

1 **Original Article:**

2 **How climatic variability is linked to the spatial distribution of range sizes:**
3 **seasonality versus climate change velocity in sphingid moths**

4 Marc Grünig^{1,2,3}, Nicolas Beerli¹, Liliana Ballesteros-Mejia^{4,5}, Ian J. Kitching⁶ & Jan Beck^{1,7*}

5

6 1) University of Basel, Biogeography, Department of Environmental Sciences, Basel, Switzerland

7 2) Agroscope, Strategic Research Division Plant Protection, Wädenswil, Switzerland

8 3) ETH Zürich, Landscape Ecology, Institute of Terrestrial Ecosystems, Zürich, Switzerland

9 4) Universidad Federal de Goiás, Laboratório de Genética e Biodiversidade, Goiania, Brazil

10 5) Sorbonne Universités, Muséum national d'Histoire Naturelle, Paris, France

11 6) Natural History Museum London, Department of Life Sciences, London, U.K.

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

13

14 *) correspondence: Jan Beck, University of Colorado, Museum of Natural History, 265 UCB, Boulder,

15 CO 80309, USA. E-mail: jan.beck@colorado.edu

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22 moths;

23 **ABSTRACT**

24 **Aim:** To map the spatial variation of range sizes within sphingid moths, and to test hypotheses on its
25 environmental control. In particular, we investigate effects of climate change velocity since the
26 Pleistocene and the mid-Holocene, temperature and precipitation seasonality, topography, Pleistocene ice
27 cover, and available land area.

28 **Location:** Old World and Australasia, excluding smaller islands.

29 **Methods:** We used fine-grained range maps (based on expert-edited distribution modelling) for all 972
30 sphingid moth species in the research region and calculated, at a grain size of 100 km, the median of range
31 sizes of all species that co-occur in a pixel. Climate, topography and Pleistocene ice cover data were taken
32 from publicly available sources. We calculated climate change velocities (CCV) for the last 21ky as well
33 as 6ky. We compared the effects of seasonality and CCV on median range sizes with spatially explicit
34 models while accounting for effects of elevation range, glaciation history and available land area.

35 **Results:** Range sizes show a clear spatial pattern, with highest median values in deserts and arctic regions
36 and lowest values in isolated tropical regions. Range sizes were only weakly related to absolute latitude
37 (predicted by Rapoport's effect), but there was a strong north-south pattern of range size decline.
38 Temperature seasonality emerged as the strongest environmental correlate of median range size, in
39 univariate as well as multivariate models, whereas effects of CCV were weak and unstable for both time
40 periods. These results were robust to variations in the parameters in alternative analyses, among them
41 multivariate CCV.

42 **Main conclusions:** Temperature seasonality is a strong correlate of spatial range size variation, while
43 effects of longer-term temperature change, as captured by CCV, received much weaker support.

44 INTRODUCTION

45 The causes of the spatial distribution of species' range sizes [have been](#) debated in biogeography
46 for at least 20 years (Brown *et al.*, 1996; Gaston, 2003; Morueta-Holme *et al.*, 2013; Veter *et al.*, 2013; Di
47 Marco & Santini, 2015). Understanding environmental correlates and ultimately the processes behind
48 range size distributions are an important step towards understanding large-scale species richness patterns
49 (Stevens, 1989; Jetz & Rahbek, 2002; Graves & Rahbek, 2005; Morueta-Holme *et al.*, 2013). Furthermore,
50 range size is negatively linked to extinction risk (Gaston, 1998; Davies *et al.* 2009; Morueta-Holme *et al.*,
51 2013), e.g. due to climatic change (Gaston, 2003; Thomas *et al.*, 2004; Ohlemüller *et al.*, 2008; Sandel *et*
52 *al.*, 2011; Garcia *et al.*, 2014) or land use and habitat fragmentation (Thomas *et al.*, 2004). A better
53 understanding of what shapes the distribution of range sizes is therefore relevant to basic ecology as well
54 as conservation (Gaston, 1996; Purvis *et al.*, 2000; Morueta-Holme *et al.*, 2013).

55 Many hypotheses have been proposed to explain patterns of range sizes. Janzen (1967) suggested
56 that species living in regions with high temperature stability throughout the year (i.e., the tropics) are
57 tolerant to a narrower range of temperatures than species in highly seasonal regions. Stevens (1989)
58 adopted this idea to explain a positive latitude-range size pattern (which he described as Rapoport's rule;
59 Letcher & Harvey, 1994; McCain & Bracy Knight, 2013; Veter *et al.*, 2013).

