

1 **How has the environment shaped geographical patterns of insect body sizes? A test**
2 **of hypotheses using sphingid moths**

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32
33 **Biosketch**

34 Nicolas Beerli completed his MSc in the research team of JB, which focusses on insect
35 macroecology and the environmental impacts on biodiversity. *Author contributions:* NB and JB
36 designed the study and analysed data, supported by FB; JB, NB, LB-M and IJK provided sphingid
37 moth data; NB, JB and IJK wrote the manuscript, with input from all authors.

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39

40 **ABSTRACT**

41 **Aim:** We mapped the geographical pattern of body sizes in sphingid moths and
42 investigated latitudinal clines. We tested hypotheses concerning their possible
43 environmental control, i.e., effects of temperature (negative: temperature size rule or
44 Bergmann's rule; positive: converse Bergmann rule), food availability, agility in densely
45 vegetated habitats, robustness to starvation during extreme weather, and seasonality.

46 **Location:** Old World and Australia/Pacific region

47 **Methods:** Body size data of 950 sphingid species were compiled and related to their
48 distribution maps. Focusing on body length, we mapped the median and maximum size
49 of all species occurring in 100 km grid cells. In a comparative approach we tested the
50 predictions from explanatory hypotheses by correlating species' size to the average
51 environmental conditions encountered throughout their range, under univariate and
52 multivariate models. We accounted for phylogeny by stepwise inclusion of
53 phylogenetically informed taxonomic classifications into hierarchical random-intercept
54 mixed models.

55 **Results:** Median body sizes showed a distinctive geographical pattern, with large species
56 in the Middle East and the Asian tropics, and smaller species in temperate regions and the
57 Afrotropics. Absolute latitude explained very little body size variation, but there was a
58 latitudinal cline of maximum size. Species' median size was correlated to net primary
59 productivity, supporting the food availability hypothesis, whereas support for other
60 hypotheses was weak. Environmental correlations contributed much less (i.e., <10%) to
61 explaining overall size variation than phylogeny (inclusion of which led to models
62 explaining >70% of variability).

63 **Main conclusion:** The intuitive impression of larger species in the tropics is shaped by
64 larger size maxima. Median body sizes are only very weakly related to latitude. Most of
65 the geographic variation in body size in sphingid moths is explained by their
66 phylogenetic past. NPP and forest cover correlate positively with the body size, which
67 supports the idea that food availability allowed the evolution of larger sizes.

68

69

70 INTRODUCTION

71 Tropical insects of impressively large body size compared to their temperate
72 counterparts are a common observation of field naturalists, as well as those admiring
73 museum collections – starting with A. v. Humboldt’s scientific explorations of the
74 Neotropics around 1800, on which he collected insects of appreciable size (Barragán *et*
75 *al.*, 2009). 50 years later his successor, Amazonian explorer H.W. Bates (1864, p.115)
76 reported accidentally shooting hawkmoths so large he mistook them for small birds.
77 However, it remains unclear whether such observations necessarily imply a larger size for
78 the average tropical insect species – it just may be that their maxima are more extreme in
79 regions of higher species richness, and it is these that capture our attention ([cf. coloration](#)
80 [in tropical birds](#); Bailey, 1978). Furthermore, it must be expected that body sizes, like
81 species richness or other trait variation, exhibit more complex geographical patterns than
82 simply a latitudinal gradient (Hawkins & Diniz-Filho, 2004). Here, using sphingid moths
83 (hawkmoths) as the exemplar, we map for the first time the body size distribution of a
84 group of insects at [near-global-spatial-extent intercontinental geographic scale \(i.e.,](#)
85 [global](#) excluding ~~only~~ the Americas) and at high spatial resolution. In a comparative
86 approach we investigate how environmental conditions and phylogenetic inertia may
87 have shaped these patterns.

88 Body size is a prime example of geographic trait variation, with important links to
89 physiological functioning, population-level processes and biodiversity as a whole
90 (Gaston & Blackburn, 2000; Blanckenhorn, 2000; Brown *et al.*, 2004). Consequently, its
91 relationships to environmental variables are of major interest (Gaston & Chown, 2013),
92 yet conclusive, large-scale studies, intra- or interspecific, have mostly been carried out on
93 endotherms (Blackburn & Hawkins, 2004; Freckleton *et al.*, 2003; Olson *et al.*, 2009).
94 Environmental gradient studies on ectotherm body sizes are scarcer, less firmly rooted in
95 theory, and provide more conflicting results at an intraspecific (Ashton *et al.*, 2003; Puzin
96 *et al.*, 2014) as well as an interspecific level (Entling *et al.*, 2010; Fattorini *et al.*, 2013;
97 Slavenko & Meiri, 2015; Zeuss *et al.*, 2017; Brehm *et al.*, 2019; [Pallares et al., 2019](#)).

