Title: Taxonomic scale dependency of Bergmann's patterns: A cross-scale comparison of hawkmoths and birds along a tropical elevational gradient

Running title: Bergmann's patterns in hawkmoths and birds

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1   **Title:** Taxonomic scale dependency of Bergmann's patterns: A cross-scale comparison of

2   hawkmoths and birds along a tropical elevational gradient

3   **Abstract**

4   Bergmann's rule predicts a larger body size for endothermic organisms in colder environments. The

5   multiplicity of patterns and processes is expected because body size and temperature are two most

6   fundamental factors on which many physiological, ecological and evolutionary processes depend,

7   affecting all levels of biological organization, from individuals to communities. The confounding

8   results from previous studies may be due to the differences in taxonomic (intraspecific, interspecific

9   and community) and spatial (latitudinal vs elevational) scales. We compared Bergmann's patterns

10   for endotherms (Aves) and ectotherms (Lepidoptera: *Sphingidae*) along a same 2.6 km elevational

11   transect in the eastern Himalayas. Using a large data spanning 3,302 hawkmoths (76 morpho-

12   species) and 15,746 birds (245 species), we compared the patterns at the intraspecific (hawkmoths

13   only), interspecific and community scales. At the interspecific scale, we account for phylogenetic

14   non-independence in body mass by using a heirarchical linear mixed effects model for hawkmoths,

15   and a phylogenetic generalised least squares model for birds. We assess the importance of using

16   abundance-weighted metrics at the community scales, after accounting for spatial auto-correlation

17   in communities. Hawkmoths exhibited positive Bergmann's pattern at the intraspecific and

18   abundance-weighted community scale. Intraspecific variation accounted for a substantial 33%

19   variation at the community level. Contrary to this, birds exhibited a strong converse-Bergmann's

20   pattern at interspecific and community scales, both with- and without-abundance. Overall, all

21   metrics which incorporate local traits and/or species abundances show stronger correlations than

22   when this information is lacking. The multiplicity of patterns at a single location provides the

23   opportunity to disentangle the relative contribution of individual- and species-level processes by

24   integrating data across multiple nested taxonomic scales for the same taxa. We suggest that future

25   studies of Bergmann's patterns should explicitly address taxonomic- and spatial-scale dependency,

26   with species relative abundance and intraspecific trait variation as essential ingredients especially at

27   short elevational scales.

28   **Key words:** Bergmann's patterns, birds, community-level, elevational gradient, hawkmoths,

29   interspecific, intraspecific, tropical

Introduction

Bergmann's rule is a popular, though contentious ecogeographical pattern which suggests a negative body size-temperature relationship in endothermic organisms. It is derived from a biophysical law which predicts better heat retention in larger-bodied animals due to their smaller surface area to volume ratio (Meiri & Dayan 2003). The direct and indirect influence of body size in many physiological, macroecological, and evolutionary processes (Bartholemew et al. 1981; Gillooly et al. 2005) and the simplicity of the initial explanation for this relationship are perhaps responsible for its popularity in ecological studies (Meiri & Dayan 2003; Watt et al. 2010; Olalla-Tárraga 2011). However, the results till date have been mixed, spanning positive, negative, and no correlation (Ashton 2002; Blackburn & Hawkins, 2004; Rodríguez et al. 2008; Olson et al. 2009; Shelomi 2012; Gutiérrez-Pinto et al. 2014; Gohli & Voje 2016; Freeman 2017; Nwaogu et al. 2018; Riemer et al. 2018).

In ectoherms, a converse Bergmann's pattern has been proposed due to the shorter seasons associated with higher latitudes and elevations, which limits developmental time and hence body size (Atkinson & Sibly, 1997; Mousseau, 1997; Chown & Gaston, 2010). However, even here, a variety of results have led to the development of several taxon- and life history-specific mechanisms including heat conservation (Zamara-Camacho et al. 2014). Some of the commonly hypothesised mechanisms, in both ectotherms and endotherms, include the starvation resistance hypothesis (Cushman et al. 1993), growing season length (Bidau & Marti 2007), water availability (Ashton 2002), converse water availability (Zug et al. 2001), primary productivity (Rosenzweig 1968), energy-water conservation (Olalla-Tárraga et al. 2009), and competition and prey-predator dynamics (McNab 1971).

52   The primary focus of research on the body size-temperature relationship has been to assess the

53   relative importance of these different processes across taxa and regions. However establishing the

54   generality of a process, even for the same organismal group, has been hindered by the differences in

55   the taxonomic scale (intraspecific, interspecific or community) at which studies are conducted

56   (Gaston et al. 2008, Olalla-Tárraga et al. 2010; Figure 1). Studies at the intraspecific scale, also

57   known as the population-approach, have documented clines along a temperature gradient (Ashton

58   2002; Yom-Tov & Geffen 2006; Fan et al. 2019) whereas interspecific studies have examined the

59   pattern across multiple species using mean values for both body size and temperature (e.g. Freeman

60   2017; Alhajeri & Steppan 2016; Beck et al. 2016). The less common community- or assemblage-

61   approach uses mean body size across all co-occurring species observed within a pre-defined area

62   such as an elevational belt or a latitudinal grid (e.g. Blackburn & Gaston 1996; Olalla-Tárraga et al.

63   2006; Rodríguez et al. 2008; Zeuss et al. 2017; Brehm et al. 2019).

