental conditions in Himalayan bird communities.

32 **Keywords:** community assembly, birds, eastern Himalaya, functional traits, phylogenetic
33 diversity

34 **1. Introduction**

35 One of the key goals of tropical ecology is to understand the relative importance of two
36 deterministic assembly processes – environmental filtering and interspecific competition –
37 across taxa and regions (Jarzyna et al. 2021). The large environmental gradients and habitat
38 heterogeneity in montane ecosystems, at relatively small scales, results in a network of local
39 communities which are subsets of the larger ‘regional’ species pool, filtered according to the
40 species’ local environmental requirements . Co-occurring species are further characterized by
41 specialized utilization of resources which minimizes competition and facilitates high local
42 diversity (MacArthur and Levins 1967). The two processes together determine the structure
43 and composition of local communities (Weiher and Keddy 1995).

44 The presence of these two processes may be inferred by examining the functional and
45 phylogenetic structure of co-occurring species within local communities (Cavender-Bares et
46 al. 2009). Environmental filtering selects for species with similar functional traits that impart
47 adaptive advantages under the local abiotic conditions, resulting in a more clustered or under-
48 dispersed trait composition relative to the regional trait pool (Weiher and Keddy 1995;
49 Swenson and Enquist 2007). Conversely, interspecific competition would tend to segregate
50 functional traits to limit similarity and reduce competition among co-occurring species,
51 resulting in an over-dispersed community trait structure. When these functional traits are
52 phylogenetically conserved – i.e., closely related species have more similar traits – similar
53 patterns of phylogenetic clustering and over-dispersion may also be expected (Coyle et al.
54 2014).

55 Lopez et al. (2016) proposed classifying functional traits as alpha and beta according to their
56 perceived importance in determining co-existence and environmental tolerance, respectively

57 (also see Ackerly and Cornwell 2007; Silvertown et al. 2006; Pavoine and Bonsall, 2011). The
58 classification is derived from the concepts of alpha and beta niche (Whittaker 1975), wherein
59 the former determines the division of resources among co-occurring species, while the latter
60 influences a species' distribution across an environmental gradient. Accordingly, functional
61 traits involved in competitive strategies such as resource acquisition or feeding strategy are
62 classified as alpha traits (e.g. plant height and root depth), and those which determine species'
63 environmental tolerances, such as the constraints imposed by temperature, oxygen and/or
64 water availability are classified as beta traits (e.g. leaf size and wood density).

65 The link between a trait and its contribution to a particular aspect of fitness is arguably easier
66 to determine in the case of plants with help of manipulative field and laboratory experiments
67 (Ruprecht et al. 2014; Pérez-Ramos et al. 2019). Not surprisingly, a majority of the studies
68 that use this classification have dealt with plants (Klimeš and Klimešová 2000; Ackerly et al.
69 2006; Silvertown et al. 2006). Classifying traits in this manner is not always straight-forward
70 with animals, based as it is largely on observations and information from species' natural
71 histories than on experimental data (Miles and Ricklefs 1984; Pigot et al. 2016). For
72 example, the beak of a bird is commonly considered an alpha trait as it is involved in resource
73 acquisition (Graham et al. 2012). However, the beak, which is uninsulated and well
74 vascularised, is also known to be involved in thermoregulation i.e. environmental tolerance
75 (Tattersall et al. 2017). The relative importance of the beak as an alpha or beta trait will
76 depend on the particular context of the community composition and the environment it
77 inhabits (Friedman et al. 2019). Similarly, body size in birds is commonly considered an
78 important beta trait determining species environmental preferences due to its role in
79 thermoregulation (Gómez et al. 2010). However, disparity in body sizes of co-occurring
80 species is known to promote coexistence (Leyequién et al. 2007); hence it plays a role as an

81 alpha trait as well (Gómez et al. 2010). Many studies of community assembly conflate data
82 from multiple traits to construct a multidimensional picture of species' niche and/or to
83 improve the statistical signal. This requires a priori knowledge of the association between a
84 trait and the specific fitness category (i.e., alpha or beta) *in the particular study context*.

85 The change in the community mean value of a trait along the gradient of a particular
86 environmental factor may be considered an indication of an adaptive role of the (functional)
87 trait vis-a-vis that environmental factor (Muscarella and Uriarte 2016). Correspondingly, the
88 dispersion in a trait associated with interspecific competition should increase with competition
89 (Adler et al. 2013). These signatures would be easiest to discern along gradients in
90 interspecific competition and environment since changes in the mean and dispersion are easier
91 to interpret than absolute values (Lopez et al. 2016).

92 Quite conveniently, elevational transects, especially in the tropics, contain within them both
93 the gradients; it is widely believed that interspecific competition decreases, while
94 environmental filtering increases, towards high elevations (Montaño-Centellas et al. 2021; but
95 see Pérez-Toledo et al. 2022). Harsh abiotic conditions at the higher altitudes, e.g. cold
96 temperatures, limited resources, higher seasonality and low partial-pressure of oxygen,
97 impose stronger environmental filtering, restricting the utility of high elevations to species
98 with traits necessary to cope with their challenges. Conversely, low variability in the abiotic
99 conditions of the lower elevations, coupled with higher productivity and higher species
100 diversity facilitates stronger competitive interactions. Phylogenetic dispersion is arguably a
101 better surrogate of ecological dispersion along such multivariate gradients (in temperature,
102 precipitation, seasonality, oxygen availability, air density, resources, etc.), especially when the
103 extent of a trait's role in competitive and environmental fitness is not known *a priori* (Webb et

104 al. 2002; Pavoine and Bonsall 2011). This is because phylogenetic dispersion should reflect
105 on the ‘net effect’ of all underlying assembly processes: phylogenetic clustering due to
106 multiple environmental factors and phylogenetic overdispersion due to competition across all
107 conserved traits.