98 The formulation of eco-geographical rules has been the cornerstone of attempts to
99 describe patterns and understand mechanisms of trait variation, and the most well-known
100 of these, Bergmann’s rule (Meiri, 2011) concerns body size. Originally [primarily](#)
101 [addressing endothermic vertebrates restricted to mammals](#), it proposes an interspecific
102 body size increase towards higher latitudes if restricted to closely related taxa. While the
103 pattern itself is well-supported (Meiri & Dayan, 2003), fewer studies have tested and
104 supported the underlying thermoregulatory mechanism (Blanckenhorn & Demont, 2004;
105 [Watt et al., 2010; Meiri, 2011; Fattorini et al., 2013; Beck et al., 2016](#)). Other
106 mechanistic, environmental effects on body size, both evolutionary and developmental,
107 have been suggested for insects and other ectotherms (Chown & Gaston, 2010, 2013;
108 Chown & Nicolson, 2013), and these may not act in a mutually exclusive manner.
109 Furthermore, body sizes are strongly affected by phylogeny, which complicates analyses
110 and the inference on environmental causes of the observed variation (Freckleton & Jetz,
111 2009).

112 Using data on size, high-resolution maps of species’ geographical ranges, and a
113 phylogenetically-informed taxonomic classification, we mapped the geographical body
114 size pattern of sphingid moths and tested its consistency with the following hypotheses
115 while accounting for phylogenetic effects.

116 (1) Bergmann’s rule expects a negative relationship between body size and
117 environmental temperature. It assumes that thermoregulation, through the ratio of
118 heat-exchanging surface and heat-producing volume, favors larger animals in colder
119 climates. Although it was originally focused on endotherms, Zamora-Camacho *et al.*

120 (2014) argued for a Bergmann-type heat preservation mechanism in an ectotherm
121 lizard. Some studies have also investigated Bergmann's rule in Lepidoptera, with
122 mixed results (e.g., Beck *et al.*, 2016, Brehm *et al.*, 2019). Furthermore, adult
123 sphingid moths are known for pre-flight thoracic muscle temperature regulation
124 (Heinrich 1993), hence temperature efficiency may ~~be not be entirely irrelevant~~.
125 Alternatively, an intraspecific effect known as the 'temperature size rule' (TSR;
126 Kingsolver & Huey, 2008; Chown & Gaston, 2010) predicts the same pattern.
127 Laboratory experiments with many ectotherms have shown that individuals develop
128 slower yet mature into a larger body size under colder temperatures (Atkinson, 1994).
129 This may be either an effect of adaptive plasticity or it may be due to non-adaptive
130 constraints of temperature on growth rates (e.g., the discrepancy between oxygen
131 supply and demands; see Makarieva *et al.*, 2005 for an interspecific approach). The
132 TSR has also been shown to apply to a sphingid moth ~~from North America~~ (*Manduca*
133 *sexta*; Davidowitz & Nijhout, 2004).

134 (2) The 'converse Bergmann pattern' expects a positive relationship of body size and
135 temperature. The reasoning here is that lower temperatures lead to lower growth rates
136 in ectotherms, favoring species that become adult (i.e., reproductive) at smaller size
137 (Meiri, 2011; Shelomi, 2012).

138 (3) The resource availability hypothesis postulates an increase of body size with
139 increased food availability (Blackburn *et al.*, 1999; Watt *et al.*, 2010).

140 Intraspecifically, lower food availability is known to result in smaller specimens
141 (Slansky & Scriber, 1985). If this mechanism was relevant interspecifically, we can
142 predict a body size increase with net primary productivity, which we use as a proxy
143 for food availability in our herbivorous study taxon.

144 ~~(4) The agility hypothesis postulates that smaller species have an advantage in agility in~~
145 ~~dense, forest covered habitats. It predicts that body size decreases with increasing~~
146 ~~forest cover. Supporting data are so far restricted to large mammals (Bro-Jørgensen,~~
147 ~~2008), where larger species are found in open habitats than in forests. Adult sphingids~~
148 ~~are known for their very fast, nocturnal flight that could be obstructed by dense~~
149 ~~vegetation, hence we considered the idea here.~~

150 ~~(5)~~(4) The starvation hypothesis postulates that larger species occur in regions with a
151 higher risk of unforeseeable starvation. With increasing body size fat storage
152 increases faster than metabolic rate, hence survival of such catastrophic events
153 becomes more likely (Chown & Gaston, 2010). This hypothesis assumes that insect
154 species in variable climates need more physiological tolerances than those in zones of
155 stable climate (Addo-Bediako *et al.*, 2000). We predict that body size increases with
156 increasing temperature extremes during their active period.

157 ~~(6)~~(5) The seasonality hypothesis (Mousseau, 1997) assumes that in seasonal habitats,
158 where a part of the year is unsuitable for growth, smaller species profit from a faster
159 completion of their reproductive cycle. We expect a negative link of seasonality and
160 body size.

161 Phylogeny plays an important role in the current spatial distribution of species'
162 traits, due to prior adaptation to past environmental conditions and the constraints of
163 evolutionary history (Gaston & Chown, 2013). It can be assumed that a part of the
164 variation in body size is explained by phylogenetic inertia. For interspecific comparisons,
165 such phylogenetic signals within the data must be accounted for to avoid spurious effects
166 on the analysis of environmental predictor variables (Freckleton & Jetz, 2009, and
167 references therein).

168 Here, we first map geographical patterns of size in sphingids moths at large
169 geographical scale by combining detailed distribution data and body size measurements.
170 We ~~test-explored~~ whether hawkmoths are larger or smaller towards the equator using a

171 simple latitudinal cline. We then tested the above hypotheses by investigating the link
172 between body size and environmental variables, such as temperature, seasonality, forest
173 cover, temperature extremes and net primary productivity (NPP). We used a comparative,
174 ‘species-focused’ approach where every species counts equally (Chown & Gaston, 2010),
175 which is evolutionarily more informative than a ‘geography-focused’ approach (i.e.,
176 comparing grid cells). The latter would be overly impacted by widespread species that
177 occur in many cells (Jetz & Rahbek, 2002). Phylogenetic information was included into
178 the analyses at different taxonomic classification levels, which helped to identify the
179 importance of phylogenetic history in comparison to environmental effects.