64   Studies of the intraspecific pattern usually focus on a single or few closely-related species which

65   exhibit large environmental (temperature) ranges (Ashton 2002; Gutiérrez-Pinto et al., 2014;

66   Freeman 2017). Thus, although critical for understanding species-specific responses, the

67   intraspecific approach may not be ideal for addressing the generality of an 'eco-geographical rule'

68   since a majority of species do not span a sufficient range of temperature to exhibit marked

69   intraspecific variation in body size (Gaston et al. 2008). The interspecific approach, on the other

70   hand, uses information on multiple species, but constraints the data to species mean body size and

71   mid-point of its elevational/latitudinal distribution. This ignores intraspecific variation, relative

72   species abundances and range overlap between species - all three of which are shown to be strong

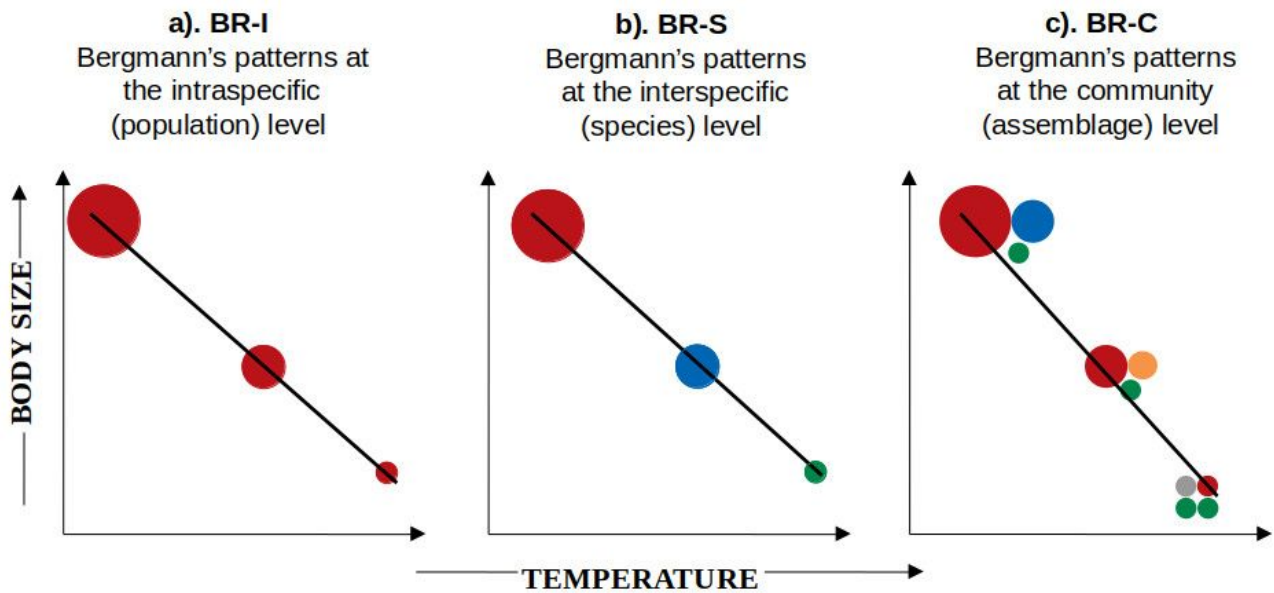73   determinants of macroecological patterns (Blackburn & Hawkins 2004).

Figure 1. Three hypothetical scenarios are shown to illustrate a positive Bergmann's pattern at three taxonomic scales: intraspecific (BR-I), interspecific (BR-S) and community (BR-C). Each circle represents an individual, colors represent different species, and the size of the circle is proportional to the body size of the individual. a). **BR-I:** In the intraspecific approach, individuals of the same species are measured at different points along a temperature gradient, and individuals observed at higher temperatures exhibit lower body size; b). **BR-S:** In the interspecific approach, multiple species are recorded along a temperature gradient, and overall smaller species are observed at higher temperatures; c). **BR-C:** In the community approach, all individuals within a pre-defined grid (or latitudinal / elevational belt) are measured and community mean body size is lower at higher temperature. The BR-C pattern can occur due to i). *Intraspecific variation* (e.g. individuals of red species are becoming smaller with increasing temperature); ii). *Interspecific variation* (e.g. blue species is replaced by the smaller orange species, which is further replaced by the even smaller grey species), or due to iii). *Variation in species abundances* (e.g. the green species of constant body size is found across the breadth of the gradient, however its abundance is higher in the community at higher temperatures).

74   Several authors have highlighted the scale-dependency of Bergmann's patterns, and the community-

75   approach is often remarked as the most appropriate way to investigate body size variation along

76   broad temperature gradients as it can account for variations at both intra- and interspecific levels

77   (Blackburn & Hawkins 2004, Meiri & Thomas 2007; Olalla- Tárraga et al., 2007). In the context of

78   a Bergmann's pattern, a greater contribution of intraspecific variation or change in species

79   abundances to the variation in community mean body size may be indicative of a stronger role of

80   size-related competition in facilitating species coexistence within a community (MacArthur &

81   Levins 1967; Siefert et al. 2015). On the other hand, stronger interspecific variation, i.e. species

82   turnover, is associated with strong environmental filtering on species' body-, and therefore range-

83   size (Keddy 1992; de la Riva et al., 2015). More importantly, the variations at the intra- and

84   interspecific scales may also occur in opposite directions, resulting in a mis-characterization of the

85   pattern or the process when either information is lacking (Vellend et al. 2014). Indeed many studies

86   in plant functional ecology have shown a congruence of patterns and processes across different taxa

87   only when individual-level data were taken into consideration (Kichenin et al. 2013; Siefert et al.

88   2015; Des Roches et al. 2018). Despite this, we found only two community level investigations of

89   Bergmann's patterns which have incorporated both, intraspecific variation and species relative

90   abundances – one on bees (Classen et al., 2017) and another on moths (Brehm et al., 2019).

91   Body size is arguably the most important animal trait, and therefore it is not surprising that its

92   variation is determined by several different processes, usually in a case- and taxon-specific manner.

93   However, more importantly, the observed "diversity of Bergmann's patterns" and the associated

94   processes is also influenced by the different contexts of the many studies. They have differed not

95   only in their taxonomic (intraspecific, interspecific or community) and spatial (latitudinal or

96   elevational) scales, but also in the metrics used for the same scales (e.g. with and without species

97   abundances/intraspecific variation for the community scale along elevational gradients; Beck et al.

98   2016; Brehm et al. 2019). Here, we investigate whether reducing the number of confounding factors

99   would make for greater uniformity of body size-temperature relationships than seen in previous

100   cross-taxa and cross-scale comparisons. We compare body size variation of endotherms (Aves) and

101   ectotherms (Lepidoptera: *Sphingidae*) along the same compact elevational transect spanning 200-

102   2770 m in the eastern Himalayas. We hypothesize that if heat conservation is the primary

103   determinant of variation in body size, then we should observe a positive Bergmann's pattern in

104   both, hawkmoths and birds, and at all three taxonomic scales – intraspecific (only hawkmoths),

105   interspecific and community, i.e. body size should increase with elevation at all taxonomic scales

106   and for both organismal groups. We further assess the importance of species relative abundances

107   and/or intraspecific variation in determining community level variation in body mass for the two

108   taxa.