60 Besides such intra-annual variability, long-time climatic oscillations were also proposed to
61 influence range sizes. Dynesius & Jansson (2000, 2002) and Jansson (2003) connected several biological
62 phenomena, including range size variation, with long-time climatic oscillations driven by changes in the
63 Earth's orbit. These have stronger effects towards the poles and therefore cause larger temperature
64 changes at higher latitudes. Dynesius & Jansson (2000) argued that areas of long-time climate stability
65 allow for the persistence of small-ranged species, while only large-ranged species (which often have high
66 climatic tolerances, are generalists and good dispersers) could survive in regions of low stability. Sandel *et*
67 *al.* (2011) built on these ideas to connect the proportion of small-ranged species with the concept of
68 climate change velocity (hereafter CVV).

69 Climate change velocity was developed as a measurement for long-time climate variability by
70 Loarie *et al.* (2009) and adopted by Sandel *et al.* (2011). CCV expresses the speed at which species have
71 to migrate to track a changing climate. CCV is influenced by a temporal gradient of change as well as the
72 spatial change of climate in a region (which is high where there is high topographic variability). Highest
73 CCV occurs in flat landscapes with a high magnitude of climatic change, while it is lowest in mountainous
74 regions with relatively stable climate (because there species do not need to travel far to reach a different
75 climatic zone; Loarie *et al.*, 2009; Ackerly *et al.*, 2010; Sandel *et al.*, 2011; Burrows *et al.*, 2014).
76 Focussing on temperature CCV since the last glacial maximum (LGM), Loarie *et al.* (2009) and Sandel *et*
77 *al.* (2011) suggested a connection between small geographic range (“endemism”) and low CCV, and
78 discussed this in the light of species’ vulnerability when exposed to high future CCVs.

79 Other potentially influencing factors include elevation range, available land area, and long- or
80 short-term variation of climatic variables other than temperature. Elevational range affects habitat rarity
81 (Hawkins & Diniz-Filho, 2006). Habitats found in highland regions typically have small area sizes. Hence,
82 many species that occur there must be expected to have relatively small ranges. Similarly, available land
83 area could be a relevant predictor in large-extent analyses (Ohlemüller *et al.*, 2008). Terrestrial species can
84 only have large ranges if there is sufficient land area available. Also, there is no ecological reason why
85 seasonality (or CCV) effects should be related to temperature variation but not to precipitation (which is a
86 relevant niche dimension for many species), or even more complex combinations of climatic variables.

87 Here we used the range size distributions of Old World sphingid moths, a family of herbivorous
88 insects, to test the above hypotheses in a competitive manner for their explanatory power. We were
89 especially interested in the recently published hypothesis of CCV effects (Sandel *et al.* 2011; i.e.,
90 temperature change velocity) in comparison to the older hypothesis of temperature seasonality (Janzen
91 1967). We also evaluated the evidence for different mechanisms acting simultaneously in shaping range
92 sizes (i.e., their relative contribution in explaining patterns after accounting for the other hypothesized
93 effects).

94 There is no a priori knowledge of what is an appropriate time window of CCV effects for a given
95 taxon – we focus here on testing Sandel *et al.*'s (2011) specific hypothesis of post-Pleistocene effects (i.e.
96 since LGM) as a general mechanism. However, we also use CCV calculations for a different time period
97 (mid-Holocene to present), as mid-Holocene temperatures in many parts of the world were warmer than
98 today. This will help to elucidate the suggested mechanism, which is not based on the direction but on the
99 speed of climate change. Thus, we expect similar relationships of range size with CCV for both time
100 periods. This also acknowledges that climate change since the LGM has not been linear (e.g., Thompson,
101 1998). **Furthermore**, we evaluated the placement of species' ranges within biomes (Olson *et al.*, 2001).
102 This will assist in assessing whether range size patterns are mainly due to large-scale habitat (i.e.,
103 vegetation) differences.

104

105 **MATERIAL & METHODS**

106 **Sphingid moths and range size data**

107 Sphingid moths are a family of large, mobile and, in some cases, extremely dispersive
108 Lepidoptera (Kitching & Cadiou, 2000). Caterpillars are folivorous with a moderate degree of hostplant
109 specialization (typically to plant family or order). Due to their popularity with amateur collectors, more is
110 known about their taxonomy, distribution and life history than for many other taxa, making them a
111 suitable model group for global-scale biogeographic studies on insects (Ballesteros-Mejia *et al.*, 2016).