180

181 METHODS

182 Hawkmoths or sphingids are a family of Lepidoptera that have attracted the
183 attention of ~~professional as well as amateur~~ insect collectors for centuries (Kitching &
184 Cadiou, 2000). Consequently, they are more extensively studied, taxonomically and
185 biogeographically, than most other insects. Recently, Ballesteros-Mejia *et al.* (2017)
186 published and analyzed detailed geographic ranges for all species occurring outside the
187 Americas (data available at www.mol.org). These maps stem from expert-edited species-
188 distribution modelling (relating published and unpublished occurrence records to climate
189 and vegetation variables, at 5 x 5 km resolution). Details on the procedures of modelling
190 and validation of geographic range maps are found in Ballesteros-Mejia *et al.* (2017). Of
191 981 species occurring in the research region, we considered ~~950-947~~ species for the
192 present analysis. The reasons for excluding some taxa were phylogenetic uncertainty
193 (~~eleven species represented taxa of i.e.~~, unreliable species status), missing environmental
194 data (~~eight small-island endemics of the far eastern Pacific, longitude beyond >180°E~~) or
195 because no male specimens (~~or pictures/images~~) were available for body size
196 measurement (see below for a further reduction to 938 species for body length measures
197 (14 species)).

198 Theoretically, body mass is the physiologically most meaningful size metric
199 (Gaston & Blackburn, 2000), but it is ~~exceedingly~~ difficult to measure when relying on
200 dried museum specimens or images. Many length measurements have been shown to
201 correlate with body mass and such linear measurements are commonly used as a proxy
202 for body size in insects (Chown & Gaston, 2010; [Brehm *et al.*, 2019](#)). We compiled data
203 on body length (head to tip of abdomen), thorax width, and forewing length (base to tip).
204 Measurements were taken from scaled pictures published in d’Abrera ([1987]; ~~471-459~~
205 species), from pictures/images that are publicly available (28 species), and unpublished
206 pictures-colour photographs (38 species, mostly from IJK’s personal photographic print
207 collection). ~~For the~~ The remaining 422 species, which were not available in scaled
208 illustrations, were measured from pinned specimens ~~from-in~~ the collection of the Natural
209 History Museum, London. Details of the measured specimens can be found in
210 Appendix ES1. All measurements were taken with a digital caliper, rounded to 0.1 mm.
211 Since there is sexual size dimorphism in some sphingid groups (e.g., tribes Smerinthini,
212 Ambulycini, where males tend to be smaller than females; Kitching & Cadiou, 2000) we
213 measured and compared only males (the more common sex in collections) for
214 consistency. In other Lepidoptera taxa, size measures for males and females are highly
215 correlated (data from Brehm *et al.*, 2019, see there also for further discussion).
216 Furthermore, we would note that any resulting size underestimates within those clades’
217 size would be controlled for by fitted random effects models for phylogenetic association
218 (in mixed models, see below).

219 As in other macro-studies (e.g., Zeuss *et al.*, 2017) we were only able to measure
220 one specimen per species (often only one picture or specimen was available).

221 ~~However,~~Although body size can be variable within species, such a sample ($n = 1$) is an
222 unbiased estimate of the mean. While~~Although~~ a single-specimen measure would be
223 unsuitable for intraspecific studies, it should yield near-identical patterns as to averages
224 based on many specimens if studied across many species. This is because randomly-
225 distributed errors will even out, and correlation analyses will provide reliable results. We
226 confirmed this theoretical expectation with subsampling simulations based on moth body
227 size data from Brehm *et al.* (2019; J. Beck & G. Brehm, unpubl.). Furthermore, we
228 ~~assessed~~ the size variability in eight abundant sphingid species, where the body lengths of
229 208 specimens (14-34 per species) were measured from scans of collection drawers
230 (Johnson *et al.*, 2013; Trueman & Yeates, 2015; data in ES1). The absolute difference
231 between mean body lengths of these specimens and the (independent) single specimen-
232 measure was on average 3.4 mm, which we find small when considering an interspecific
233 body length range of 55.8 mm (from 12.5 to 68.3 mm) in our dataset. Thus, while
234 intraspecific effects may not be entirely negligible, they are probably relatively
235 small/irrelevant in comparison to interspecific variability in a dataset with many
236 hundreds of species. Over our large sample of ~~93850~~ species they may ~~have just added~~
237 some additional random noise. Furthermore, intraspecific variability in Lepidoptera
238 often appears large due to occasional ‘dwarf specimens’, but these do not tend to be
239 illustrated ~~on~~ in pictures whenever ‘normal’ specimens are available. Measuring tens of
240 thousands of specimens to fully appreciate species’ intraspecific variation was simply
241 beyond of the scope of this research project. Data for the size measures for all species in
242 analysis are available in ES1.

243

244 Environmental predictors

245 To test our hypotheses on the environmental control of body size, we considered the
246 mean annual temperature of frost-free months, net primary production, forest cover,
247 extreme temperatures and seasonality. Additionally, absolute latitude was used as a non-
248 environmental predictor.