109   Sphingidae, commonly known as hawkmoths, are relatively easy to identify to the species level, and

110   comprise over 1600 species globally with the highest diversity in the tropics (Beck et al. 2006a;

111   2006b, 2009; Kitching 2020). Birds are popular targets of studies of Bergmann's pattern due to their

112   high and easily identifiable diversity, well documented geographical distributions (Orme et al. 2006;

113   Quintero & Jetz 2018), morpho-trait measurements (Ali & Ripley 1972; Rasmussen & Anderton

114   2005; Wilman et al. 2014), evolutionary relationships (Jetz et al. 2012), and perhaps their role in the

115   original study (Salewski & Watt 2017).

116   **Materials and Methods**

117   *Study region and the data*

118   The study area and the hawkmoth data are described in Mungee & Athreya (2020a; 2020b). Briefly,

119   hawkmoth individuals were sampled at 13 elevations separated by approximately 200 m between

120   200 and 2770 m in Eaglenest Wildlife Sanctuary in the eastern Himalayas of Arunachal Pradesh,

121   northeast India. The region is one of the world's 8 '*hottest hotspots*' of biodiversity and endemism

122   (Myers et al., 2000) with a rich avifauna (Orme et al. 2005; Price 2012). A novel photogrammetric

123   method was used for morphological measurements of individuals of (unfettered) hawkmoths which

124   settled on a UV light screen (Mungee & Athreya 2020a).

125   We carried out transect counts of birds along the same elevational gradient, but with a higher

126   elevational resolution of 50 m. Each elevational transect was sampled on 12x2=24 occasions during

127   0600-1200 hrs in April-June, 2012-2014. We minimised systematic differences in bird activity

128   across the 6-hr sampling window by subdividing it into three periods of 2 hour each – early (0600-

129   0800 hrs), mid (0800-1000 hrs) and late (1000-1200 hrs). The 12 replicates at each elevation were

130   equally distributed across these 3 periods. We could not sample below 500 m inside Eaglenest due

131   to accessibility issues. Therefore, we sampled the lowest elevation (i.e. 200 m) in the adjoining

132   Pakke Tiger Reserve, about 20 km from the 500 m transect in Eaglenest. Species mean body mass

133   were obtained from published resources (Ali & Ripley 1972; Rasmussen & Anderton 2005;

134   Schumm et al. 2020). Due to a strong linear relationship between temperature and elevation across

135   our steep study site ($r^2 = 0.98$; $p < 0.001$), we use elevation as the independent variable in all

136   analyses (Mungee & Athreya 2020b).

137   **Statistical analyses**

138   ***Intraspecific Bergmann's pattern (BR-I)***

139   We investigated the intraspecific pattern only for hawkmoths since we did not measure traits of

140   individual birds. We estimated the pattern for hawkmoths as a group by using normalised body

141   mass and elevation with species mean values:

142
$$B_{ij}^{norm} = \frac{B_{ij} - \mu_{Bj}}{\mu_{Bj}} \quad \text{and} \quad E_{ij}^{norm} = E_{ij} - \mu_{Ej} \quad ,$$

143   where B is body mass, E is elevation, μ is the species mean, and the indices indicate the *i-th*

144   individual of the *j-th* species. With this normalisation we were able to pool the data from all

145   individuals regardless of species and elevation to derive the intraspecific relationship between body

146   mass and elevation for the 'community' as a whole. We also examined the intraspecific pattern for

147   individual species which had more than 20 individuals and spanned more than 800 m (sampled at 4

148   or more elevations) in elevational range.

149   ***Interspecific Bergmann's pattern (BR-S)***

150 For the interspecific analysis, the species' mean body mass (mean across all individuals from all

151 elevations for hawkmoths; published mean values for bird species) was determined as a function of

152 the midpoint of the elevational range for the species using ordinary least squares regression.

153 Following previous practice we used $\log_{10}$(body mass) as the dependent variable at this level.

154 However, body mass may be phylogenetically conserved across species leading to non-

155 independence of residuals in a linear regression. To account for this, we used different approaches

156 for hawkmoths and birds depending on the availability of information on phylogenetic relatedness

157 among species.

158 In case of hawkmoths, we used the phylogenetically informed taxonomic classification assembled

159 by Beerli et al. (2019) to perform a stepwise hierarchical linear mixed effect model with subfamily,

160 tribe and genus as random effects and elevation as the fixed effect. Response (body mass) and

161 explanatory (elevation) variables were standardized to zero mean and unit variance to make the

162 coefficient estimates comparable within and between the hierarchical models. In case of birds, we

163 used the phylogenetic tree provided by Schumm et al. (2020) for birds of eastern Himalayas. We

164 added 13 missing species to this tree using the latest global avian phylogeny (Jetz et al. 2012). To

165 do this, we scaled their branches to convert them into ultrametric trees, and used the relative branch

166 lengths and placement from the global phylogenetic tree. We ran a phylogenetic generalized least

167 square (PGLS) regression and estimated the phylogenetic signal of body mass by maximum-

168 likelihood estimated values of Pagel's lambda (Pagel, 1999).

169 ***Community-scale Bergmann's pattern (BR-C)***

170 For the community approach (BR-C), we calculated three metrics to assess the importance of

171 species abundances and/or intraspecific variation in characterizing the community-level variation in

172 body mass of hawkmoths and birds:

173   i.   *CM-S (Community mean using species data):* Mean body mass across all co-occurring
174   species at an elevation without considering their relative abundance. For hawkmoths, a
175   single 'regional' mean (across all individuals from all elevations) body mass value was used
176   for each species; this is the usual method while assessing grid-level assemblage patterns
177   across latitudinal gradients (Olalla-Tárraga et al., 2010); it depends only on turnover in
178   species richness *i.e.,* species occurrences.

