

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

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4 Nicolas Beerli¹, Florian Bärtschi^{1,2}, Liliana Ballesteros-Mejia³, Ian. J. Kitching⁴ & Jan
5 Beck^{1,5*}

6

7 1) University of Basel, Department of Environmental Science, Basel, Switzerland

8 2) Umweltbüro Bärtschi, Basel, Switzerland

9 3) Muséum national d'Histoire naturelle, Sorbonne Université, Institut de Systématique, Évolution,
10 Biodiversité (ISYEB). UMR 7205 - CNRS, MNHN, UPCM, EPHE, Paris, France

11 4) Department of Life Sciences, Natural History Museum London, London, UK

12 5) University of Colorado, Museum of Natural History, Boulder, USA

13 *) Correspondence: Jan Beck, University of Colorado, Museum of Natural History, 265 UCB,
14 Boulder, CO 80309, USA. E-mail: jan.beck@colorado.edu

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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 intercontinental geographic scale (i.e., global excluding the Americas)
85 and at high spatial resolution. In a comparative approach we investigate how
86 environmental conditions and phylogenetic inertia may have shaped these patterns.

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

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

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

114 (1) Bergmann’s rule expects a negative relationship between body size and
115 environmental temperature. It assumes that thermoregulation, through the ratio of
116 heat-exchanging surface and heat-producing volume, favors larger animals in colder
117 climates. Although it was originally focused on endotherms, Zamora-Camacho *et al.*
118 (2014) argued for a Bergmann-type heat preservation mechanism in an ectotherm
119 lizard. Some studies have also investigated Bergmann’s rule in Lepidoptera, with

120 mixed results (e.g., Beck *et al.*, 2016, Brehm *et al.*, 2019). Furthermore, adult
121 sphingid moths are known for pre-flight thoracic muscle temperature regulation
122 (Heinrich 1993), hence temperature efficiency may be relevant. Alternatively, an
123 intraspecific effect known as the ‘temperature size rule’ (TSR; Kingsolver & Huey,
124 2008; Chown & Gaston, 2010) predicts the same pattern. Laboratory experiments
125 with many ectotherms have shown that individuals develop slower yet mature into a
126 larger body size under colder temperatures (Atkinson, 1994). This may be either an
127 effect of adaptive plasticity or it may be due to non-adaptive constraints of
128 temperature on growth rates (e.g., the discrepancy between oxygen supply and
129 demands; see Makarieva *et al.*, 2005 for an interspecific approach). The TSR has also
130 been shown to apply to a sphingid moth (*Manduca sexta*; Davidowitz & Nijhout,
131 2004).

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

136 (3) The resource availability hypothesis postulates an increase of body size with
137 increased food availability (Blackburn *et al.*, 1999; Watt *et al.*, 2010).
138 Intraspecifically, lower food availability is known to result in smaller specimens
139 (Slansky & Scriber, 1985). If this mechanism was relevant interspecifically, we can
140 predict a body size increase with net primary productivity, which we use as a proxy
141 for food availability in our herbivorous study taxon.

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

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

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

160 Here, we first map geographical patterns of size in sphingids moths at large
161 geographical scale by combining detailed distribution data and body size measurements.
162 We explored whether hawkmoths are larger or smaller towards the equator using a simple
163 latitudinal cline. We then tested the above hypotheses by investigating the link between
164 body size and environmental variables, such as temperature, seasonality, forest cover,
165 temperature extremes and net primary productivity (NPP). We used a comparative,
166 ‘species-focused’ approach where every species counts equally (Chown & Gaston, 2010),
167 which is evolutionarily more informative than a ‘geography-focused’ approach (i.e.,
168 comparing grid cells). The latter would be overly impacted by widespread species that
169 occur in many cells (Jetz & Rahbek, 2002). Phylogenetic information was included into

170 the analyses at different taxonomic classification levels, which helped to identify the
171 importance of phylogenetic history in comparison to environmental effects.