108 In this study, we first analyzed the variation in phylogenetic dispersion in communities of
109 birds along an east Himalayan elevational transect (200–2800m) to test the expected decline in
110 the relative dominance of interspecific competition, and increase in environmental filtering.
111 We then analyzed the variation in mean and dispersion of several commonly used avian
112 functional traits which have been associated with either one, or both aspects of fitness –
113 environmental and competitive – by previous studies, shown in Table 1. We concluded that a
114 functional trait is: (i) an alpha-trait if the dispersion in the community trait distribution
115 decreases with elevation, and (ii) a beta-trait if its community-mean value exhibits directional
116 variation with elevation

117 Our study transect is characterized by a steep decline in temperature, resource availability and
118 habitat complexity – all of which may impose environmental stress on ecological
119 communities. The transect also hosts an exceptionally high regional and local bird diversity,
120 and high rates of species turnover (Mungee et al. 2021), providing an ideal system to detect
121 signatures of competitive overdispersion. Further, our fine-scale primary data (50 m
122 elevational resolution) provides a fair picture of ‘local’ communities of co-occurring, and
123 likely interacting species.

124 **2. Materials and Methods**

125 **2.1 Study region, species and trait data**

126 We sampled birds between 200 and 2800 m along a single elevational transect in Eaglenest
127 wildlife sanctuary in the eastern Himalayan global biodiversity hotspot. Birds were recorded
128 visually or aurally along 48 transects of 100 m length, separated from their neighbours by 0.5-
129 2 km of distance and 50 m in elevation, during April-July from 2011 to 2014. A detailed
130 description of the study region and primary data can be obtained from Mungee et al. (2021).
131 We compiled four species-level morphological traits: beak size (the product of length, width
132 and depth), wing length, tarsus length and body mass. We corrected the (other) morphological
133 traits for allometry with body-mass using linear regression ($R^2 = 0.28-0.89$; Supporting
134 Information; Figure S1); i.e. for each morphological trait y ,
135 $residual_y = \log_{10}(y) - intercept - slope * \log_{10}(body-mass)$.

136 We also compiled the species' behavioral and ecological preferences including primary
137 substrate, foraging mode, primary diet and habitat preferences (Price et al. 2014; Wilman et
138 al. 2014; Schumm et al. 2020; Athreya, 2006; Tobias et al. 2022). All numerical traits were
139 standardized using mean and standard deviation before analyses. Trait-trait correlations were
140 assessed using pairwise Spearman's correlations.

141 **2.2 Phylogenetic data and evolutionary signal**

142 We used Schumm et al.'s (2020) phylogeny of the Himalayan avifauna to estimate
143 evolutionary relationships of species present in our data. The sixteen species absent from this
144 phylogeny were added to their respective clades as polytomies using the global avian
145 phylogeny in Jetz et al. (2012). We used Pagel's lambda (λ ; Pagel 1999) to determine the
146 strength and significance of the phylogenetic signal in each functional trait; i.e. to determine
147 phylogenetic niche conservatism. We chose Pagel's λ over Blomberg's K (Blomberg et al.
148 2003) as it is more robust in the presence of incompletely resolved phylogenies and missing

149 branch-length information (Molina-Venegas and Rodríguez 2017). A value of zero indicates
150 no phylogenetic signal, whereas values ≥ 1 indicate a strong phylogenetic signal (Pagel 1999).
151 We estimated the statistical significance of λ by using likelihood ratio tests which compare the
152 observed trait values to those expected with $\lambda = 0$.

153 **2.3 Community trait and phylogenetic dispersion along the elevational gradient**

154 We calculated phylogenetic and trait dispersion using Mean Pairwise Distance (MPD) and
155 Mean Nearest Taxon Distance (MNTD; Webb et al. 2002). MPD is the average functional or
156 phylogenetic distance between all co-occurring species in a community. Its value is influenced
157 by the lengths of the branches connecting the deep or ‘basal’ nodes of the functional or
158 phylogenetic tree. On the other hand, MNTD is calculated as the average distance between
159 each species and its closest relative in the local community. Therefore, MNTD is more
160 informative on the dispersion in the ‘terminal’ nodes of the functional/phylogenetic tree. For
161 both metrics, MPD and MNTD, higher values indicate higher trait/phylogenetic dispersion
162 while lower values indicate clustering (Webb et al. 2002).

163 We calculated MPD and MNTD for (i) each individual functional trait – e.g. MPD_{BEAK} and
164 $MNTD_{\text{BEAK}}$ (for beak size), (ii) multivariate functional diversity – MPD_{F} and $MNTD_{\text{F}}$, i.e. all
165 the functional traits pooled together, and (iii) phylogenetic diversity – MPD_{P} and $MNTD_{\text{P}}$. In
166 the multivariate analysis, we used equal weights for each trait. The functional trait
167 dendrogram (needed to calculate MPD and MNTD) was generated using Gower distances
168 (Gower 1971) since it can accommodate both numerical and categorical traits.

169 We used null models to determine if the MPD and MNTD metrics differed significantly (over-
170 or under-dispersion) from a random distribution (Webb et al. 2002). Null models that maintain

171 within-community trait-abundance link but randomize habitat occurrences i.e. across
172 community randomization, perform better when estimating under-dispersion in response to
173 environmental filtering. On the other hand, within-community over-dispersion as a result of
174 interspecific interactions are better detected with null models that do not maintain the
175 connection between species abundances and trait values (Götzenberger et al. 2016).
176 Accordingly, we tested the data using the “*frequency*” null model (*Null-1*) which performs
177 across-habitat randomizations, and the “*independentswap*” null model (*Null-2*) which ignores
178 the link between abundances and traits (Götzenberger et al. 2016). In both cases, we used all
179 species present across all elevations to populate the regional species pool as there are no
180 physical barriers along our study gradient and birds are active dispersers. For more details on
181 the randomization procedures and null models see Supporting Information Table S2.