112 Distribution maps for all 972 sphingid species found in the research region were available at 5 km
113 grain size. These data were based on a carefully processed multi-source compilation of specimen records,
114 combined with species distribution modelling techniques (SDM; based on climatic variables and
115 vegetation cover) and then expert-edited to account for dispersal limitation (for details and validation see
116 Ballesteros-Mejia *et al.*, 2016; maps can be browsed in Map of Life, www.mol.org). For each species,
117 range size was calculated (Appendix S1). We then used up-scaled distribution maps to a 100 km grain to

118 calculate the median range size of the species co-occurring in each pixel (i.e., a 2-D version of “Steven’s
119 method”; Gaston *et al.*, 1998; Sizing *et al.*, 2009). To provide comparable data with published studies
120 (Hawkins & Diniz-Filho, 2006; Morueta-Holme *et al.*, 2013) we also calculated average range sizes after
121 log-transforming the data.

122

123 **Environmental predictors**

124 The calculation of the climate change velocity (CCV) followed Sandel *et al.* (2011) and Loarie *et*
125 *al.* (2009), who described CCV as the temporal gradient of temperature change divided by its spatial
126 gradient, resulting in a unit of distance per time. We used mean annual temperatures for current conditions
127 (averages 1950-2000), mid-Holocene (6’000 years before present) and Last Glacial Maximum (LGM;
128 21’000 years before present). LGM data were derived from two coupled Atmosphere-Ocean General
129 Circulation Models (AOGCM), CCSM4 and MIROC 3.2 (averaged values). Present and LGM data were
130 available from WorldClim (www.worldclim.org; Hijmans *et al.*, 2005; accessed Aug. 2013) at a resolution
131 of 2.5 arcmin (~5 km). Mid-Holocene data was downloaded from PMIP2 (<https://pmip2.lsce.ipsl.fr/>;
132 Braconnot *et al.*, 2007; accessed Aug. 2013).

133 The PMIP2 data has a lower resolution (2.5 degree), which misses more localized climatic effects
134 caused, e.g., by topography. To obtain data at the same resolution as for WorldClim data (2.5 arcmin), we
135 interpolated the raster. The same interpolation was applied to the PMIP2 current temperature data. We
136 then calculated the difference in current temperature between WorldClim and PMIP2 data and added it to
137 the mid-Holocene data from PMIP2 database to account for elevation effects (and other time-stable
138 anomalies). This method (A. Wilson, pers. comm.) follows the assumptions that (a) local adiabatic effects
139 on temperatures have not changed much since the mid-Holocene, and (b) that topographies have remained
140 stable. To verify this procedure we repeated all steps to calculate a map for the LGM with data from
141 PMIP2 database and obtained a high correlation with WorldClim data (Pearson’s $r = 0.987$; equivalent
142 Mid-Holocene data are now also available at www.worldclim.org).

143 We calculated the temporal gradient as the difference between present and past temperatures in
144 each cell after converting all temperatures to Kelvin (K). We converted differences to absolute values to
145 retrieve positive velocities independent of their sign. We calculated the spatial gradient as the slope of the
146 temperature over distance, i.e. rate of change for each cell from a 3 x 3 cell neighborhood. Spatial change
147 rates are mainly driven by elevation difference due to the adiabatic relationship of temperature with air
148 pressure. We used the slope of current temperatures because the temperature slopes of past climates
149 correlate very well with these (e.g., current vs. LGM rate, Pearson's $r = 0.997$). Values < 0.01 K/km were
150 changed to 0.01 K/km to avoid dividing by zero (or near-zero). The temporal change rates (K/y) were then
151 divided by the spatial change rates (K/km) and then multiplied with 1000 to yield data in units of m/y. We
152 denote the velocity from LGM to present as CCV21, the velocity from the mid-Holocene to the present as
153 CCV6.

154 To allow for a multidimensional interpretation of climate and CCV (i.e., extending the original
155 hypothesis of temperature change effects towards precipitation changes and other climatic variation), we
156 applied methodology developed by Hamann *et al.* (2015). This method for predicting CCV effects
157 involves an ordination of climatic data, so it does not allow a direct test of the 'temperature CCV'-
158 hypothesis of Sandel *et al.* (2011). However, it assures that other, more complex and multivariate CCV
159 effects within the given time window are not overlooked. As these analyses did not alter our conclusion,
160 we present them in the [Appendix \(S6\)](#).