- 249 ○ *Mean annual temperature* was calculated for those months with an average monthly
250 temperature above 0°C. Data were based on monthly temperature data from the
251 WorldClim database (resolution 30 arc-second, time period 1950-2000; Hijmans *et*
252 *al.*, 2005). Excluding cold winter months is reasonable because sub-zero winter
253 temperatures are quite irrelevant for diapausing organisms while including them into
254 averages would bias relevant temperatures downward.
- 255 ○ *Net primary production* (NPP) data was taken from remotely sensed normalized
256 differential vegetation index values (NDVI), corrected for modelled periods of water
257 limitation (Running *et al.*, 2004; time period 2000-2014). In this dataset ‘No Data’
258 values caused by lack of green reflection were set to zero where they occurred on
259 land, as vegetation-free landscapes (e.g., deserts, glaciers) must be interpreted as
260 unproductive for our purposes, rather than being excluded from analysis.
- 261 ○ *Forest cover* (in percent) was based on Tuanmu & Jetz (2014), who provided 12
262 generalized land cover maps based on a consensus land cover dataset. Four of these
263 land cover categories were forests (evergreen/deciduous needleleaf trees; evergreen
264 broadleaf trees; deciduous broadleaf trees, mixed/other trees). Percentages from these
265 four forest types were summed (and corrected to 100% where this value was
266 exceeded due to integer rounding).
- 267 ○ *Temperature extremes* data were based on temperature data from Smith *et al.* (2008)
268 at a resolution of 5°. For every grid cell, data included monthly temperature deviation
269 of a long-term average (128 years: 1880-2008). In the northern hemisphere, we

270 excluded data north of 35°N for November, December, January and February to
271 account for diapause; analogously we excluded data south of 35°S for May, June,
272 July and August in the southern hemisphere. We then counted within each grid cell
273 the months with temperature values that were below one standard deviation (SD)
274 from the grid cell mean (referring to SD of all grid cells in analysis). The number of
275 months was divided by the estimated length of the hawkmoths' activity period (nine
276 months above 35° S/N and 12 in the other areas) to render them comparable. This
277 provided a metric of extreme negative temperature events (i.e.,
278 $\frac{\text{months} | \text{temp.} \leq \text{mean} - \text{SD}}{\text{months of activity per year}}$ in 128 years of data). Finally, the data were interpolated to a
279 finer resolution using inverse distance weighting (search radius 6 points), to make
280 data comparable with other environmental data. The higher our metric, the more
281 months with extremely low temperatures occurred.

282 ○ *Temperature seasonality* data were used from the WorldClim database (Hijmans *et al.*, 2005). It is the standard deviation of the annual temperature seasonality,
283 multiplied by 100.
284

285 Predictor data were re-projected to a Mollweide World equal area projection
286 (bilinear resampling) to match moth data. Pixels in oceans, seas or lakes >1 km² were
287 excluded from all raster datasets. We carried out the handling and extraction of spatial
288 data in ArcGIS 10.3 (<http://desktop.arcgis.com>), subsequent data compilation and all
289 further analyses were done in R 3.3 (<https://cran.r-project.org/>; packages *ade4*, *ape*,
290 *caper*, *data.table*, *ecodist*, *lme4*, *matrix*, *nlme*, *xtable*).

291 We used two different approaches to map interspecific body size clines. In an
292 assemblage-based (Chown & Gaston, 2010) (or grid cell-based) approach we mapped the
293 median body length of all species occurring in 100 x 100 km grid cells. Grid-cells
294 containing ≤5 species were removed to reduce random noise. We measured the
295 variability of body length with the interquartile range, as well as the maximum body
296 length (i.e., largest species per cell). We used this approach for map visualizations and
297 for assessing body size variation with (absolute) latitude (using adequate techniques to
298 account for spatial autocorrelation in statistical tests, details in ES3). However, our main
299 analyses did not follow this grid cell-based approach as it is weakened by not accounting
300 for phylogenetic effects, and by pseudo-replication due to one species occurring in
301 several (or many) grid cells (Jetz & Rahbek, 2002; Entling *et al.*, 2010).

302 In our comparative approach (individual-species focus) we treated each species as
303 one data point. This also allowed inclusion of phylogenetic effects into models. To
304 associate environmental predictors with each species, for all environmental variables
305 (except forest cover) we calculated the mean across those 5 x 5 km pixels where the
306 species occur (according to our range maps). For forest cover, we calculated the median
307 at point localities of raw distribution records of high spatial accuracy (≤1 km uncertainty)
308 to minimize error on habitat association, excluding ten species with ≤5 distribution
309 records.

310

311 Data analyses

312 We replaced 24 'No Data' values for forest cover by the means of the variable so
313 as not to lose these species from multivariate models (Zuur *et al.*, 2010). Furthermore, all
314 data were standardized with a z -transformation ($\frac{x - \mu}{\sigma}$, where μ is the mean and σ is the
315 standard deviation) to make model coefficients comparable across different analyses.
316 Body sizes, temperature extremes and seasonality were log₁₀-transformed after visual
317 inspection of histograms to reach normality prior to the z -transformations, whereas

318 temperature data was x^3 -transformed. NPP data (already normally distributed) and forest
319 cover data (percent values) were standardized without transformation. We assured the
320 fulfillment of model assumptions by checking visually for residual normality, outliers
321 and heteroscedasticity (using R diagnostic plots).