179   ii. *CM-A (Species Community mean with species abundance):* Mean of species mean trait
180   value, weighted by elevation-specific abundance. This has been usually termed Community
181   Weighted Mean (CWM) in previous studies (Cornwell & Ackerly 2009) but we suggest that
182   the terminology used here brings out the differences in the three metrics in an easier manner;
183   this metric encapsulates turnover in species diversity i.e., both species richness and
184   abundance.

185   iii. *CM-I (Community mean using individual data; only hawkmoths):* Mean of all co-occurring
186   individuals at an elevation, regardless of their species; it includes turnover in richness and
187   abundance, and intraspecific variation.

188 We calculated the linear regression of the BR-C metrics with elevation, with and without weighting
189 the communities using species richness (following Meiri & Thomas 2007). Additionally, for the
190 metric CM-A, we also compare the patterns using community-weighted median, instead of mean.
191 For all community level plots, we evaluated spatial autocorrelation in mean body mass by using
192 Akaike Information Criterion (AIC) and the Likelihood Ratio (LR) tests of residuals (Diniz-Filho et
193 al. 2003).

194 For hawkmoths, we also assessed the relative contributions of intra- and interspecific variability
195 effects on community mean body mass along the elevational gradient following the variance

196   decomposition method proposed by Lepš et al. (2011). This method is based on the decomposition

197   of the total sum of squares ($SS_{specific}$) of the community-level trait variance along an environmental

198   gradient (elevation) into three additive components: 'fixed' (SS_{fixed}), 'intraspecific' ($SS_{intraspecific}$) and

199   'covariation' (SS_{cov}) effects:

$$SS_{specific} = SS_{fixed} + SS_{intraspecific} + SS_{cov}$$

201   The two community-mean metrics used for this decomposition i.e. 'fixed' and 'specific' averages

202   correspond to our CM-A and CM-I metrics. The 'specific' community-average body mass is

203   calculated using the 'local' species body mass i.e. mean across individuals measured at that

204   elevation (thus includes both inter- and intraspecific effects), and 'fixed' community-average body

205   mass uses 'regional' species body mass i.e. mean across all individuals from all elevations along the

206   gradient (includes only the interspecific effects). The effect of 'intraspecific' community mean is

207   then calculated as the difference between 'specific' and 'fixed' averages. Linear regressions of the

208   'specific', 'fixed' and 'intraspecific' community averages are assessed, with elevation as an

209   explanatory variable. The sums of squares for each of the three community-average measures

210   explained by elevation is then used to assess the relative contributions of the intra- and interspecific

211   components (Lepš et al., 2011). SS_{cov} component reflects the effect of covariation between inter-

212   and intraspecific trait variability. We used 999 bootstraps to assess the significance of the three

213   components.

214   All statistical analyses were performed in R 3.6.3 (R Core Development Team 2013) and the

215   following packages were used: *spdep 1.1.3* (Bivand et al. 2018), *vegan 2.5.6 (*Oksanen et al. 2019),

216   *cati 0.99.3* (Taudiere & Violle 2015), *ape 5.3* (Paradis & Schlip 2018), *lmerTest 3.1.3* (Kuznetsova

217   et al. 2017), *caret 6.0.86* (Kuhn 2020).

218 **Results**

219 We recorded a total of 4,731 hawkmoth individuals spanning 80 morphospecies, 30 genera and 3

220 subfamilies (Figure S1; Table S1). We measured traits for 3,302 individuals from 76 species; the

221 remaining either did not sit on the gridded screen or could not be measured due to poor image

222 quality. We have presented the patterns at all taxonomic scales using only the "trait" sample of

223 3,302 individuals, since we wished to compare results across taxonomic levels with the same data.

224 Adding the rest of the sample, i.e. abundance-weights for the CM-A metric in the community

225 approach, from the 4,731 individuals data did not change the results in any significant manner

226 (Supporting Information Figure S2). We recorded 15,746 individual birds from 245 species, 150

227 genera and 50 families (Table S1).

228 *BR-I*

229 At the pooled intraspecific level, hawkmoth body mass showed a weak, but significant positive

230 correlation with elevation (Table 1; Figure 2a; $r^2 = 0.001, p < 0.05$). The intraspecific patterns of

231 the 24 species in our data which had an elevational range of 800 m or more and had more than 20

232 individuals were idiosyncratic (Table S2; Figure S1). Of them, the patterns of 17 (71%) species

233 were not statistically significant, and only 6 (25%) species (*Acosmeryx naga, Acosmeryx omissa,*

234 *Cechetra lineosa, Callambulyx rubricosa, Eupanacra sinuata* and *Rhagastis lunata)* exhibited weak

235 but positive correlations, and one species a negative correlation (*Theretra clotho*) (Table S2; Figure

236 S1).

237 *BR-S*

238 We found no support for an interspecific Bergmann's pattern in hawkmoths using ordinary least

239 squares regression (Table 1; Figure 2b; $r^2 = -0.01, p = 0.6)$. Across the three hierarchical models,

240 the explained variance (*pseudo-r^2*) was consistently high (>0.5) and increased with each nested

Table 1. Linear regression between body size variation and elevation for hawkmoths and birds, at different taxonomic levels. All slopes significant at p < 0.1 are in bold.