161 Temperature seasonality (T_{seas}) is measured as the standard deviation of monthly mean
162 temperatures throughout the year, and precipitation seasonality ($\text{Precip}_{\text{seas}}$) as its coefficient of variation
163 (data from www.worldclim.org; Hijmans *et al.*, 2005).

164 We calculated available land area as the area of land cells in a given radius around a cell
165 (Morueta-Holme *et al.*, 2013). As it is somewhat arbitrary what **radius** is to be used for this calculation, we
166 tested (in preliminary trials) different radii that lead to circles with maximum areas of the lower quartile,
167 median and upper quartile of range sizes. We found that the radius related to the upper quartile of ranges

168 sizes (i.e., 955 km) led to the best model fits and we used the resulting area calculations for further
169 analyses.

170 All further GIS manipulations and analyses were carried out in Mollweide World equal area
171 projection at 100 km grain size. Climate data, originally processed at 2.5 arcmin, were aggregated and
172 projected to this grid. Pleistocene ice extent (Ehlers *et al.*, 2011) was coded as one (ice) and zero (no ice).
173 Elevation range was calculated from a digital elevation model (Stein *et al.*, 2015). Furthermore, we used a
174 broad classification of zoogeographic realms from Holt *et al.* (2013).

175 We restricted the study region in various ways to reduce unwanted variability and bias. First, all
176 smaller islands were excluded to avoid effects of dispersal limitation of island endemics on range data (as
177 these will not contribute to our understanding of the general drivers of range size). Exceptions were made
178 for the British Isles, Sumatra, Borneo, Madagascar and New Guinea, because they are either large enough
179 to develop range size variability within the island, or were connected to continental regions in the relevant
180 past (i.e., LGM). Since the connectivity argument cannot be made for Madagascar (but for all others of the
181 large islands), we also re-run analyses without Madagascar (which did not change conclusions; data not
182 shown).

183 Second, we excluded cells with a species richness <5 , because random effects in the data have
184 great potential to introduce noise into ecological patterns. This restriction affected mostly desert regions in
185 North Africa and Western Australia, as well as much of north-eastern Siberia. Third, we excluded coastal
186 cells to avoid unwanted effects due to area size variation of cells. After applying these restrictions, 762
187 species continued to contribute to range size data in 7,108 pixels.

188

189 **Statistical analyses**

190 All data (predictors and response) were standardized to a mean of zero and a standard deviation of
191 one, which makes model coefficients directly comparable. All variables except land area were \log_{10} -

192 transformed prior to standardization to reach normality. We tested predictor data for collinearity, finding
193 that all correlations between variable pairs were weak ($r^2 < 0.26$). In a preliminary analysis step, we used
194 model selection (Burnham & Anderson, 2005) to compare a full model with all hypothesized effects (no
195 interactions) to simplified models of various subsets of these predictors. [We present both the Bayesian](#)
196 [Information Criterion \(BIC\) to account for very large sample sizes, as well as Akaike's Information](#)
197 [Criterion \(AIC\) for comparison.](#)

198 We based the main analyses on univariate regression of the above predictors, as well as on their
199 combination in a multivariate linear model. Because our dataset contained spatially structured data,
200 ordinary least square (OLS) models are most likely to be biased in significance assessments and possibly
201 also in coefficient estimates (Bini *et al.*, 2009). Therefore, we also present results from a spatial
202 simultaneous autoregressive error (SAR) model (function *errorsarlm* in R-package *spdep*; neighbourhood
203 distance of 5000 km, based on preliminary trials; residual autocorrelation remained high only over very
204 short distances of < 200 km (concluded from correlograms of residuals), which we considered acceptable
205 at our data resolution and extent). [By comparing results for OLS and SAR the reader can appreciate the](#)
206 [potential effects of spatial structure in our data.](#)

207 Zoogeographic regions differ in their evolutionary history, but it is unclear to what extent this may
208 affect range sizes (e.g., whether or not range size data carry phylogenetic signal; Jablonski, 2008; Cardillo,
209 2015). Furthermore, available zonations are based on vertebrate taxa, which may be different to the
210 appropriate (yet unknown) zonation for sphingid moths. For these reasons, we calculated all analyses with
211 and without additional consideration of zoogeographic regions (as binary dummy predictors). Because
212 they led to the same conclusions, we present only models without zoogeographic regions in the main text
213 (see [Appendix S4](#) for inclusion).