172

173 **METHODS**

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

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

208 As in other macro-studies (e.g., Zeuss *et al.*, 2017) we were only able to measure
209 one specimen per species (often only one picture or specimen was available). Although
210 body size can be variable within species, such a sample ($n = 1$) is an unbiased estimate of
211 the mean. Although a single-specimen measure would be unsuitable for intraspecific
212 studies, it should yield near-identical patterns to averages based on many specimens if
213 studied across many species. This is because randomly-distributed errors will even out,
214 and correlation analyses will provide reliable results. We confirmed this theoretical
215 expectation with subsampling simulations based on moth body size data from Brehm *et*
216 *al.* (2019; J. Beck & G. Brehm, unpubl.). Furthermore, we assessed the size variability in
217 eight abundant sphingid species, where the body lengths of 208 specimens (14-34 per
218 species) were measured from scans of collection drawers (Johnson *et al.*, 2013; Trueman
219 & Yeates, 2015; data in ES1). The absolute difference between mean body lengths of

220 these specimens and the (independent) single specimen-measure was on average 3.4 mm,
221 which we find small when considering an interspecific body length range of 55.8 mm
222 (from 12.5 to 68.3 mm) in our dataset. Thus, while intraspecific effects may not be
223 entirely negligible, they are probably irrelevant in comparison to interspecific variability
224 in a dataset with many hundreds of species. Over our large sample of 938 species they
225 may just add some additional random noise. Furthermore, intraspecific variability in
226 Lepidoptera often appears large due to occasional ‘dwarf specimens’, but these do not
227 tend to be illustrated in pictures whenever ‘normal’ specimens are available. Measuring
228 tens of thousands of specimens to fully appreciate species’ intraspecific variation was
229 simply beyond of the scope of this research project. Data for the size measures for all
230 species in analysis are available in ES1.

231

232 Environmental predictors

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

237 ○ *Mean annual temperature* was calculated for those months with an average monthly
238 temperature above 0°C. Data were based on monthly temperature data from the
239 WorldClim database (resolution 30 arc-second, time period 1950-2000; Hijmans *et*
240 *al.*, 2005). Excluding cold winter months is reasonable because sub-zero winter
241 temperatures are quite irrelevant for diapausing organisms while including them into
242 averages would bias relevant temperatures downward.

243 ○ *Net primary production* (NPP) data was taken from remotely sensed normalized
244 differential vegetation index values (NDVI), corrected for modelled periods of water
245 limitation (Running *et al.*, 2004; time period 2000-2014). In this dataset ‘No Data’
246 values caused by lack of green reflection were set to zero where they occurred on
247 land, as vegetation-free landscapes (e.g., deserts, glaciers) must be interpreted as
248 unproductive for our purposes, rather than being excluded from analysis.

249 ○ *Forest cover* (in percent) was based on Tuanmu & Jetz (2014), who provided 12
250 generalized land cover maps based on a consensus land cover dataset. Four of these
251 land cover categories were forests (evergreen/deciduous needleleaf trees; evergreen
252 broadleaf trees; deciduous broadleaf trees, mixed/other trees). Percentages from these
253 four forest types were summed (and corrected to 100% where this value was
254 exceeded due to integer rounding).

255 ○ *Temperature extremes* data were based on temperature data from Smith *et al.* (2008)
256 at a resolution of 5°. For every grid cell, data included monthly temperature deviation
257 of a long-term average (128 years: 1880-2008). In the northern hemisphere, we
258 excluded data north of 35°N for November, December, January and February to
259 account for diapause; analogously we excluded data south of 35°S for May, June,
260 July and August in the southern hemisphere. We then counted within each grid cell
261 the months with temperature values that were below one standard deviation (SD)
262 from the grid cell mean (referring to SD of all grid cells in analysis). The number of
263 months was divided by the estimated length of the hawkmoths' activity period (nine
264 months above 35° S/N and 12 in the other areas) to render them comparable. This
265 provided a metric of extreme negative temperature events (i.e.,
266 $\frac{\text{months} | \text{temp.} \leq \text{mean} - \text{SD}}{\text{months of activity per year}}$ in 128 years of data). Finally, the data were interpolated to a
267 finer resolution using inverse distance weighting (search radius 6 points), to make

268 data comparable with other environmental data. The higher our metric, the more
269 months with extremely low temperatures occurred.