HAWKMOTHS			
Taxonomic level	**Model**	**Slope ± SE**	**R^2**
Intraspecific	Normalised(BM) ~ Normalised(Elevation); OLS	**$(1.525 \pm 0.742) \times 10^{-5}$**	**0.001****
Interspecific	$\log_{10}$(BM) ~ Elevation; OLS	$(2.714 \pm 5.179) \times 10^{-5}$	-0.01
	Standardised(BM) ~ Standardised(Elevation) + (1|Subfamily); LME	Pseudo-r^2 (Explained Deviance) = 0.57	
	Standardised(BM) ~ Standardised(Elevation) + (1|Tribe); LME	Pseudo-r^2 (Explained Deviance) = 0.67	
	Standardised(BM) ~ Standardised(Elevation) + (1|Genus); LME	Pseudo-r^2 (Explained Deviance) = 0.80	
Community	CM-S ~ Elevation; OLS	**$(-1.148 \pm 0.578) \times 10^{-4}$**	**0.20***
	CM-A ~ Elevation; OLS	**$(1.069 \pm 0.408) \times 10^{-4}$**	**0.33****
	CM-I ~ Elevation; OLS	**$(1.373 \pm 0.573) \times 10^{-4}$**	**0.28****
	Community median BM ~ Elevation; OLS	**$(1.901 \pm 0.564) \times 10^{-4}$**	**0.46****
	CM-A ~ Elevation; SAR	**$(1.254 \pm 0.385) \times 10^{-4}$**	**0.43****
BIRDS			
Taxonomic level	**Regression Variables**	**Slope ± SE**	**R^2**
Interspecific	$\log_{10}$(BM) ~ Elevation; OLS	**$(-1.98 \pm 0.478) \times 10^{-4}$**	**0.06*****
	$\log_{10}$(BM) ~ Elevation; PGLS	**$(-3.830 \pm 0.522) \times 10^{-4}$**	-
Community	CM-A ~ Elevation; OLS	**$(-3.806 \pm 0.525) \times 10^{-2}$**	**0.81*****
	CM-S` ~ Elevation; OLS	**$(-2.489 \pm 0.379) \times 10^{-2}$**	**0.78*****
	Community median BM ~ Elevation; OLS	**$(1.149 \pm 0.190) \times 10^{-2}$**	**0.75****
	CM-A ~ Elevation; SAR	**$(-3.428 \pm 0.605) \times 10^{-2}$**	**0.84*****

BM: Body mass; OLS = Ordinary Least Squares Regression; LME = (Heirarchical) Linear Mixed Effects Model with random intercept; SAR = Spatial Autoregressive model (Nagelkerke Pseudo R^2 values are reported for SAR models); CM-S: Community mean body mass across all co-occurring species without considering their local abundance; CM-A: Community mean body mass across all co-occurring species, weighted by local abundance; CM-I: Community mean body mass of all co-occurring individuals, regardless of species; * p < 0.1; ** p < 0.05; *** p < 0.01

241   level (*subfamily = 0.57; tribe = 0.67; and genus = 0.80*). Overall, integration of the phylogenetic

242   information did not affect the significance of the BR-S pattern (*p = 0.12 − 0.67*). Contrary to

243   hawkmoths, we found a significant converse-Bergmann's pattern for birds at the interspecific level

244   (Table1; Figure 3a; *r^2 = 0.06, p < 0.01*). Phylogenetic generalised least square (PGLS) models gave

245   similar results (Table1; *λ = 0.88;* 95% confidence interval = [0.85, 0.90]), hence we discuss only
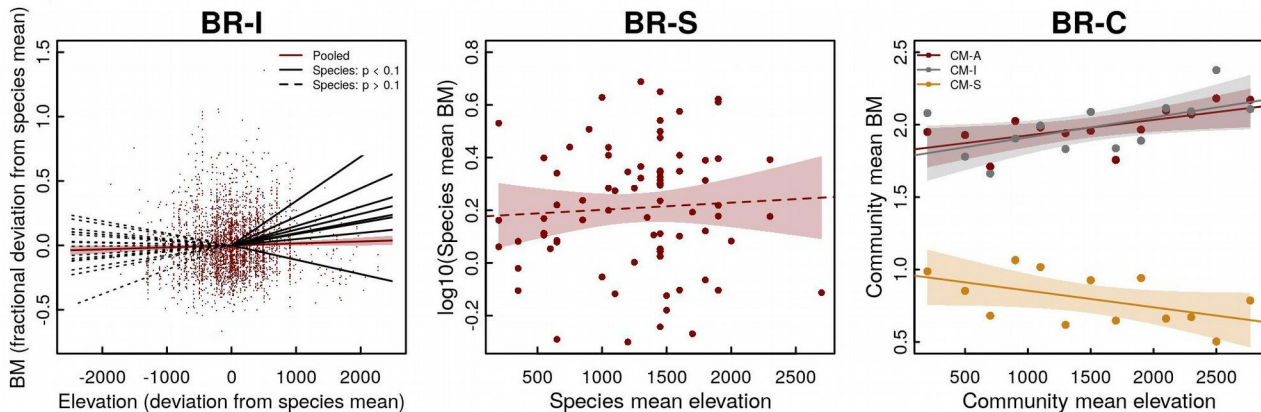
246   OLS results below.

Figure 2. Relationship between elevation and body mass (BM) for hawkmoths at different taxonomic scales. *a) BR-I:* average intraspecific pattern obtained by pooling data of all individuals from all species. The red line represents the regression fit for the pooled data, while the black lines represent the 24 individual species which were sufficiently numerous (also see Figure S1); *b) BR-S:* interspecific pattern using species mean body size and midpoint of the elevational range; *c) BR-C: (i) CM-S (Community mean using species data):* Mean body mass across all co-occurring species at an elevation without considering their relative abundance (orange), *(ii) CM-A (Species Community mean with species abundance):* Mean of species mean trait value, weighted by elevation-specific abundance (red); *(iii) CM-I (Community mean using individual data):* Mean of all co-occurring individuals at an elevation, regardless of their species (grey). Regression coefficients for all the linear fits are listed in Table 1. All fits significant at p < 0.1 are shown as solid lines, the rest are as dashed lines.