182 We calculated Standardized Effect Sizes (SES, Gotelli and McCabe 2002) to quantify the
183 difference between the observed and the null (simulated) values of the metric X (MPD or

184 MNTD) using $SES = \frac{X_{OBS} - X_{\mu NULL}}{X_{SD NULL}}$, where μ and SD are the mean and standard deviation of

185 999 random simulations of the null model. A negative SES value suggests an under-dispersed
186 community indicative of strong environmental constraints. On the other hand, a positive value
187 suggests over-dispersion which is associated with interspecific competition. We compared the
188 results from null models calculated using species abundance and also presence-absence data
189 using Fisher’s Z-test; the former is expected to increase the sensitivity of detecting under- or
190 over-dispersion (Götzenberger et al. 2016; Tucker et al. 2016). We investigated the
191 relationship between different dispersion metrics and elevation using linear models.

192 **2.4 Community trait mean along the elevational gradient**

193 We calculated community-weighted mean (CWM) values for each local community for each
194 trait (Lavorel et al. 2008). For a quantitative trait (relative beak, relative tarsus, relative wing
195 and body mass) CWM is the mean trait value of all species present in the community,
196 weighted by their local abundances. For categorical traits (diet, foraging mode, primary
197 substrate and habitat), CWM is the proportion of each ‘category’ of the trait in the community,
198 i.e. their relative abundance compared to other categories, i.e. functional groups (Lavorel et al.
199 2008). All calculations were done in the R programming environment (Version 4.3.0; R
200 Foundation for Statistical Computing 2009, <http://www.r-project.org/>). Pagel’s λ was
201 calculated using the functions “*fitContinuous*” and “*fitDiscrete*” of the R package *Geiger*
202 (Pennell et al. 2014); pairwise species functional distances were computed using the function
203 “*gowdis*” from the package *FD* (Laliberté et al. 2014a; Laliberté et al. 2014b); pairwise
204 species phylogenetic distances were computed with “*cophenetic.phylo*” from package *ape*
205 (Paradis 2010; Paradis et al. 2019); MPD and MNTD metrics, and their SES values were all
206 generated using the package *PICANTE* (Kembel et al. 2010); package *lmtree* was used to
207 compare the slopes of linear models between abundance-based and incidence-based datasets
208 (Hothorn et al. 2015); all CWM values were computed using “*functcomp*” from the package
209 *FD* (Laliberté et al. 2014a; Laliberté et al. 2014b).

210 **3. Results**

211 We recorded 15,867 individual birds, spanning 245 species, 150 genera and 50 families. We
212 found strong and significant phylogenetic signal in all functional traits ($\lambda = 0.78-0.99$) except
213 habitat affinity ($\lambda = 0.01$), indicating that closely related species possess similar morphology
214 and ecology in our data (Table S1). Standardized effect sizes (SES) for MPD and MNTD were
215 similar across the two null models, Null-1 and Null-2. This was true for each individual trait
216 as well as multivariate functional and phylogenetic metrics. Therefore, in the remaining

217 sections we discuss only the results from Null-1, while results using Null-2 are included in the
218 Supporting Information (Figure S2 - S4).

219 MPD_F , but not $MNTD_F$, exhibited significant decline with elevation with respect to both
220 observed and SES values (Figure 1). Abundance-based $SES-MPD_F$ exhibited a steeper decay
221 with elevation than its incidence-based counterpart ($z = 1.2$; $p < 0.05$) (Table 2). MPD_p and
222 $MNTD_p$ were similar to the multivariate functional metrics (Table 2, Figure 1). Mean Pairwise
223 Distances (MPD) exhibited a negative relationship with elevation for all traits, except primary
224 substrate (Table 2, Figure 2 and 3). There were significant differences between the linear
225 regression slopes of abundance- and incidence-based MPD in four traits: relative wing
226 (Fisher $z = -3.72$; $p < 0.001$), tarsus ($z = -3.34$; $p < 0.001$), beak ($z = 4.51$; $p < 0.001$), and
227 primary substrate ($z = -3.98$; $p < 0.001$; Table 2).

228 The negative relationship with elevation was also seen when MPD was replaced by SES-
229 MPD. We point out that the negative relationships, indicating a change of dispersion with
230 elevation, are significant even though a majority of community-specific SES values lie within
231 ± 1.96 SD of the null distribution. The abundance-based metrics exhibited a steeper decay with
232 elevation for all traits except body-mass, habitat, and primary substrate (Table 2). Observed
233 values of MNTD are more variable across the different traits (Table 2, Figure 2 and 3). A
234 significant decline was observed only for relative wing length, beak and body mass. A
235 majority of community SES values lie within ± 1.96 SD (Figure 3). Relative tarsus and
236 relative beak size show U-shaped patterns of variation in observed-MNTD and SES-MNTD
237 (Figure 2).

238 CWM of relative wing length, relative beak size, and body mass decreased with elevation (R^2
239 ranging from 0.29 to 0.71), while that of relative tarsus length increased along the gradient (R^2
240 = 0.60). The patterns were less consistent and generally non-linear for the ecological and
241 behavioral (*contra* morphological) traits (Figure 4; Supporting Information Figures S5 – S8).
242 There was a strong reduction in the relative abundance of frugivorous birds, while the
243 insectivores and nectarivores increased towards the highest elevations.

244 **4. Discussion**

245 We studied the variation in dispersion and mean of functional traits for bird communities
246 along a 200-2800 m elevational transect in the eastern Himalayas. Along large elevational
247 gradients, environmental stress increases while resource specialization and interspecific
248 competition decreases with elevation. Under these conditions, beta functional traits should
249 exhibit a directional change of their mean value while alpha traits may be identified by a
250 decrease in their dispersion with elevation. We tested this for a set of commonly used
251 functional traits for birds. However, we found that most traits exhibited both trends: their
252 dispersion decreased with elevation, and their mean exhibited a significant relationship with
253 elevation. This suggests that, at least in the context of Himalayan birds, most of the
254 commonly used avian functional traits are implicated in both environmental and competitive
255 fitness.

256 It is widely believed that interspecific competition decreases while environmental filtering
257 increases towards higher elevations along mountain systems (Graham et al. 2009). This
258 phenomenon, commonly referred to as the Stress-Dominance Hypothesis (SDH), is attributed
259 to the more stressful environment of high elevations which leads to a stabilizing selection of
260 competitively dominant functional strategies, i.e. a convergent or under-dispersed functional
261 trait structure (Weiher and Keddy 1995; Swenson and Enquist 2007; Coyle et al. 2014).