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

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

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

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

298

299 Data analyses

300 We replaced 24 ‘No Data’ values for forest cover by the means of the variable so
301 as not to lose these species from multivariate models (Zuur *et al.*, 2010). Furthermore, all
302 data were standardized with a z-transformation ($\frac{x-\mu}{\sigma}$, where μ is the mean and σ is the
303 standard deviation) to make model coefficients comparable across different analyses.
304 Body sizes, temperature extremes and seasonality were log₁₀-transformed after visual
305 inspection of histograms to reach normality prior to the z-transformations, whereas
306 temperature data was x^3 -transformed. NPP data (already normally distributed) and forest
307 cover data (percent values) were standardized without transformation. We assured the
308 fulfillment of model assumptions by checking visually for residual normality, outliers
309 and heteroscedasticity (using R diagnostic plots).

310 Statistical analyses were conducted for all three body size measures (forewing
311 length, thorax width, body length) as well as the product of body length x thorax width as
312 response variables, but we present only body length analyses in the main text. This
313 variable is less affected by different body shapes among subfamilies (e.g., systematic
314 differences in thorax/wing length ratios). Models with body length as a response also
315 received the highest pseudo-r²s in environmental models. We report results for the other

316 metrics in the Electronic Supplement (ES5). In some specimens, no body lengths could
317 be measured due to missing abdomens (a common issue in Lepidoptera collections where
318 abdomens may be removed for genitalia dissection or simply be lost over time), which
319 reduced sample size for these analyses to 938 species.

320

321 Phylogenetic effects

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

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

345

346 Univariate models

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

352

353 Multivariate models

354 Multivariate analyses were conducted to investigate the independent influence of
355 each predictor variable, using all predictors except latitude. Unlike for univariate *lme*
356 models, we used maximum likelihood (ML) fitting for multivariate *lme* models because
357 AICs from models with a different structure of fixed effects can only be compared when
358 based on ML fits (even though REML fits are less biased; Zuur, 2009). With large
359 sample sizes, differences in models fitted with the two different methods diminish (Zuur,
360 2009).

361 To detect and account for collinearity among the predictor variables, the variance
362 inflation factor (VIF) of the multivariate model with all predictor variables was

363 calculated. Zuur *et al.* (2010) recommend dropping the predictor variable with the highest
364 VIF, then recalculating the VIF values with the new model, repeating this until the VIF
365 values are <3.

366

367 **Results**

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

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

388 Fig. 2 shows raw data relationships of body length with latitude and the
389 environmental predictors; Fig. 3 highlights the main characteristics of univariate
390 correlations (i.e., model coefficients and explained variance; further test statistics in ES4,
391 Table S4.1). Across all models, explained variance is low (pseudo- $r^2 < 0.2$) if no or only
392 higher-level phylogenetic classifications are integrated into models, while adding genus-
393 level classification (hierarchically within higher-level classifications) yields pseudo- r^2
394 > 0.7 . Integrating phylogenetic information weakens all fitted environmental effects, but it
395 does not affect the rank order of their strengths, their sign, or their significance (all p
396 < 0.001) except for mean annual temperature ($p < 0.05$ when genus-level phylogeny is
397 included).

398 Univariate correlations best support the resource availability hypothesis (positive
399 correlation of body length and NPP). More weakly, data were also compatible with the
400 'converse Bergmann-hypothesis' (positive correlation of body length and mean
401 temperature; Fig. 3) and the seasonality hypothesis (negative correlation of seasonality
402 and size). Univariate correlations are inconsistent in sign with predictions from the TSR
403 and Bergmann rule (both expecting a negative link with mean temperature), and the
404 starvation hypothesis (expecting positive links with temperature extremes).

405 Multivariate modelling (Fig. 4; details in ES4, Table S4.2), as in the univariate
406 models, features low pseudo- r^2 's unless genus-level classifications are integrated into the
407 models. They also support the link of body length with NPP (i.e., resource availability
408 hypothesis) whereas the positive link with temperature (converse Bergmann hypothesis)
409 is weaker, in particular when phylogenetic data are included. Seasonality effects are weak
410 and inconsistent depending on how much phylogenetic information is included. As in the
411 univariate analyses, multivariate models indicated larger, not smaller species in forested

412 habitat. This pattern is not because forests feature higher NPP (which is accounted for in
413 models). Unlike with the univariate models, temperature extremes show positive
414 coefficients with body length in multivariate models (as expected by the starvation
415 hypothesis), but links are weak, non-significant, and VIF analysis indicated predictor
416 collinearity issues.