BR-C

We found a significant positive Bergmann's pattern in hawkmoths at the community level for the abundance-weighted metric without incorporating intraspecific variation i.e. CM-A (Table 1; Figure 2c; $r^2 = 0.33$; $p < 0.05$) and for the abundance-weighted metric which incorporates intraspecific variation i.e. CM-I ($r^2 = 0.28$; $p < 0.05$). However, surprisingly, we found a significant negative pattern using the metric CM-S which does not incorporate 'local' abundance or intraspecific variation (Table 1; Figure 2c; $r^2 = 0.20$; $p < 0.1$). Similar to the interspecific analysis, community mean body mass exhibited a significant converse-Bergmann's patterns in birds (Figure 3b). Unlike in hawkmoths, the pattern was consistent between CM-A ($r^2 = 0.81$; $p < 0.01$) and CM-S ($r^2 =$
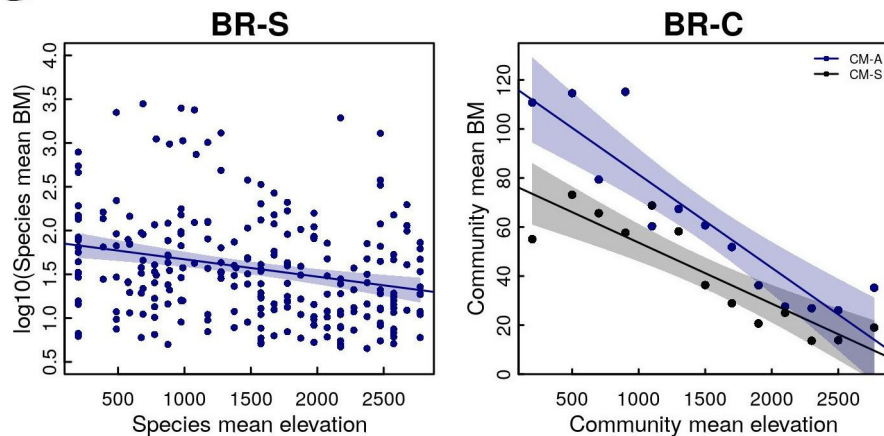
Figure 3. Relationship between elevation and body mass (BM) for birds at two taxonomic scales. ***a)*** ***BR-S:*** interspecific pattern using species mean body size and midpoint of elevational range; ***b) BR-C:*** *(i) CM-S (Community mean using species data):* Mean body mass across all co-occurring species at an elevation without considering their relative abundance, *(ii) CM-A (Species Community mean with species abundance):* Mean of species mean trait value, weighted by elevation-specific abundance; regression coefficients for all the linear fits are listed in Table 1. The regression lines were all significant at p < 0.1.

256   *0.78; p < 0.01*). Weighting the communities by species richness (Table S3), or using median instead

257   of mean (Table 1) did not significantly affect the parameter estimates, for both hawkmoths and

258   birds. Variance partitioning of hawkmoth community mean body mass showed that interspecific

259   variation (STV) and intraspecific variation (ITV) contributed 54.2 ± 8.1% and 33.0 ± 5.5%

260   respectively, with an overall 12.8 ± 8.4% positive co-variation between the two (Figure 4).

261   **Discussion**

262   We have shown that hawkmoths and birds exhibit contrasting body size-elevation relationships at

263   the abundance-weighted community level along the same 2600 m elevational transect in the east

264   Himalayas. Interestingly, endothermic birds exhibited a strong converse-Bergmann's pattern while

265   ectothermic hawkmoths showed a positive Bergmann's pattern. Statistically, the patterns varied

266   across different taxonomic scales within each group, although qualitatively they were similar only
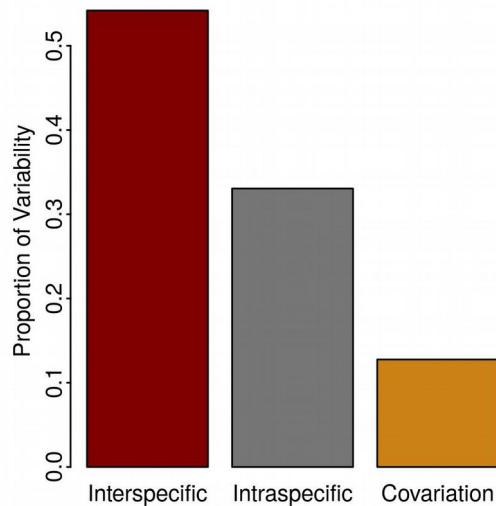
Interspecific (Species turnover)	Intraspecific	Covariation
0.54 ± 0.081	0.33 ± 0.055	0.13 ± 0.084

Figure 4. For hawkmoths, the relative contribution of intraspecific trait variation, species turnover (richness + abundance), and their covariation was assessed using the variance partitioning approach proposed by Léps et al. 2011.

267 in case of birds. Hawkmoths exhibited significant Bergmann's patterns at the intraspecific (BR-I)

268 and the community scales (CM-I and CM-A), but not when the metric did not include local trait or

269 abundance (i.e. interspecific approach; BR-S). Interestingly, the community scale pattern which did

270 not include local species abundances (i.e. CM-S) was contrary to that of abundance-based metrics,

271 i.e. community species mean decreased with elevation. Some of the more abundant hawkmoth

272 species for which we could test the intraspecific pattern individually showed a variety of patterns

273 including positive, negative and no correlation. On the other hand, we detected the converse-

274 Bergmann's pattern in birds at all investigated taxonomic scales (i.e. BR-S, BR-CM-S & BR-CM-

275 A). However, statistically it was strongest for the abundance-weighted community mean and the

276 least for the interspecific approach. In the absence of traits of individual birds we could not test for

277 the metrics which required individual trait measurements. Clearly, thermoregulation is not the only

278 or even the primary mechanism influencing the body size-temperature relationship, even in

279 endotherms. More importantly, overall, all metrics which incorporate local traits and/or abundance

280 show stronger correlations of body mass with elevation, than when this information is lacking.

281 The variety in the observed patterns of the body size-temperature relationship has largely been

282 attributed to life-history related traits of different taxa (*e.g.* endotherms vs ectotherms; mesotherms

283 vs exotherms). However, our study provides evidence for differing patterns for the same taxon,

284 across different taxonomic scales (intraspecific, interspecific or community), and with different

285 metrics (e.g. with or without abundance; with or without individual trait measurements), even when

286 using the same data set. Clearly, the scale and the metric with which Bergmann's pattern is tested

287 influences the conclusion of a study; i.e. each combination of metric and scale, presumably

288 reflecting a different process, has its own body size-temperature pattern. Therefore, it may be best

289 to treat 'Bergmann's Rule' simply as a label for a pattern associated with the negative relationship

290 between body size and temperature; identifying the underlying process necessarily requires an

291 understanding of the metric and the scale involved, as also an appreciation of how the pattern

292 changes with these two, even for the same data.