262 Conversely, the greater specialization needed for sustaining co-existence in the species rich
263 low elevations leads to an over-dispersed trait structure (MacArthur 1969). Conformity to
264 SDH in birds has been observed in a number of studies in tropical mountains (Graham et al.
265 2009; Dehling et al. 2014; Boyce et al. 2019; Montaña-Centellas et al. 2019; Jarzyna et al.
266 2021) and for elevational studies across the world (García-Navas et al. 2021; Jarzyna et al.
267 2021; Montaña-Centellas et al. 2019; He et al. 2018; Ding et al. 2021).

268 Our results appear to be consistent with the SDH. We found that phylogenetic (and
269 multivariate functional) dispersion decreased with elevation (Figure 1). Our study transect
270 spanning 2600 m in elevation is characterized by a steep decline in temperature, resource
271 availability and habitat complexity – all of which may impose environmental stress on
272 ecological communities. Our spatial sampling (transects 100 m in length, separated from its
273 neighbour by ~1 km in distance, and 50 m in elevation) defines communities in which the
274 individuals may be assumed to co-occur and compete directly for local resources. In fact,
275 Weiher and Keddy (1995), while formulating Stress Dominance Hypothesis, remarked that
276 over-dispersion is likely to be “restricted to small-scales....where competitive adversity
277 predominates”.

278 Across all measured dispersion values – phylogenetic, multivariate functional and individual
279 traits – we observed a significant negative relationship between dispersion and elevation
280 using MPD. This relationship was consistently weaker or absent in the case of MNTD
281 (Figures 1-3). The stronger influence of elevation on deeper evolutionary relations (i.e. MPD
282 *contra* MNTD) suggests early radiation and colonization, followed by subsequent emergence
283 of specialization and competitive niche differences. This is consistent with one earlier study
284 from the region which showed that species accumulation in the (eastern) Himalayas is limited

285 by competition for niche space, rather than elevational expansion (Price et al. 2014). Our
286 study reveals that this specialization occurs at much finer scales than previously shown
287 (within 50 m elevational bands). The discussion of the relationship between dispersion and
288 elevation will be confined to MPD in the rest of this paper.

289 Previous studies have recommended the use of different null models for detecting over- and
290 under-dispersion, especially when simultaneous affects of environmental filtering and
291 interspecific competition are to be expected, as in the present scenario (Gotelli 2000;
292 Götzenberger et al. 2016; Tucker et al. 2016). Typically, the *frequency* null model has been
293 suggested to capture processes resulting in higher dispersion than the null, while the
294 *independentswap* null model reveals processes related to under-dispersion. Overall, our results
295 were similar across both null models (Figure S2-S4). However, we also note that in all cases
296 the dispersion values lie within ± 1.96 S.D. of both the null models. Nevertheless, the
297 reduction in dispersion is both highly significant and consistent across the elevation axis,
298 indicating a gradual but consistent shift in the nature of the dominant assembly process across
299 the elevational transect. We think this strong signal is due to the physical nature of our study
300 transect and data – a smooth, compact but steep environmental gradient sampled at 48
301 regularly spaced locations. It is quite likely that in the absence of such fine-grain sampling
302 across so many locations the linear correlation would not have been sufficiently strong to
303 compensate for the lack of data outside ± 1.96 S.D.

304 We found that incorporating species abundances in the null models, and in the calculation of
305 the different dispersion metrics improved the strength of the negative slope in most cases
306 (Table 2). Indeed, in a review spanning 2000-2014, Perrone et al. (2017) found that processes
307 related to limiting similarity are better detected with abundance data, although only a few

308 studies have specifically investigated this issue using empirical data (Bernard-Verdier et al.
309 2012). Our study provide further evidence on the importance of using species abundances
310 when assessing patterns of under- and over-dispersion along environmental gradients in
311 natural communities (also see HilleRisLambers et al. 2012; Münkemüller et al. 2012;
312 Götzenberger et al. 2016). More importantly, our results suggest that the contradictory
313 conclusions among many previous studies may stem, in part, from the use of presence-
314 absence, as opposed to abundance data.

315 Beak size in birds is most commonly associated with resource-related competition, and
316 therefore alpha-niche (Moermond and Denslow 1985; Dehling et al. 2014). We found a
317 reduction in MPD_{BEAK} with elevation (Figure 2), indicating the expected decrease in
318 competitive interactions for resources. Schoener (1971) observed a similar higher dispersion
319 in beak sizes of tropical insectivorous birds along a latitudinal gradient, and attributed this to
320 the greater diversity of available prey sizes. This suggests beak sizes as important alpha-traits
321 – although not unambiguously, since their community mean value also exhibited a strong
322 decline with increasing elevation (Figure 4). The reduction in beak size is contrary to their
323 expected role in thermoregulation (beta trait; Tattersall et al. 2017), and may be related to the
324 reduction in the size of arthropod prey with elevation (Schumm et al. 2020). We note that 90%
325 of the birds at the highest elevation are insectivores (Figure 4), suggesting resource size,
326 rather than thermoregulatory constraints, driving the beak size variation along the study
327 gradient (Boyce et al. 2019).

328 The body-mass, and to a lesser extent, wing and tarsus, have previously been considered beta-
329 traits due to their role in stress-tolerance associated with lower temperatures (Gómez et al.
330 2010). However, the reduction in wing length and body-mass in our study contradicts these

331 expectations (Bergmann's rule, Allen's rule) but is in line with previous studies from tropical
332 elevational gradients (Boyce et al. 2019; Schumm et al. 2020). The strong reduction in body
333 size has been attributed to a reduction in the sizes of arthropod preys along the study region
334 (Schumm et al. 2020). The higher elevations in our study region are also characterized by a
335 simpler habitat structure with reduced under-storey which may select for ground foraging
336 species with longer tarsi and smaller relative wings explaining the observed patterns in these
337 traits. Overall, our results indicate a stronger influence of resource and habitat structure, rather
338 than temperature or air density, on all morphological traits. Nevertheless, a strong directional
339 change in their mean value, and a decline in their dispersion suggests their role in both, beta
340 and alpha niches.