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

427

428 **DISCUSSION**

429 For 950 sphingid species, occurring from the northern temperate through the
430 African and Asian tropics to the southern temperate zone, we observed distinct
431 geographical patterns of average body size (Fig. 1) that were only weakly related to
432 absolute latitude. Rather, they featured larger species in the Middle East through South-
433 and Southeast-Asia to Melanesia, and smaller species elsewhere, including the African
434 tropics. However, species richness in the Middle East is low (Ballesteros-Mejia *et al.*,
435 2017), which increases chance effects (i.e., very high values on the Arabian Peninsula are
436 based on few species per pixel). A comparative, species-focused analysis revealed
437 landscape productivity (NPP) as the strongest correlate of body size, supporting the
438 ‘resource availability’ hypothesis. Other hypotheses of environmental control of body
439 size were weakly (i.e., ‘converse Bergmann’; seasonality) or not at all supported; for
440 some hypotheses (i.e., TSR, starvation) even the sign of the expected relationship was not
441 met by data. These conclusions held for univariate and multivariate modelling
442 approaches, with or without the inclusion of phylogenetic relatedness of taxa.

443 However, broad environmental conditions, even NPP, generally explained
444 relatively little of the variability of body sizes (i.e., <10%) whereas hierarchically
445 including phylogeny to genus-level consistently produced sound predictions of the global
446 variability in sizes (i.e., >70% of size variability explained). This implies that
447 phylogenetic inertia in body sizes, combined with the unknown, past evolutionary events
448 that shaped the sizes of today’s higher-level taxonomic groups’ ancestors are much more
449 relevant for predicting observed body size distributions than current environments.

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

456

457 **Resource availability effects**

458 Our data best supported the idea that body size increases with food availability,
459 which we approximated with productivity (NPP; Blackburn *et al.*, 1999). However, a

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

477

478 Other hypotheses

479 We found only weak coefficients for the 'converse Bergmann' and seasonality
480 hypotheses, and multivariate analyses suggest predictor collinearity issues or other
481 artefacts. Recently, Zeuss *et al.* (2017) presented similar data on geographic patterns of
482 size in European Lepidoptera (and Odonata). While our study went beyond Zeuss *et al.*
483 (2017) in some important aspects (i.e., larger geographic coverage, more fully including
484 global environmental gradients; comparative analyses accounting for phylogenetic
485 effects), they had data for, and highlighted, a key variable to at least potentially
486 disentangle some mechanistic effects, i.e., voltinism (the number of generations per
487 year). Several hypothetical mechanisms assume, naively, a constant and consistent
488 number of generations per year, which is known to be untrue for many well-studied
489 insect taxa (Zeuss *et al.*, 2017; and references therein). If longer favorable growing
490 seasons or warmer temperatures lead to more generations, this may offset any potential
491 body size increases as postulated by 'converse Bergmann' or seasonality hypotheses.

492 For the other tested hypotheses (i.e., Bergmann/TSR, agility) we did not even
493 observe correlations of the correct sign, which clearly rules them out within the following
494 limitations. The starvation hypothesis postulates that larger species have a lower risk of
495 death due to unexpected climate events, such as starvation or desiccation (Chown &
496 Gaston, 2010). We did not find any support for this idea from negative temperature
497 extremes (which would limit movement and hence foraging), while we could not test, due
498 to data limitations, effects of unusual drought events. However, most growth in sphingid
499 larvae happens during the last instar (e.g., 90% in *Manduca sexta*; D'Amico *et al.*, 2001),
500 so adult body sizes may not provide a suitable test of postulated starvation effects on the
501 size of earlier instars (i.e., phenology may be more relevant than final size). However, in
502 other insects there has also been little support for this hypothesis except for ants, which
503 are a special case because of their eusocial behavior (Kaspari & Vargo, 1995). Support
504 for the TSR in the literature is mainly from intraspecific studies (including a sphingid;
505 Davidowitz & Nijhout, 2004), but its role is apparently small when it comes to explaining
506 interspecific patterns.