322 Statistical analyses were conducted for all three body size measures (forewing
323 length, thorax width, body length) as well as the product of body length \times thorax width as
324 response variables, but we present only body length analyses in the main text. This
325 variable is less affected by different body shapes among subfamilies (e.g., systematic
326 differences in thorax/wing length ratios). Models with body length as a response also
327 received the highest pseudo- r^2 s in environmental models. We report results for the other
328 metrics in the Electronic Supplement (ES5). In some specimens, no body lengths could
329 be measured due to missing abdomens (a common problem issue in Lepidoptera
330 collections where abdomens may be removed for genitalia dissection or simply be lost
331 over time), which reduced sample size for these analyses to 938 species.

332

333 Phylogenetic effects

334 It must be assumed that a substantial part of body size variation is due to
335 phylogenetic inertia – i.e., closely related species are similar in size. Such phylogenetic
336 signal must be accounted for in interspecific comparisons to avoid spurious effects of
337 non-independent data. We employed a stepwise, hierarchical approach to do so,
338 accounting for the fact that we had a reliable, phylogenetically informed taxonomic
339 classification, but not a true phylogeny with branch lengths, available for analyses (this
340 would be required for many other approaches). Our classification was based on the
341 *Sphingidae Taxonomic Inventory* (<http://sphingidae.myspecies.info>), which builds on the
342 tribal-level molecular phylogeny of Kawahara *et al.* (2009) and integrates most recent
343 findings of phylogenetic and taxonomic studies, molecular and morphology-based. The
344 classification is available in ES2.

345 We started with environmental models containing no phylogenetic information,
346 using a generalized least squares (*gls*) model. In three further models, we added
347 information on subfamily, tribe and genus associations stepwise into hierarchical linear
348 mixed effect models (*lme*) as random intercept effects, whereas links with the
349 environment were modelled as fixed effects (Zuur, 2009); see Stone et al. (2011) for
350 mixed models as a method to account for phylogenetic effects). To assess the effect of
351 phylogeny onto body size variability, we compared model Akaike information criteria
352 (AICs) and pseudo- r^2 values (i.e., correlation of predicted vs. observed values), as well as
353 the standardized coefficients fitted for environmental effects. For the model without
354 random effects, we had to use a different algorithm (*gls*) to that used for models with
355 random effects (*lme*). However, the *gls* and *lme* model coefficients are comparable
356 (Pinheiro & Bates, 2006).

357

358 Univariate models

359 We correlated body length in separate models with every environmental predictor
360 variable, using the stepwise approach described above to account for phylogeny. All
361 univariate *lme* analyses were conducted with restricted maximum likelihood estimation
362 (REML), since this is required for a comparison between models with differently nested
363 random structure (Zuur, 2009).

364

365 Multivariate models

366 Multivariate analyses were conducted to investigate the independent influence of
367 each predictor variable, using all predictors except latitude. Unlike for univariate *lme*
368 models, we used maximum likelihood (ML) fitting for multivariate *lme* models because
369 AICs from models with a different structure of fixed effects can only be compared when
370 based on ML fits (even though REML fits are less biased; Zuur, 2009). With large
371 sample sizes, differences in models fitted with the two different methods diminish (Zuur,
372 2009).

373 To detect and account for collinearity among the predictor variables, the variance
374 inflation factor (VIF) of the multivariate model with all predictor variables was
375 calculated. Zuur *et al.* (2010) recommend dropping the predictor variable with the highest
376 VIF, then recalculating the VIF values with the new model, repeating this until the VIF
377 values are <3 .

378

379 Results

380 There is no clear latitudinal cline in median body lengths (Fig. 1A). Rather,
381 species in the Arabian Peninsula, in South Asia and in the Indo-Australian tropics are
382 distinctively larger than temperate as well as Afrotropical taxa. A grid cell-based
383 correlation of median BL with distance from the equator yields $r^2 = 0.19$, but it is non-
384 significant due to high spatial non-independence of data (ES3, Fig. S3.4). However, when
385 comparing temperate Eurasia and Africa it becomes clear that the variability in body
386 lengths is larger in the Afrotropics, i.e., there are smaller and larger species than in
387 temperate regions, leading to similar medians. Variability (Fig. 1B) is also high in desert
388 regions of Africa and Asia, despite relatively low species richness (not shown;
389 Ballesteros *et al.*, 2017). Interquartile ranges are significantly negatively correlated with
390 distance from the equator ($r^2 = 0.47$; ES3, Fig. S3.5), and maximum body length per grid
391 cell) is strongly and significantly negatively correlated to distance from the equator ((Fig.
392 1C; $r^2 = 0.54$, ES3, Fig. S3.6). A map of minimum BL (ES3, Fig. S3.3) shows that the
393 tropics also have smaller species than temperate regions, which supports the assessment
394 that the latitudinal variation of maximum body size is mainly a function of greater
395 variability in more species-rich regions (i.e., larger sample sizes).

396 Plotting median data in a comparative approach (Fig. 2) revealed a weak
397 latitudinal pattern; species occurring at higher absolute latitudes are smaller, on average,
398 than those at low latitudes. This relationship is significant but has almost no explanatory
399 value ($r^2 = 0.02$ †; ES4, Table S4.1).