341

342 Primary substrate, i.e., the principal place a bird obtains its food, forms an important
343 component of species' behavioral and foraging niche and is a commonly used surrogate for
344 defining interspecific competitive-axis. In our study, we did not find any evidence of
345 reduction in dispersion for primary substrate, although we did observe variation in the
346 dominance structure across the five individual categories. For example, tree-canopy
347 specialists dominated at the lowest and highest elevations, whereas species obtaining their
348 food from bushes peaked at mid-elevations, co-occurring with ground, mid-canopy and tree-
349 canopy species. Other aspects of species behavioral and resource niches tested here, i.e.
350 foraging mode, diet and habitat, exhibited the expected decline in their dispersion with
351 elevation (Figure 3). We also observed an elevational dependence in the mean values of the
352 different categories of these three traits (Figure 4) though the variation is clearly non-linear.
353 Many previous studies have associated morphological traits in birds with in multiple
354 ecological axes. Our results suggest that even ecological and behavioural traits may be
355 implicated as response traits for both competition and environmental filters, via their response

356 to changing environment and habitat which requires a change in the dominant behavioral, and
357 resource acquisition strategy.

358 **Conclusion**

359 Ecological studies have relied on natural history observations to associate some of the
360 commonly measured functional traits with either competitive (alpha) or environmental (beta)
361 fitness. Our study indicates that this dichotomy is an oversimplification. While the global
362 associations between avian morphology and ecological function are widely acknowledged—
363 for instance, the beak serving as the primary tool for capturing and processing food, and
364 wings, tails, and legs being linked to locomotion—the extent to which these functions
365 contribute to competition or environmental tolerance is contingent upon the specific
366 circumstances of the species and its environment. We argue that unambiguous classification
367 of functional traits, exclusively associated with either alpha or beta niches, is not
368 straightforward. In future studies employing such classifications, it is crucial to rigorously
369 examine patterns of variation in the mean and dispersion of individual traits before assigning
370 a trait solely to a specific aspect of fitness.

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374 **Declarations**

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378 **Conflict of Interest:** We declare that we do not have any conflict of interest.

379 **Ethics approval:** Ethics approval is not applicable in this study

380 **Consent to participate:** Not applicable

381 **Consent for publication:** Not applicable

382 **Availability of data and material :** The datasets used during the current study will be made
383 publicly available on Dryad upon acceptance.

384 **Code availability:** Publicly available software and packages were used in this manuscript and
385 have been adequately mentioned and cited throughout.

386 **Authors' contributions:** MM and RA conceived the ideas and designed methodology; RP
387 collected the data; MM analyzed the data; MM wrote the original draft of the manuscript;
388 MM and RA led the editing and review of the manuscript. All authors gave final approval for
389 publication.

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561 **Table 1. Functional traits of birds used in the present study to assess variation in**
 562 **community-mean and community-dispersion along an east Himalayan elevational**
 563 **gradient.** Classifying functional traits as alpha or beta (according to their perceived
 564 importance in determining co-existence and environmental tolerance, respectively) has been
 565 suggested to associate patterns in trait dispersion (clustering/overdispersion) with specific
 566 community assembly processes (environmental filtering/interspecific competition; see text for
 567 more details). However, individual traits may be associated with single, or multiple ecological
 568 strategies in birds as shown below.

Trait	Competitive/environmental fitness	References
Beak size	<ol style="list-style-type: none"> 1. Resource-related competition (α-niche) 2. Visual and acoustic signalling (α-niche) 3. Thermoregulatory function (β-niche) 	Gómez et al. 2010; Graham et al. 2012; Luck et al. 2012; Boyce et al. 2019; Pigot et al. 2016
Body-mass	<ol style="list-style-type: none"> 1. Stress tolerance related to thermoregulation (β-niche) 2. Stress tolerance related to resource availability (β-niche) 3. Resource competition (α-niche) 	
Wing-length	<ol style="list-style-type: none"> 1. Stress tolerance related to air density (β-niche) 2. Stress tolerance related to resource availability; long-distance dispersal for foraging flights (β-niche) 3. Aligned with movement capacity which in turn influences resource use (α-niche) 	
Tarsus-length	<ol style="list-style-type: none"> 1. Resource and habitat competition, foraging niche and foraging stratum (α-niche) 2. Stress tolerance related to thermoregulation (β-niche) 	
Primary Substrate	Resource and habitat competition, foraging niche (α -niche)	
Foraging Mode		
Primary Diet	Resource competition (α -niche)	
Habitat	Habitat competition (α -niche)	

569 **Table 2. Variation of community dispersion metrics (MPD and MNTD) of bird**
 570 **functional and phylogenetic diversity along an east Himalayan elevational gradient.** Adj.
 571 R^2 (goodness of fit) represents the proportion of variance explained by the model; *p. values*
 572 represent the significance of slope ($p < 0.01^{**}$, $p < 0.05^*$). *z*-statistic and associated *p. values*
 573 are the statistics from Fisher's Z-test for comparison of abundance versus incidence datasets
 574 for the respective trait and metric.