507 Our results are, at least in parts, in conflict with some recent, more localized
508 studies on the body sizes of Lepidoptera and other taxa. Brehm *et al.* (2019) reported a
509 size increase with elevation in Costa Rica moths, which was best explained by a negative
510 effect of temperature (cf. Bergmann, TSR) but not by an effect of productivity. Beck *et al.*
511 (2016) also found increasing moth sizes with higher elevations, although they could
512 not link this to flight-time temperatures in their highly seasonal study region, the Swiss
513 Alps. While inconsistent results from ectotherm body size patterns and their causes are
514 common in the scientific literature so far (e.g., Entling *et al.*, 2010; Fattorini *et al.*, 2013;
515 Slavenko & Meiri, 2015; Zeuss *et al.*, 2017; Pallares *et al.*, 2019), it is particularly
516 surprising that sphingids, well-known for their (partial) thermoregulation as adults
517 (Heinrich, 1993), did not follow a pattern interpretable towards Bergmann's rule and
518 heat-preservation whereas other moths groups did show such trends in elevational
519 gradient studies. We cannot assess whether methodological differences, peculiarities of
520 elevational studies, a generally high potential for spurious results when dealing with
521 small effect sizes, or other factors may have caused these discrepancies.

522

523 Limitations of the study

524 This study tested, and rejected, some of the global hypotheses regarding
525 environment-body size relationships, based on currently available data on adult sphingid
526 moth sizes. However, our database is necessarily imperfect, and we need to briefly
527 discuss how this may have biased the conclusions of our analyses. First, we used an up-
528 to-date, but nevertheless coarse and incomplete taxonomic classification as a proxy for a
529 complete, time-calibrated phylogeny with branch length data. Our step-wise inclusion of
530 lower-taxon information gradually increased the explanatory value of statistical models
531 while reducing the tested environmental effects (Fig. 3). We therefore assume that the
532 predominance of phylogeny, as opposed to current environment, in explaining size
533 patterns would be even more pronounced with a more detailed, finely-resolved
534 phylogeny. Second, we only had adult size data available, but many of the mechanistic
535 explanations proposed may apply more strongly to the larval stage, where growth occurs.
536 Thus, concluding that a given hypothesis does not explain observed adult sizes remains
537 valid, but this does not rule out that the proposed mechanisms might play some role in
538 shaping the life histories of juvenile stages, which can differ in important aspects (among
539 them, in sphingids, thermoregulation; Heinrich, 1993; Kingsolver *et al.*, 2015). Third,
540 ignoring intraspecific size variation essentially means that we had to view our
541 measurements as a (small) statistical sample around an unknown per-species mean. We
542 do not see any obvious directional bias in this, but it implies that our data may contain
543 considerable random noise simply due to occasionally measuring unusually large or small
544 specimens of a species. As a consequence, the tested effects may be underestimated to an
545 unknown degree. However, the relatively large sample size (i.e., 950 species) would help
546 to counter such chance effects. Programs of computer-aided photography and
547 measurement of specimens in museum collections are under way but they may not
548 directly provide reliable data for solving this issue (Johnson *et al.*, 2013; Trueman &
549 Yeates, 2015). Fourth, our analytical setup involved two potentially confounding effects,
550 phylogenetic inertia and spatial autocorrelation. It is exceedingly complex to control
551 analyses for both effects (Freckleton & Jetz, 2009), and we choose to account in our
552 models for the more important of the two, phylogeny. Strong phylogenetic effects on
553 body size have been repeatedly reported in the literature, and they were shown on our
554 data. Spatial autocorrelation occurs in most geographic data and has the potential to
555 affect significance assessments and possibly also coefficient estimates (Bini *et al.*, 2010).
556 However, while we do not wish to give the impression of taking this lightly, it is our
557 assessment that statistically strong patterns rarely lead to changing conclusions when

558 applying spatially explicit modelling, whereas the phylogenetic inertia of body sizes most
559 probably has the potential to affect conclusions in empirical studies (Diniz-Filho &
560 Torres, 2002).