400 Fig. 2 shows raw data relationships of body length with latitude and the
401 environmental predictors; Fig. 3 highlights the main characteristics of univariate
402 correlations (i.e., model coefficients and explained variance; further test statistics in ES4,
403 Table S4.1). Across all models, explained variance is low (pseudo- $r^2 < 0.2$) if no or only
404 higher-level phylogenetic classifications are integrated into models, while adding genus-
405 level classification (hierarchically within higher-level classifications) yields pseudo- r^2
406 > 0.7 . Integrating phylogenetic information weakens all fitted environmental effects, but it
407 does not affect the rank order of their strengths, their sign, or their significance (all p
408 < 0.001) except for mean annual temperature ($p < 0.05$ when genus-level phylogeny is
409 included).

410 Univariate correlations best support the resource availability hypothesis (positive
411 correlation of body length and NPP). More weakly, data were also compatible with the
412 ‘converse Bergmann-hypothesis’ (positive correlation of body length and mean

413 temperature; Fig. 3) and the seasonality hypothesis (negative correlation of seasonality
414 and size). Univariate correlations are inconsistent in sign with predictions from the TSR
415 and Bergmann rule (both expecting a negative link with mean temperature), ~~the agility~~
416 ~~hypothesis (expecting a negative link with forest cover)~~, and the starvation hypothesis
417 (expecting positive links with temperature extremes).

418 Multivariate modelling (Fig. 4; details in ES4, Table S4.2), as in the univariate
419 models, features low pseudo- r^2 's unless genus-level classifications are integrated into the
420 models. They also support the link of body length with NPP (i.e., resource availability
421 hypothesis) whereas the positive link with temperature (converse Bergmann hypothesis)
422 is weaker, in particular when phylogenetic data are included. Seasonality effects are weak
423 and inconsistent depending on how much phylogenetic information is included. As in the
424 univariate analyses, multivariate models indicated larger, not smaller species in forested
425 habitat, ~~contrary to the agility hypothesis~~. This pattern is not because forests feature
426 higher NPP (which is accounted for in models). Unlike with the univariate models,
427 temperature extremes show positive coefficients with body length in multivariate models
428 (as expected by the starvation hypothesis), but links are weak, non-significant, and VIF
429 analysis indicated predictor collinearity issues.

430 Based on VIF we simplified this full multivariate model by first dropping
431 seasonality, then temperature extremes. In a final step we also dropped mean annual
432 temperature although it had a very low VIF value because univariate analyses had
433 suggested that it was non-significant and yielded higher AIC values than a model
434 consisting only of forest cover and NPP (ES4, Table S4.2). Finally, a comparison of NPP
435 and forest cover showed that they truly express quite independent aspects of the
436 environment (correlation: $r^2 = 0.26$). Notably, multivariate models do not explain
437 substantially more variance overall than univariate models if phylogeny is fully included.
438 Models using other body size metrics as responses, whether univariate or multivariate,
439 lead to the same conclusions (ES5).

440

441 DISCUSSION

442 For 950 sphingid species, occurring from the northern temperate through the
443 African and Asian tropics to the southern temperate zone, we observed distinct
444 geographical patterns of average body size (Fig. 1) that were only weakly related to
445 absolute latitude. Rather, they featured larger species in the Middle East through South-
446 and Southeast-Asia to Melanesia, and smaller species elsewhere, including the African
447 tropics. However, species richness in the Middle East is low (Ballesteros-Mejia *et al.*,
448 2017), which increases chance effects (i.e., very high values on the Arabian Peninsula are
449 based on few species per pixel). A comparative, species-focused analysis revealed
450 landscape productivity (NPP) as the strongest correlate of body size, supporting the
451 'resource availability' hypothesis. Other hypotheses of environmental control of body
452 size were weakly (i.e., 'converse Bergmann'; seasonality) or not at all supported; for
453 ~~many-some~~ hypotheses (i.e., TSR, ~~agility~~, starvation) even the sign of the expected
454 relationship was not met by data. These conclusions held for univariate and multivariate
455 modelling approaches, with or without the inclusion of phylogenetic relatedness of taxa.

456 However, broad environmental conditions, even NPP, generally explained
457 relatively little of the variability of body sizes (i.e., <10%) whereas hierarchically
458 including phylogeny to genus-level consistently produced sound predictions of the global
459 variability in sizes (i.e., >70% of size variability explained). This implies that
460 phylogenetic inertia in body sizes, combined with the unknown, past evolutionary events

461 that shaped the sizes of today's higher-level taxonomic groups' ancestors are much more
462 relevant for predicting observed body size distributions than current environments.

463 In light of this it is not surprising that, consistent with other invertebrate studies
464 (Shelomi, 2012), the much-discussed latitudinal gradient of (average) body sizes,
465 although statistically observable in data (Fig. 2), is buried under random noise and
466 explains very little of the data variability (Table S3.1). Because this scatter is wider with
467 higher species richness towards the tropics (Fig. 2), maximum body sizes feature a much
468 stronger latitudinal pattern, which shapes the intuitive perception of the pattern (Fig. 1).