293 Along with taxonomic scales, another important consideration when comparing body size variation

294 across studies is the difference in the spatial scales (Levins 1992; Chase & Knight 2013; Chase et

295 al. 2018). Most studies of Bergmann's pattern have been conducted across continental scales (i.e.,

296 latitudinal gradients; Olalla-Tárraga et al. 2006; Rodríguez et al. 2008; Ollala-Tarraga et al. 2010;

297 Zeuss et al. 2017). It has been suggested that the dominance of species turnover obviates the need to

298 incorporate intraspecific or abundance variation at latitudinal scales, whereas intra-community

299 dynamics, such as competition, play a stronger role in facilitating co-existence for shorter

300 elevational transects where the environment changes substantially within a small geographic scale

301 (Siefert et al. 2015). However, a large number of intraspecific analyses of Bergmann's patterns have

302 shown that many species can exhibit substantial phenotypic or genetic variation in body mass even

303 across continental scales (Ashton 2002; Adams & Church 2007; Hassall 2015; Goldberg et al.

304 2018). To our best knowledge, no study has yet assessed the role of intraspecific/abundance

305   variation in determining community-level Bergmann's patterns across broad latitudinal gradients,

306   although examples exist in the plant functional ecology literature (Siefert et al. 2015).

307   In our study, which spans a geographically compact transect, metrics which used abundance show

308   higher significance of correlation, more so for hawkmoths than for birds. The difference in role of

309   species abundance between hawkmoths and birds may be related to their beta diversities: 0.68 for

310   hawkmoths and 0.93 for birds (Sørensen Indices; Supporting Information Figure S3), suggesting the

311   presence of species with broader rangers in the former. Intraspecific variation and change in

312   abundance may play a greater role in the change in community mean trait in taxa containing species

313   with large geographical ranges. This also corroborates the lack of any significant correlation in the

314   BR-S and BR-CM-S approach for hawkmoths, both of which lacked species relative abundances.

315   On the other hand, turnover in species occurrences dominated the community-mean variation in

316   birds and hence the negative body mass-elevation correlation was detected with and without

317   abundance in both BR-S and BR-C.

318   Further, while latitudinal and elevational transects are most often viewed as similar through the

319   prism of temperature, they differ in several important, but rarely considered, determinants of animal

320   body size like oxygen availability (Körner 2007), air density (Dillon et al. 2006), UV-radiation

321   (Mani 1968), etc. which may have contrasting influence on organismal body size through multiple

322   pathways (Klepsatel et al. 2014). For instance, temperature seasonality is more prominent at high

323   latitudes than at high elevations in the tropics (Rahbeck 1997; Körner 2000). Contrasting patterns of

324   body size variation between latitudinal and elevational gradients has been reported for both

325   endotherms and ectotherms (Gutiérrez-Pinto et al. 2014; Klepsatel et al. 2014; Sun et al. 2017) and

326   therefore, coherence between latitudinal and elevational Bergmann's patterns is not always to be

327   expected.

Bergmann's patterns in hawkmoths

328

329 At the intraspecific scale, the co-added data from individuals of all hawkmoth species exhibited a

330 weak but statistically significant positive Bergmann's pattern. It should be noted that this is the

331 average intraspecific value for the entire community. Of the 24 species tested separately, 6 (25%)

332 exhibited a significant Bergmann's pattern while 1 species exhibited a converse Bergmann's pattern.

333 Two of these (*Cechetra lineosa* and *Acosmeryx naga),* represent the most abundant species in the

334 region (> 25% in our data set) and span almost the entire sampled elevational extent. It has been

335 previously remarked that intraspecific clines in body size are generally expected only for the

336 'common' species with large geographic ranges (*sensu* Chown & Gaston 2010). One reason for this

337 may be the lack of statistical power for the smaller samples of the less abundant species for a given

338 effort. Another reason for this may come from the generally smaller geographical, and hence

339 environmental ranges associated with rare species. Therefore the intrinsic dispersion in the trait

340 values within such a species would be a larger fraction of the width in environmental optimum

341 across the geographical range. Whether the intraspecifc Bergmann's clines in species of hawkmoths

342 of our study region are due to genetic adaptation or phenotypic plasticity remains to be investigated.

343 At the species level, we did not find any significant correlation between body mass and elevation,

344 which is in agreement with the three previous studies of the interspecific Bergmann's pattern in

345 moths: of hawkmoths across latitude (Beerli et al. 2019), of Geometridae across elevation (Brehm

346 & Fiedler 2004), and of macrolepidoptera in general across elevation (Beck et al. 2016). Beerli et al.

347 (2019) reported a support for the resource availability hypothesis for hawkmoths at a latitudinal

348 scale which links adult body size to resource availability during the developmental phase

349 (Rosenzweig 1968). Our results do not support this, since productivity was strongly negatively

350 correlated with elevation along our study transect (NDVI ~ elevation: $r^2 = 0.84; p < 0.01$).

351   No previous work has assessed community level variation in body size for the hawkmoth family.

352   Brehm & Fiedler (2004) found no significant trend for the family *Geometridae* at the community

353   level, although their smaller sampled elevational range (1000-2700 m) may have made the detection

354   more difficult. On the other hand, Zeuss et al. (2017) found a converse-Bergmann's pattern for

355   lepidopteran assemblages at a continental scale. They showed that voltinism, or the number of

356   generations per year, may limit adult body size in macrolepidoptera by affecting the time available

357   for development during the larval stage, although with species-specific exceptions. We note that the

358   non-abundance weighted community-mean metric yielded a converse-Bergmann's pattern in our

359   study also, though we are not in a position to test for voltinism at this stage. Brehm et al. (2019)

360   reported a positive Bergmann's pattern in the ectothermic *Geometridae* and *Arctiinae* moths in

361   Costa Rica, and ruled out thermoregulation as the primary mechanism. It has been suggested that

362   hawkmoths should be considered as (behavioural) endotherms – for the purpose of Bergmann's

363   pattern – because of their active 'shivering' of thoracic muscles to heat up the body (Heinrich 1993;

364   Beerli et al. 2019) which explains the positive body size-elevation relationship at the community

365   level in our study. However, it may be noted that the only other community-approach to

366   Bergmann's patterns in moths, which incorporates both – intraspecific variation and species relative

367   abundances – and was conducted along a tropical elevational gradient for a direct comparison, also

368   revealed a strong positive Bergmann's patterns along the elevational gradient in strictly ectothermic

369   groups i.e. *Geometridae* and *Arctiinae* (Brehm et al. 2019). This raises an important question of

370   whether this similarity is methodological, or mechanistic.