561

562 Conclusions

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

577

578 References

- 579 Addo-Bediako, A., Chown, S. L. & Gaston, K. J. (2000) Thermal tolerance, climatic
580 variability and latitude. *Proceedings of the Royal Society (B)*, **267**, 739–745.
- 581 Ashton, K. G., Feldman, C. R. & Garland Jr, T. (2003) Bergmann's rule in nonavian
582 reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, **57**, 1151–1163.
- 583 Atkinson, D. (1994) Temperature and organism size—A biological law for ectotherms?
584 *Advances in Ecological Research*, **25**, 1–58.
- 585 Bailey, S. F. (1978) Latitudinal gradients in colors and patterns of passerine birds. *Condor*, **80**, 372–
586 281.
- 587 Ballesteros-Mejia, L., Kitching, I. J., Jetz, W. & Beck, J. (2017) Putting insects on the
588 map: Near-global variation in sphingid moth richness along spatial and
589 environmental gradients. *Ecography*, **40**, 698–708.
- 590 Barragán, Á. R., Dangles, O., Cárdenas, R. E. & Onore, G. (2009) The history of
591 Entomology in Ecuador. *Ann. soc. entomol. Fr. (n.s.)*, **45**, 410–423.
- 592 Bates, H. W. (1864) *The naturalist on the river Amazons*, 2nd ed. Murray, London.
- 593 Beck, J., Liedtke, H. C., Widler, S., Altermann, F., Loader, S., Hagmann, R., Lang, S. &
594 Fiedler, K. (2016) Patterns or mechanisms? Bergmann's and Rapoport's rule in
595 moths along an elevational gradient. *Community Ecology*, **17**, 137–148.
- 596 Bini, L. M., Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., Albuquerque, F. S., Araújo, M. B.,
597 Baselga, A., Beck, J., Bellocq, M. I., Böhning-Gaese, K., Borges, P. A. V., Cabrero-Sañudo,
598 F. J., Castro-Parga, I., Chey, V. K., De Marco, P., Ferrer-Castán, D., Field, R., Filloy, J.,
599 Fleishman, E., Gómez, J. F., Greve, M., Guil, N., Hortal, J., Iverson, J. B., Kerr, J. T.,
600 Kissling, D., Kitching, I. J., León-Cortés, J. L., Levi, C., Lobo, J. M., Oberdorff, T., Olalla-
601 Tarraga, M. Á., Pausas, J. G., Qian, H., Rahbek, C., Rodríguez, M. Á., Ruggiero, A.,
602 Sackman, P., Sanders, N. J., Williams, P. & Hawkins, B. A. (2009) Coefficient shifts in

- 603 geographical ecology: an empirical evaluation of spatial and non-spatial regression.
604 *Ecography*, **32**, 193–204
- 605 Blackburn, T. M. & Hawkins, B. A. (2004) Bergmann's rule and the mammal fauna of
606 northern North America. *Ecography*, **27**, 715–724.
- 607 Blackburn, T. M., Gaston, K. J. & Loder, N. (1999) Geographic gradients in body size: a
608 clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.
- 609 Blanckenhorn, W. U & Demont, M. (2004) Bergmann and Converse Bergmann
610 latitudinal clines in arthropods: Two Ends of a Continuum? *Integrative and*
611 *Comparative Biology*, **44**, 413–424.
- 612 Blanckenhorn, W. U. (2000) The evolution of body size: what keeps organisms small?
613 *Quarterly Review of Biology*, **75**, 385–407.
- 614 Brehm, G., Colwell, R. & Zeuss, D. (2019) Moth body size increases with elevation
615 along a complete tropical elevational gradient for two hyperdiverse clades.
616 *Ecography*, online first (doi: 10.1111/ecog.03917)
- 617 Bro-Jørgensen, J. (2008) Dense habitats selecting for small body size: a comparative
618 study on bovids. *Oikos*, **117**, 729–737.
- 619 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004) Toward a
620 metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- 621 Chown, S. L. & Gaston, K. J. (2010) Body size variation in insects: a macroecological
622 perspective. *Biological Reviews*, **85**, 139–169.
- 623 Chown, S. L. & Nicolson, S. (2004) *Insect physiological ecology: mechanisms and*
624 *patterns*. Oxford University Press, Oxford.
- 625 d'Abbrera, B. ([1987] 1986) *Sphingidae Mundi: hawk moths of the world*. EW Classey
626 Ltd., Faringdon (UK).
- 627 D'Amico, L. J., Davidowitz, G. & Nijhout, H. F. (2001) The developmental and
628 physiological basis of body size evolution in an insect. *Proceedings of the Royal*
629 *Society (B)*, **268**, 1589–1593.
- 630 Damuth, J. (2007) A macroevolutionary explanation for energy equivalence in the scaling
631 of body size and population density. *American Naturalist*, **169**, 621–631.
- 632 Davidowitz, G. & Nijhout, H. F. (2004) The physiological basis of reaction norms: the
633 interaction among growth rate, the duration of growth and body size. *Integrative*
634 *and Comparative Biology*, **44**, 443–449.
- 635 Diehl, E. W. ([1982]) Die Sphingiden Sumatras. *Heterocera Sumatrana*, **1**, 1-97.
- 636 Diniz-Filho, J. A. F & Torres, N. M. (2002) Phylogenetic comparative methods and the
637 geographic range size – body size relationship in new world terrestrial carnivore.
638 *Evolutionary Ecology*, **16**, 351–367.
- 639 Entling, W., Schmidt-Entling, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2010) Body
640 size-climate relationships of European spiders. *Journal of Biogeography*, **37**,
641 477–485.
- 642 Fattorini, S., Lo Monaco, R., Di Giulio, A. & Ulrich, W. (2013) Latitudinal trends in
643 body length distributions of European darkling beetles (Tenebrionidae). *Acta*
644 *Oecologica*, **53**, 88–94.