	Obs. MPD		Obs. MNTD		SES-MPD		SES-MNTD	
	Adj. R^2	<i>z</i>	Adj. R^2	<i>z</i>	Adj. R^2	<i>z</i>	Adj. R^2	<i>z</i>
Functional (all traits)	0.34 ^{**}	-0.81	0.09 [*]	-0.86	0.33 ^{**}	1.20 [*]	0.08 [*]	-0.28
Phylogenetic	0.56 ^{**}	-0.93	0.09 [*]	-0.86	0.52 ^{**}	2.30 ^{**}	0.07 [*]	-0.66
Relative Wing length	0.39 ^{**}	-3.72 ^{**}	0.14 ^{**}	-2.42 ^{**}	0.34 ^{**}	-2.95 ^{**}	0.12 [*]	-2.16 ^{**}
Relative Tarsus length	0.43 ^{**}	-3.34 ^{**}	0.01	-0.37	0.39 ^{**}	-1.98 ^{**}	0.01	-0.21
Body-mass	0.28 ^{**}	1.30	0.28 ^{**}	-0.50	0.24 ^{**}	1.08	0.26 ^{**}	-1.16
Relative beak size	0.05	4.51 ^{**}	0.04	1.34	0.05	4.34 ^{**}	0.04	0.66
Primary Substrate	0.01	-3.98 ^{**}	0.12 ^{**}	0.74	-0.01	-4.47 ^{**}	0.11 [*]	-0.25
Foraging Mode	0.13 ^{**}	0.16	-0.02	0.80	0.12 [*]	2.93 ^{**}	-0.02	0.68
Diet	0.19 ^{**}	0.93	-0.20	1.59	0.20 ^{**}	2.49 ^{**}	-0.02	1.67 ^{**}
Habitat	0.19 ^{**}	0.94	-0.02	1.59	0.20 ^{**}	2.53 ^{**}	-0.02	1.72 ^{**}

575 **Figure 1. Variation in multivariate functional (all traits pooled) and phylogenetic dispersion for**
576 **birds along an east Himalayan elevational transect in northeast India.** Within each local
577 community, functional and phylogenetic dispersion was measured using two metrics: mean pairwise
578 distance (MPD) and mean nearest taxon distance (MNTD). The observed values for the two metrics
579 (Observed-MPD and Observed-MNTD) were compared against a randomized (null) community using
580 the standardized effect sizes (SES-MPD and SES-MNTD). Within each plot, higher values indicate
581 over-dispersion, while lower values indicate clustering in the community's trait structure. Significantly
582 clustered assemblages are those with SES values ≤ -1.96 , and significantly over-dispersed
583 assemblages were those with SES values ≥ 1.96 . However, a significant relationship of dispersion
584 (SES) with elevation is itself an indication of change in clustering/dispersion across the gradient.
585 Fitted linear models are shown only for significant relationships with elevation.

586 **Figure 2. Variation of dispersion in four functional traits (wing and tarsus length, body**
587 **mass and beak size) for birds along an elevational transect in the Eastern Himalaya of**
588 **northeast India.** Within each local community, dispersion was measured using two metrics: mean
589 pairwise distance (MPD) and mean nearest taxon distance (MNTD). The observed values for the two
590 metrics (Observed-MPD and Observed-MNTD) were compared against a randomized (null)
591 community using the standardized effect sizes (SES-MPD and SES-MNTD). Fitted linear models are
592 shown only for significant relationships with elevation.

593 **Figure 3. Variation of dispersion in four functional traits (primary substrate, foraging**
594 **mode, diet and habitat) for birds along an elevational transect in the Eastern Himalaya**
595 **of northeast India.** Within each local community, dispersion was measured using two metrics: mean
596 pairwise distance (MPD) and mean nearest taxon distance (MNTD). The observed values for the two
597 metrics (Observed-MPD and Observed-MNTD) were compared against a randomized (null)
598 community using the standardized effect sizes (SES-MPD and SES-MNTD). Fitted linear models are
599 shown only for significant relationships with elevation.

600 **Figure 4. Variation in community weighted mean (CWM) for the different functional**

601 **traits of birds along an east Himalayan elevational transect in northeast India.** CWM

602 values are shown for the four morphological traits in the first row (wing length, tarsus length,

603 body mass and beak size), and the individual categories of different ecological traits in the

604 subsequent rows. For categorical traits (diet, primary substrate and foraging mode, in second,

605 third, and fourth rows, respectively), CWM is the proportion of each functional group in the

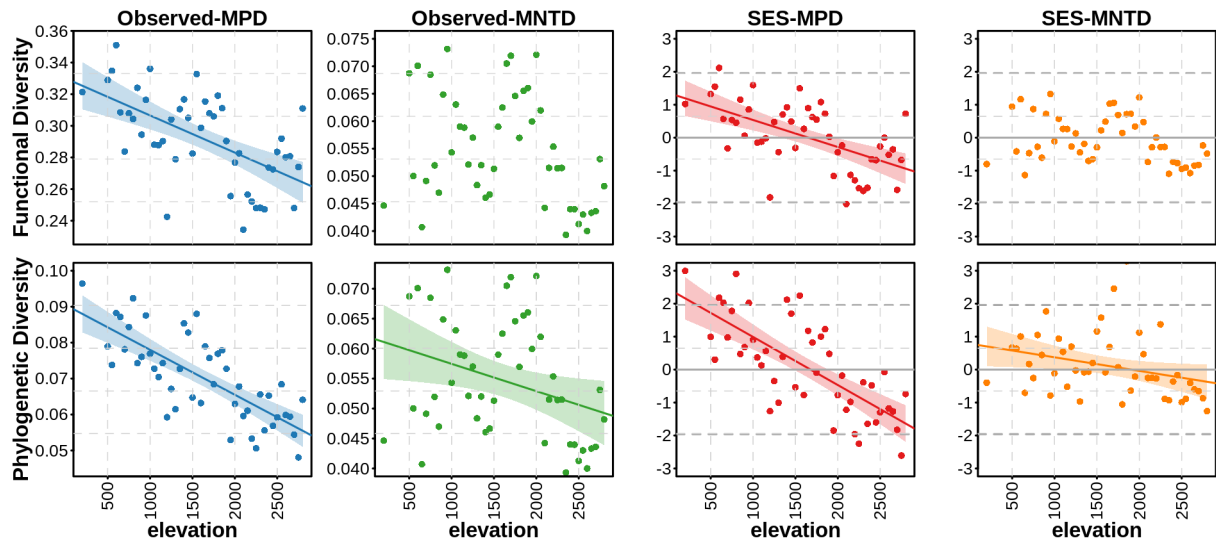
606 community, i.e. their relative abundance compared to other functional groups (Lavorel et al.