469

470 Resource availability effects

471 Our data best supported the idea that body size increases with food availability,
472 which we approximated with productivity (NPP; Blackburn *et al.*, 1999). However, a
473 mechanism whereby plant productivity constrains consumers' body size appears in
474 conflict with the idea of 'energy equivalence' (Damuth, 2007; Brown *et al.*, 2004), which
475 postulates that the variability of species richness, not body size, offsets variability in
476 energy availability. In light of these theoretical uncertainties, we caution against
477 interpreting our statistical support, or that of other studies, as unequivocal proof for the
478 postulated mechanism of the food availability hypothesis. However, we see additional
479 *post-hoc* support for interspecific food limitation effects on body size in the positive
480 correlation of forest and size. We had ~~originally included~~ considered forests in
481 preliminary analyses to test the agility hypothesis (dense forest benefitting small, agile
482 species in large mammals; Bro-Jørgensen, 2008), ~~but removed this idea from our~~
483 ~~presentation as quite unreasonable for flying insects (data rejecting rejected it~~
484 ~~comprehensively, not shown it because we found positive, not negative links with size).~~
485 Although forest data appear statistically independent of NPP (Table S3.2), the
486 recovered ~~is~~ positive correlation may be due to the fact that a sizable portion of NPP in
487 some regions derives from grassland habitats. However, sphingid caterpillars are
488 folivorous and only a single genus, *Leucophlebia*, is confirmed as feeding on Poaceae
489 (Diehl, [1982]). The absence of forests may therefore pinpoint where there is little food
490 for sphingids even if NPP may not be particularly low (i.e., in grasslands).

491

492 Other hypotheses

493 We found only weak coefficients for the 'converse Bergmann' and seasonality
494 hypotheses, and multivariate analyses suggest predictor collinearity issues or other
495 artefacts. Recently, Zeuss *et al.* (2017) presented similar data on geographic patterns of
496 size in European Lepidoptera (and Odonata). While our study went beyond Zeuss *et al.*
497 (2017) in some important aspects (i.e., larger geographic coverage, more fully including
498 global environmental gradients; comparative analyses accounting for phylogenetic
499 effects), they had data for, and highlighted, a key variable to at least potentially
500 disentangle some mechanistic effects, i.e., voltinism (the number of generations per
501 year). Several hypothetical mechanisms assume, naively, a constant and consistent
502 number of generations per year, which is known to be untrue for many well-studied
503 insect taxa (Zeuss *et al.*, 2017; and references therein). If longer favorable growing
504 seasons or warmer temperatures lead to more generations, this may offset any potential
505 body size increases as postulated by 'converse Bergmann' or seasonality hypotheses.

506 For the other tested hypotheses (i.e., Bergmann/TSR, agility) we did not even
507 observe correlations of the correct sign, which clearly rules them out within the following
508 limitations. The starvation hypothesis postulates that larger species have a lower risk of

509 death due to unexpected climate events, such as starvation or desiccation (Chown &
510 Gaston, 2010). We did not find any support for this idea from negative temperature
511 extremes (which would limit movement and hence foraging), while we could not test, due
512 to data limitations, effects of unusual drought events. However, most growth in sphingid
513 larvae happens during the last instar (e.g., 90% in *Manduca sexta*; D'Amico *et al.*, 2001),
514 so adult body sizes may not provide a suitable test of postulated starvation effects on the
515 size of earlier instars (i.e., phenology may be more relevant than final size). However, in
516 other insects there has also been little support for this hypothesis except for ants, which
517 are a special case because of their eusocial behavior (Kaspari & Vargo, 1995). Support
518 for the TSR in the literature is mainly from intraspecific studies (including a sphingid;
519 Davidowitz & Nijhout, 2004), but its role is apparently small when it comes to explaining
520 interspecific patterns.

521 Our results are, at least in parts, in conflict with some recent, more localized
522 studies on the body sizes of Lepidoptera and other taxa. Brehm *et al.* (2019) reported a
523 size increase with elevation in Costa Rica moths, which was best explained by a negative
524 effect of temperature (cf. Bergmann, TSR) but not by ~~not~~ an effect of productivity. Beck
525 *et al.* (2016) also found increasing moth sizes with higher elevations, although they could
526 not link this to flight-time temperatures in their highly seasonal study region, the Swiss
527 Alps. While inconsistent results ~~on~~ from ectotherm body size patterns and their causes are
528 common in the scientific literature so far (e.g., Entling *et al.*, 2010; Fattorini *et al.*, 2013;
529 Slavenko & Meiri, 2015; Zeuss *et al.*, 2017; Pallares *et al.*, 2019), it is particularly
530 surprising that sphingids, well-known for their (partial) thermoregulation as ~~image~~adults
531 (Heinrich, 1993), did not follow a pattern interpretable towards Bergmann's rule and
532 heat-preservation whereas other moths groups ~~showed~~ did show such trends in elevational
533 gradient studies. We cannot assess whether methodological differences, peculiarities of
534 elevational studies, a generally high potential for spurious results when dealing with
535 small effect sizes, or other factors may have caused these discrepancies.