- 645 Freckleton, R. P. & Jetz, W. (2009) Space versus phylogeny: disentangling phylogenetic
646 and spatial signals in comparative data. *Proceedings of the Royal Society (B)*, **276**,
647 21–30.
- 648 Freckleton, R. P., Harvey, P. H. & Pagel, M. (2003) Bergmann's rule and body size in
649 mammals. *American Naturalist*, **161**, 821–825.
- 650 Gaston, K. J. & Blackburn, T. M. (2000) *Pattern and process in macroecology*.
651 Blackwell Science, Oxford (UK).
- 652 Gaston, K. J. & Chown, S. L. (2013) Macroecological patterns in insect body size.
653 *Animal Body Size: Linking Pattern and Process across Space, Time and*
654 *Taxonomic Group* (eds. F. A. Smith & S. K. Lyons), pp. 13–61. University of
655 Chicago Press, Chicago.
- 656 Hawkins, B. A. & Diniz-Filho, J. A. F. (2004) 'Latitude' and geographic patterns in
657 species richness. *Ecography*, **27**, 268–272.
- 658 Heinrich, B. (1993) *The hot-blooded insects: strategies and mechanisms of*
659 *thermoregulation*. Harvard University Press, Cambridge, MA.
- 660 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high
661 resolution interpolated climate surfaces for global land areas. *International*
662 *Journal of Climatology*, **25**, 1965–1978.
- 663 Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species
664 richness. *Science*, **297**, 1548–1551.
- 665 Johnson, L., Mantle, B., Gardner, J., & Backwell, P. (2013). Morphometric
666 measurements of dragonfly wings: the accuracy of pinned, scanned and detached
667 measurement methods. *ZooKeys*, **276**, 77–84.
- 668 Kaspari, M. & Vargo, E. L. (1995) Colony size as a buffer against seasonality:
669 Bergmann's rule in social insects. *American Naturalist*, **145**, 610–632.
- 670 Kawahara, A. Y., Mignault, A. A., Regier, J. C., Kitching, I. J. & Mitter, C. (2009)
671 Phylogeny and biogeography of hawkmoths (Lepidoptera: Sphingidae): evidence
672 from five nuclear genes. *PLoS ONE*, **4**, e5719.
- 673 Kingsolver, J. G. & Huey, R. B. (2008) Size, temperature, and fitness: three rules.
674 *Evolutionary Ecology Research*, **10**, 251.
- 675 Kingsolver, J. G., Higgins, J. K. & Augustine, K. E. (2015) Fluctuating temperatures and
676 ectotherm growth: distinguishing non-linear and time-dependent effects. *Journal*
677 *of Experimental Biology*, **218**, 2218–2225.
- 678 Kitching, I. J. & Cadiou, J.-M. (2000) *Hawkmoths of the world: an annotated and*
679 *illustrated revisionary checklist (Lepidoptera: Sphingidae)*. The Natural History
680 Museum & Cornell University Press, London & Ithaca, 227 pp.
- 681 Makarieva, A. M., Gorshkov, V. G. & Li, B.-L. (2005) Temperature-associated upper
682 limits to body size in terrestrial poikilotherms. *Oikos*, **111**, 425–436.
- 683 Meiri, S. (2011) Bergmann's rule—what's in a name? *Global Ecology and Biogeography*,
684 **20**, 203–207.
- 685 Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of*
686 *Biogeography*, **30**, 331–351.
- 687 Mousseau, T. A. (1997) Ectotherms follow the converse to Bergmann's rule. *Evolution*,
688 **51**, 630.