607 2008). Wing length, tarsus length and beak sizes were corrected for body-mass allometry prior

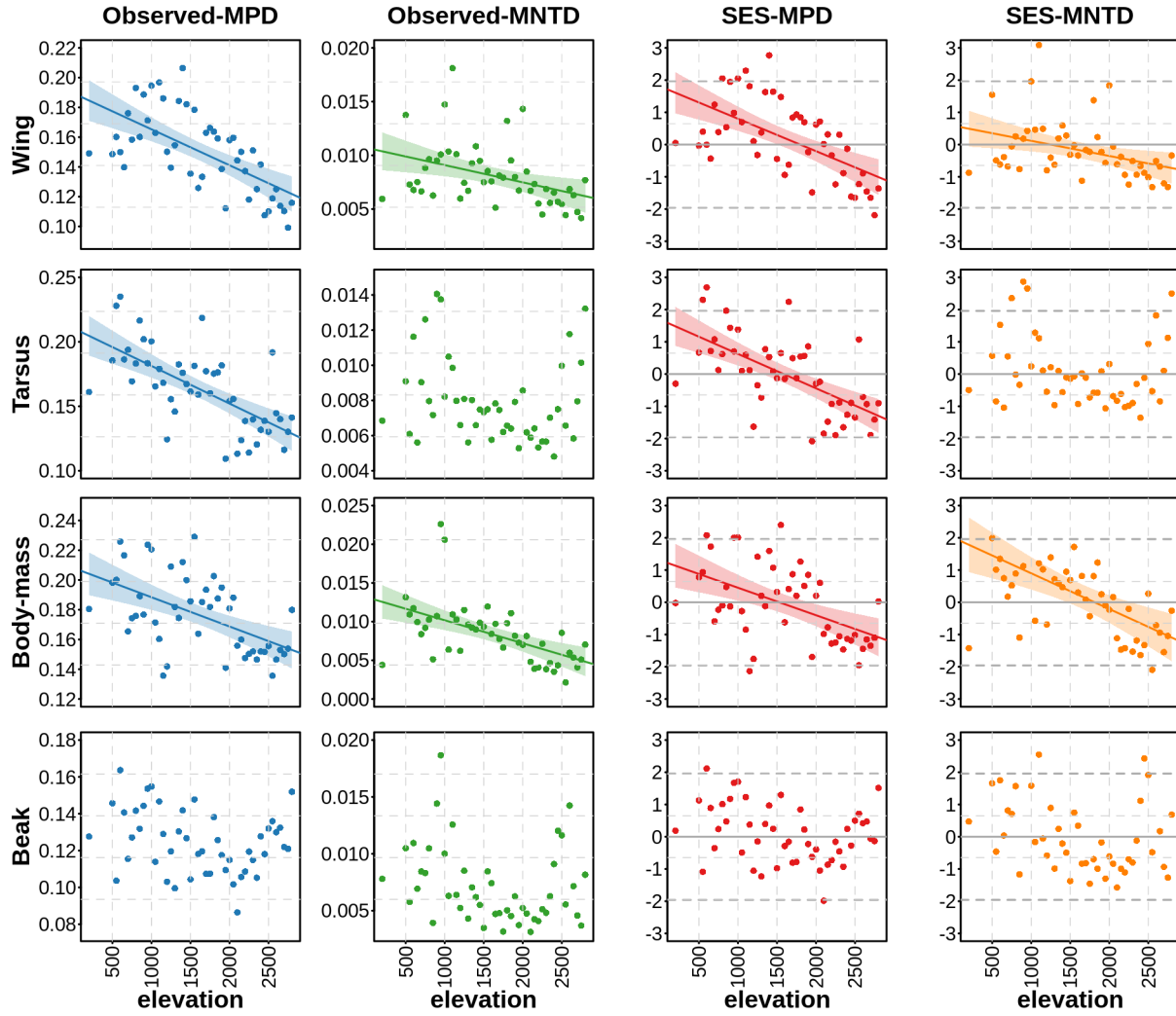
608 to the calculation of CWM values (see text for more details). For categorical traits, only four

609 representative categories are shown here. All remaining categories and the remaining