371   Overall, interspecific variation of species turnover accounted for an average 54%, where as

372   intraspecific variation accounted for 33% of the total community-level body mass variance in

373   hawkmoths as shown through variance partitioning. This result is consistent with a growing body of

374 literature advocating the use of both individual and species-specific traits to investigate community

375 level trait-environment relationships (Jung et al. 2014, Siefert et al. 2015, Enquist et al. 2015;

376 Classen et al. 2017). Only few studies have explored the extent of intraspecific variability in insect

377 communities till date, and obtained very contrasting values (e.g. < 5% for dung beetles (*Insecta:*

378 *Coleoptera*) by Griffiths et al. 2016; < 1% for stonefly assemblages (*Insecta: Plecoptera*) by

379 Garcia-Raventós et al. 2017; and > 70% for spider communities (Arachnida: Araneae) by Dahirel et

380 al. 2017). Interestingly, our results are very similar to the values reported for several plant

381 communities (reviewed in Auger & Shipley 2013 and global meta-analysis in Siefert et al. 2015).

382 Other taxa have reported mixed results (33% for tadpoles by Xavier Jordani et al. 2019; 70% in

383 lichens by Asplund & Wardle 2014). It is suggested that community-level trait variation, especially

384 across broad environmental gradients, is driven primarily by species turnover, but the relative

385 importance of intraspecific variation depends strongly on the trait, environmental factor, and spatial

386 scale considered (Araújo & Costa-Pereira 2013; Siefert etal. 2014). In the context of Bergmann's

387 pattern, our results suggest that intraspecific variation should be an important consideration for

388 groups with low beta diversity (i.e. large ranges of species within the study site), and at shorter

389 spatial scales (e.g. local elevational transects). However, more studies will be needed to affirm the

390 generality of this observation.

391 **Converse-Bergmann's Patterns in Birds**

392 We found a converse Bergmann's pattern in birds at both community and interspecific scales. This

393 is entirely against the expectation from the classical thermoregulatory mechanism in endothermic

394 organisms, but matches with the previous (interspecific) pattern observed in the region (Schumm et

395 al. 2020). Schumm et al. (2020) reported a decreasing trend for forest species and positive

396 relationship for open habitat species and an initial decrease followed by increase above 3500 m

397 elevation for the entire community. We note that this transition in pattern occurred above our

398 sampling limit. Freeman (2017) found no significant relationship between species body mass and

399 elevational range mid-point for passerines in New Guinea, Peru and Costa Rica and suggested that

400 thermoregulation may not be the primary determinant for avian body mass along tropical

401 elevational transects.

402 Birds are among the most studied of animal groups and ecologists have a better understanding of

403 the various life-history traits that characterise this speciose group. Not surprisingly, Bergmann's

404 pattern has been explored along multiple life-history dimensions to understand their impact on the

405 basic thermoregulatory paradigm. We have already discussed the issue of beta diversity impacting

406 Bergmann's pattern. While thermoregulation may cause body size to increase with decreasing

407 temperature, resource (food) availability may result in a positive correlation due to reduced primary

408 productivity at low temperatures. In this context, it has been reported that the decrease of avian

409 body size with elevation in the eastern Himalayas is correlated with decreasing arthropod (their

410 prey) body size (Price et al. 2014; Schumm et al. 2020). But, results from Brehm et al. (2019) and

411 this work show that all insect groups do not show such a decrease, especially when local

412 abundances are incorporated.

413 The expected Bergmann's pattern has been seen more regularly in birds across latitudinal gradients,

414 but even here the results suggest the modifying influence of life-history traits: weaker pattern for

415 species which are migratory and/or have sheltered nesting in the western Palearctic (Mainwaring &

416 Street 2019); contrasting pattern for endemics and non-endemics in the Andes, both along

417 latitudinal and elevational gradients; successful establishment of alien species is less dependent on

418 thermoregulatory considerations than the location of introduction (Blackburn et al. 2019). On the

419 other hand, Olson et al. (2009) concluded from a global analysis of over 9000 species that the

420 positive Bergmann's pattern was driven by a combination of temperature and resource availability.

421   Analysing a large data set of North American birds, Goodman et al. (2012) found that body size was

422   more impacted by climatic variability and primary productivity than mean ambient temperature. We

423   re-emphasize that taxonomic and spatial scales are important considerations for comparing

424   mechanistic processes, however we did not find any previous study that has assessed body size

425   variation in birds along elevational transects using abundance-weighted community mean, for a

426   direct comparison.

427   **Conclusion**

428   Despite a large body of literature on characterizing Bergmann's patterns, no study has yet

429   empirically demonstrated geographic gradients in body size at the population, species and

430   community level using the same data. Our cross-taxon and cross-scale comparison using

431   hawkmoths and birds along the same 2600 m elevational gradient revealed discrepant patterns for

432   the two taxa, and at different taxonomic scales. We suggest that drawing taxon-specific

433   generalization of processes, on the basis of results from across taxonomic scales is premature. We

434   further highlight the importance of species abundances and intraspecific variation for characterizing

435   geographic gradients in body size at the level of communities, and suggest that the validity of the

436   current approach of using assemblage-means based on species occurrences and mean body sizes

437   needs to be empirically verified, especially along elevational gradients that may span the entire

438   geographic ranges of several species within a taxa. Methodologically, we argue for a community-

439   oriented approach in future studies for addressing the generality of Bergmann's pattern because of

440   its potential in resolving the relative importance of individual and species-level processes. Our

441   study, though not conducted to explicitly test any particular mechanism, provides strong support

442   against the classical thermoregulatory mechanism in endotherms, and warrants further

443   investigations into the likely mechanism (including heat conservation) governing body size patterns

444   for ectotherms. More in-depth analysis across different taxonomic scales, especially in a

445 comparative frame-work across different taxa along the same transect are required for an accurate

446 charachterization of the Bergmann's pattern. We conclude by reiterating the key lesson from this

447 study: that every study should consider, and address, the taxonomic- and spatial-scale dependency

448 of Bergmann's patterns, and species relative abundance and intraspecific trait variation may be

449 essential ingredients for doing so.

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