- 689 Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M.,
690 Gaston, K. J., Owens, I. P. F. & Bennett, P. M. (2009) Global biogeography and
691 ecology of body size in birds. *Ecology Letters*, **12**, 249–259.
- 692 Pallares, S., Lai, Michele, Abellan, P., Ribera, I. & Sanchez-Fernandez, D. (2019) An
693 interspecific test of Bergmann’s rule reveals inconsistent body size patterns across
694 several lineages of water beetles (Coleoptera: Dytiscidae). *Ecological*
695 *Entomology*, in press (DOI: 10.1111/een.12701).
- 696 Pinheiro, J. & Bates, D. (2006) *Mixed-effects models in S and S-PLUS*. Springer Science
697 & Business Media, Berlin.
- 698 Puzin, C., Leroy, B. & Pétilion, J. (2014) Intra-and inter-specific variation in size and
699 habitus of two sibling spider species (Araneae: Lycosidae): taxonomic and
700 biogeographic insights from sampling across Europe. *Biological Journal of the*
701 *Linnean Society*, **113**, 85–96.
- 702 Running, S. W., Nemani, R. R., Heinsch, F. A., Zhao, M., Reeves, M. & Hashimoto, H.
703 (2004) A continuous satellite-derived measure of global terrestrial primary
704 production. *Bioscience*, **54**, 547–560.
- 705 Shelomi, M. (2012) Where are we now? Bergmann’s rule sensu lato in insects. *American*
706 *Naturalist*, **180**, 511–519.
- 707 Slansky, F. & Scriber, J. (1985) Food consumption and utilization. *Comprehensive Insect*
708 *Physiology, Biochemistry and Pharmacology*, **4**, 87–163.
- 709 Slavenko, A. & Meiri, S. (2015) Mean body sizes of amphibian species are poorly
710 predicted by climate. *Journal of Biogeography*, **42**, 1246–1254.
- 711 Smith, T. M., Reynolds, R. W., Peterson, T. C. & Lawrimore, J. (2008) Improvements to
712 NOAA’s Historical Merged Land–Ocean Surface Temperature Analysis (1880–
713 2006). *Journal of Climate*, **21**, 2283–2296.
- 714 Stone, G. N., Nee, S. & Felsenstein, J. (2011) Controlling for non-independence in comparative
715 analysis of patterns across populations within species. *Philosophical Transactions of the*
716 *Royal Society B*, **366**, 1410–1424
- 717 Trueman, J. W. H. & Yeates, D. K. (2015) Can whole-drawer images measure up? A
718 reply to Johnson et al. (2013). *ZooKeys*, **500**, 141–149.
- 719 Tuanmu, M.-N. & Jetz, W. (2014) A global 1-km consensus land-cover product for
720 biodiversity and ecosystem modelling: Consensus land cover. *Global Ecology*
721 *and Biogeography*, **23**, 1031–1045.
- 722 Watt, C., Mitchell, S. & Salewski, V. (2010) Bergmann’s rule; a concept cluster? *Oikos*,
723 **119**, 89–100.
- 724 Zamora-Camacho, F. J., Reguera S. & Moreno-Rueda, G. (2014) Bergmann’s rule rules body size
725 in an ectotherm: heat conservation in a lizard along a 2200-metre elevational gradient.
726 *Journal of Evolutionary Biology*, **27**, 2820–2828.
- 727 Zeuss, D., Brunzel, S. & Brandl, R. (2017) Environmental drivers of voltinism and body size in
728 insect assemblages across Europe. *Global Ecology and Biogeography*, **26**, 154–165.
- 729 Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009) *Mixed effects*
730 *models and extensions in ecology with R*. Springer Science & Business Media,
731 Berlin.

732 Zuur, A. F., Ieno, E. N. & Elphick, C. S. (2010) A protocol for data exploration to avoid
733 common statistical problems: Data exploration. *Methods in Ecology and*
734 *Evolution*, **1**, 3–14.

735

736

737 **Data Accessibility Statement**

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

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

745

746 **Appendices: Electronic Supplements**

747 **ES1** Body size data and specimen sources (spreadsheet in csv-format)

748 **ES2** Taxonomic classification as used for analyses

749 **ES3** Supplementary maps and figures

750 **ES4** Supplementary model statistics

751 **ES5** Model output for other body size metrics

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

753

754 **FIGURE CAPTIONS**

755

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

760

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

763

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

769

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