536

537 Limitations of the study

538 This study tested, and rejected, some of the global hypotheses regarding
539 environment-body size relationships, based on currently available data on adult sphingid
540 moth sizes. However, our database is necessarily imperfect, and we need to briefly
541 discuss how this may have biased the conclusions of our analyses. First, we used an up-
542 to-date, but nevertheless coarse and incomplete taxonomic classification as a proxy for a
543 complete, time-calibrated phylogeny with branch length data. Our step-wise inclusion of
544 lower-taxon information gradually increased the explanatory value of statistical models
545 while reducing the tested environmental effects (Fig. 3). We therefore assume that the
546 predominance of phylogeny, as opposed to current environment, in explaining size
547 patterns would be even more pronounced with a more detailed, finely-resolved
548 phylogeny. Second, we only had adult size data available, but many of the mechanistic
549 explanations proposed may apply more strongly to the larval stage, where growth occurs.
550 Thus, concluding that a given hypothesis does not explain observed adult sizes remains
551 valid, but this does not rule out that the proposed mechanisms might play some role in
552 shaping the life histories of juvenile stages, which can differ in important aspects (among
553 them, in sphingids, thermoregulation; Heinrich, 1993; Kingsolver *et al.*, 2015). Third,
554 ignoring intraspecific size variation essentially means that we had to view our
555 measurements as a (small) statistical sample around an unknown per-species mean. We
556 do not see any obvious directional bias in this, but it implies that our data may contain
557 considerable random noise simply due to occasionally measuring unusually large or small
558 specimens of a species. As a consequence, the tested effects may be underestimated to an

559 unknown degree. However, the relatively large sample size (i.e., 950 species) would help
560 to counter such chance effects. Programs of computer-aided photography and
561 measurement of specimens in museum collections are under way but they may not
562 | directly provide reliable data for solving this issue ([Johnson *et al.*, 2013](#); Trueman &
563 Yeates, 2015). Fourth, our analytical setup involved two potentially confounding effects,
564 phylogenetic inertia and spatial autocorrelation. It is exceedingly complex to control
565 analyses for both effects (Freckleton & Jetz, 2009), and we choose to account in our
566 models for the more important of the two, phylogeny. Strong phylogenetic effects on
567 body size have been repeatedly reported in the literature, and they were shown on our
568 data. Spatial autocorrelation occurs in most geographic data and has the potential to
569 affect significance assessments and possibly also coefficient estimates (Bini *et al.*, 2010).
570 However, while we do not wish to give the impression of taking this lightly, it is our
571 assessment that statistically strong patterns rarely lead to changing conclusions when
572 applying spatially explicit modelling, whereas the phylogenetic inertia of body sizes most
573 probably has the potential to affect conclusions in empirical studies (Diniz-Filho &
574 Torres, 2002).

575

576 Conclusions

577 Average sphingid moth body sizes show distinctive geographic patterns, but they
578 vary only very weakly with absolute latitude. However, maximum body sizes per cell,
579 which are affected by species richness, indicate an increase towards the tropics, which
580 creates the impression of an overall size increase towards the tropics. Among various
581 hypotheses regarding how the environment is shaping such patterns globally, we found
582 strongest support for the food availability hypothesis, as sizes increase with net primary
583 productivity. There was no support at all (i.e., opposite sign of effect) for Bergmann's
584 rule or the temperature size rule, the agility hypothesis, or the starvation hypothesis,
585 while support for the seasonality hypothesis or the converse Bergmann pattern was weak
586 and potentially unreliable. However, phylogenetic effects were much more relevant than
587 any of the tested environmental factors in shaping the observed size data. This implies
588 that past environmental factors in the regions of occurrence of today's higher taxon's
589 ancestors may have shaped observed size patterns, which will be exceedingly challenging
590 to test.

591

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749

750

751 **Data Accessibility Statement**

752 As electronic supplements to this article we publish our data on sphingid body sizes
753 (ES1), a taxonomic classification of species (ES2) as used in analysis, and GIS-
754 compatible data of Fig. 1 (ES6). Environmental data used in our analysis are from the
755 public domain. Raw distribution maps of sphingid species can be accessed at Map of
756 Life, www.mol.org. *

757 *) currently only for browsing, by the time of acceptance of this paper they will be
758 available for download in GIS format.

759

760 **Appendices: Electronic Supplements**

761 | **ES1** Body size data [and specimen sources](#) (spreadsheet in csv-format)

762 | **ES2** Taxonomic classification as used for analyses

763 | **ES3** Supplementary maps and figures

764 | **ES4** Supplementary model statistics

765 | **ES5** Model output for other body size metrics

766 | **ES6** Body size distribution maps (median, interquartile, maxima; ASCII-format)

767

768 **FIGURE CAPTIONS**

769

770 **Figure 1** Geographical pattern of the median body length (A), its interquartile range (B)
771 and maximum body length found in each cell (C). Grid cells with ≤ 5 species were
772 removed (map resolution: 100 x 100 km, Mollweide World geographical projection). See
773 ES3 for additional maps; data for Fig. 1 are available in GIS-compatible format (ES6).

774

775 **Figure 2** Body length plotted against all predictor variables. LOESS (locally weighted
776 scatterplot smoothing) is fitted to indicate main data trends.

777

778 **Figure 3** Summary of univariate model results (response: body length) with stepwise
779 hierarchical inclusion of phylogenetic information. Bars (right y-axis) indicate the
780 variance explained by the models, line plots (left axis) the fitted coefficients for the
781 different predictors. Because data are standardized, coefficients can be compared across
782 models as a measure of effect size.

783

784 **Figure 4** Summary of multivariate model results (response: body length) with stepwise
785 hierarchical inclusion of phylogenetic information. Bars (right y-axis) indicate the overall
786 variance explained by the multivariate model models, line plots (left axis) the fitted
787 coefficients for the different predictors.