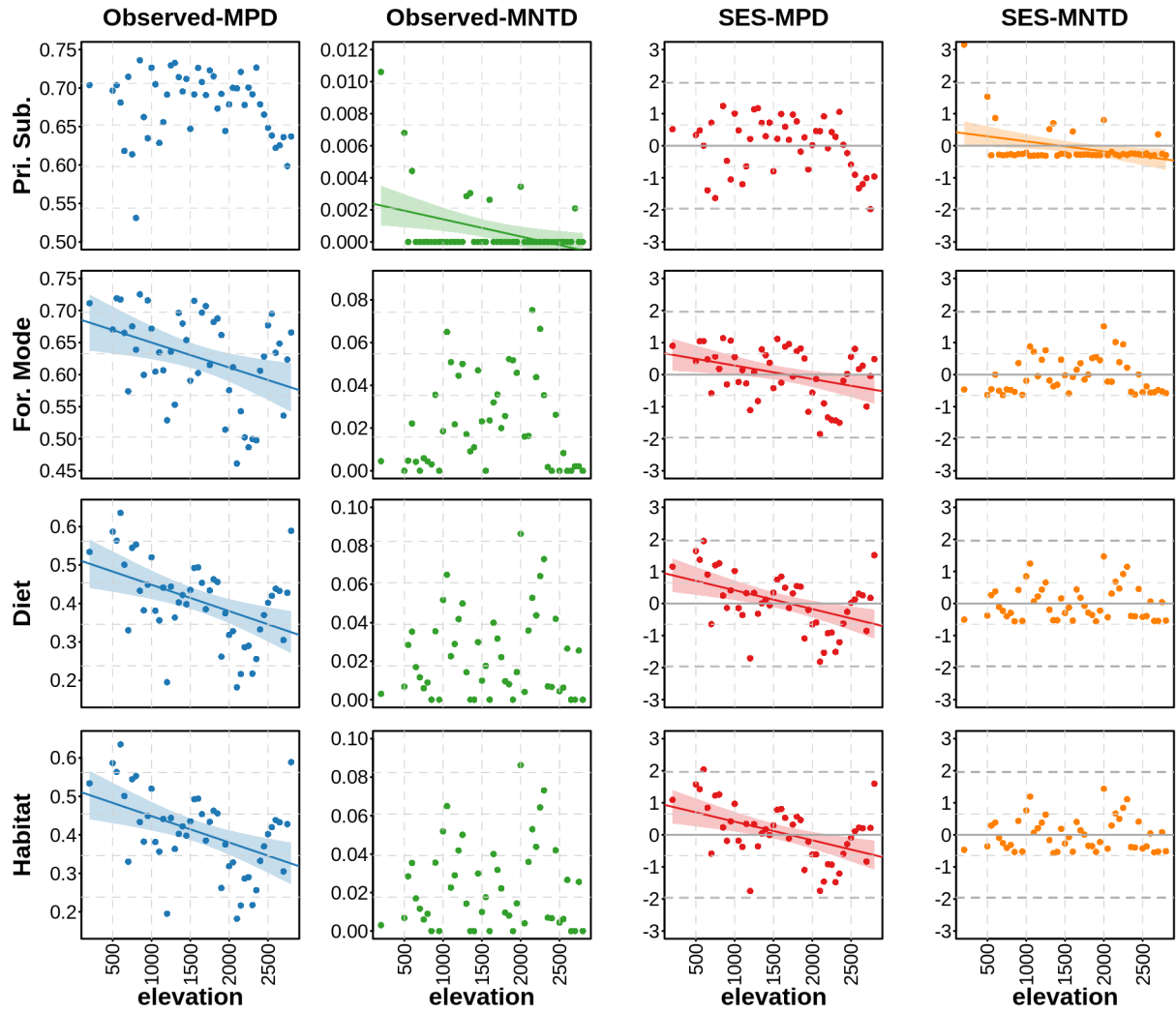
610 ecological trait (Habitat) are included as Supporting Information (Figure S5-S8).



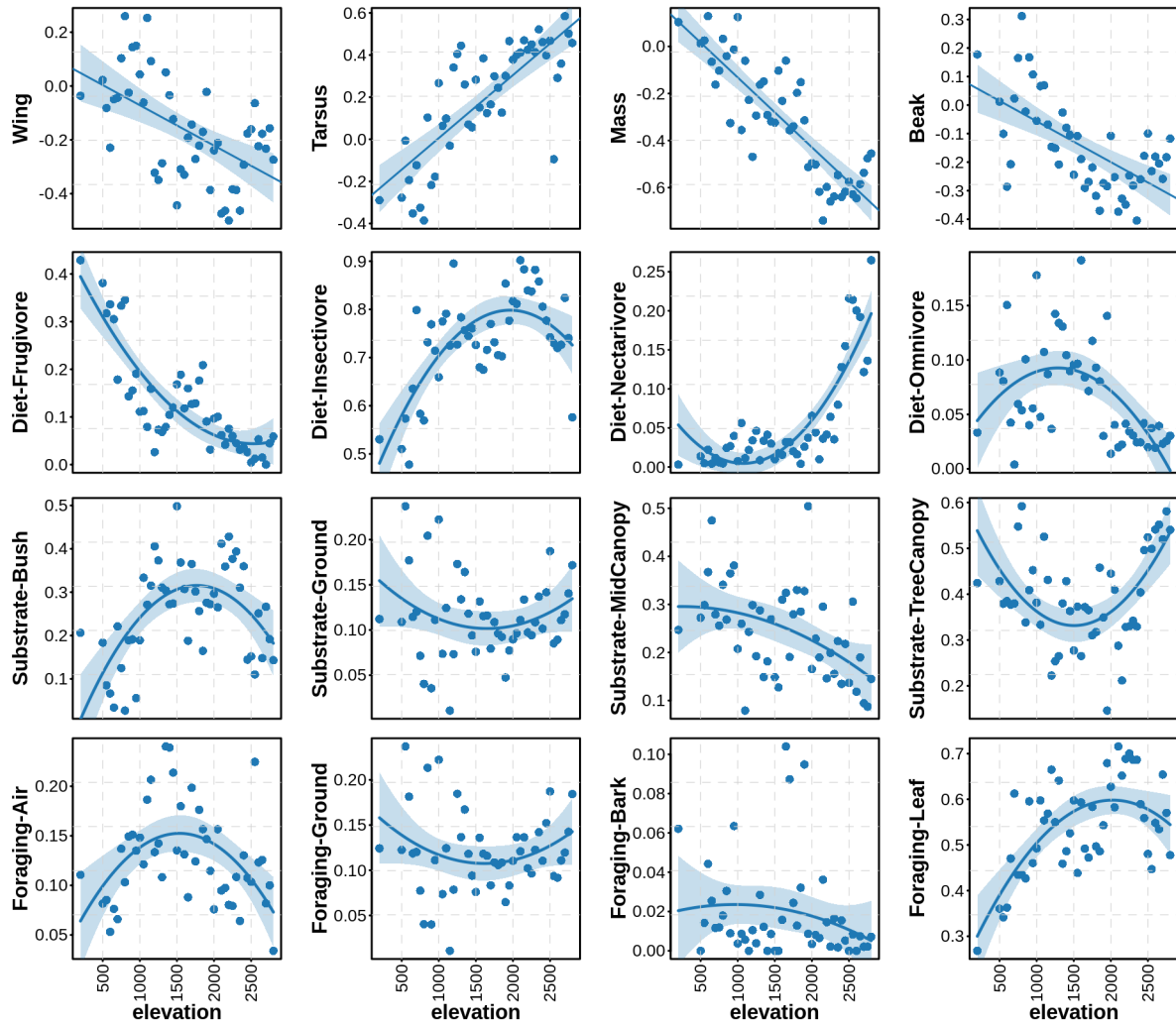
611 **Figure 1**



612 Figure 2



613 Figure 3



614 **Figure 4**