214 Analyses were carried out in R 3.3 (incl. packages *spdep*, *ncf*). We present pseudo- R^2 values of
215 the (likelihood-fitted) models, calculated from a linear regression of model prediction vs. observed data.

216

217 **RESULTS**

218 Estimated range sizes varied over seven orders of magnitude, from 75 to 53.4×10^6 km² (for raw
219 data see Appendix S1). Range size data resembled a left-skewed log-normal distribution (Fig. S2.1 in
220 Appendix S2), as commonly observed in such data (Gaston, 2003); there are many more small-ranged
221 than large-ranged species. Fig. 1 maps median range sizes across the research region. Largest range sizes
222 were concentrated in the deserts of North Africa and the Middle East, as well as the Arctic. Small range
223 sizes were common in Madagascar, New Guinea and Australia. Notably, in the Eastern Palearctic as well
224 as the Pamir/Hindukush region, small to medium range sizes stretch much further north than in the
225 Western part of the research region. There is a clear North-South decline in range sizes (Pearson's $r =$
226 0.656), while a correlation of range size with absolute latitude, as expected by Rapoport's effect (Stevens
227 1989), is weak (Pearson's $r < 0.225$).

228

229 **Environmental correlates of range size variation.**

230 Patterns of all environmental predictors are mapped in Fig. 2. Climate change velocities derived
231 for the period from LGM to the present (CCV21) exhibit a very different pattern to that from the mid-
232 Holocene to the present (CCV6). Likewise, temperature seasonality is distributed differently than
233 precipitation seasonality. Univariate models with median range sizes (Fig. 3, Table 1) indicate strong
234 positive effects of temperature seasonality and land area, slightly weaker, negative correlations with
235 elevation range, and almost no effect of precipitation seasonality. CCV measures are relatively weak and
236 inconsistent in strength (positive for CCV21, negative for CCV6; note that this is not due to opposite
237 temperature gradients, as velocities are based on absolute change).

238 Model selection based on AIC as well as BIC (Appendix S3) showed that models containing all

239 (or nearly all) predictors were most useful for predicting range size variability. In particular, the full model
240 (7 predictors) was considered best if biogeographic regions were not included ($\Delta\text{AIC} = 16$, $\Delta\text{BIC} > 8$ to
241 second-best model; Table S3.1). For models including biogeographic regions as predictors (Table S3.2),
242 all top-models had 5-7 predictors (additional to biogeographic regions), whereas the full model was
243 ranked second ($\Delta\text{AIC} = 1.7$) or third ($\Delta\text{BIC} = 8.6$), depending on the information criterion. For
244 consistency among the following analyses, we therefore chose to always use the full models for in-depth
245 assessments of predictor effect.

246 Table 2 shows results for multivariate models containing all predictor variables. Both modelling
247 approaches (spatial and non-spatial) confirmed strong positive effects of temperature seasonality and land
248 area, and negative effects of elevation range. Positive effects of LGM ice extent were weaker but
249 consistent, whereas we could neither find unequivocal support for partial effects of precipitation
250 seasonality, nor for both CCV measures. Relatively weak effects of CCV21, in particular, changed sign
251 depending on whether OLS or SAR models were used, whereas CCV6 effects were different in direction
252 to those proposed by the hypothesis (i.e., higher climate change velocity was associated with smaller
253 ranges). Fig. 3 shows partial effects for selected variables.

254 Model selection (Appendix S3) as well as OLS and SAR including effects of biogeographic realm
255 (Appendix S4), led to the same conclusions. Furthermore, analyses for average log-transformed range
256 sizes (instead of medians; Appendix S5) were consistent with these assessments. Using a multivariate
257 metric of CCV (Hamann *et al.*, 2015), based on six climatic variables, did not alter our conclusion of weak
258 CCV effects compared to those of temperature seasonality alone (Appendix S6). Range size patterns were
259 not related to biome area sizes (Fig. S7.2 in Appendix S7), hence biome size does not provide an
260 alternative, arguably more parsimonious explanation of range size patterns.

261

262 **DISCUSSION**

263 Our data indicated that, for sphingid moths within the geographic restrictions of our analyses (i.e.,
264 continental Old World & Australia), current intra-annual temperature variability explains statistically the
265 spatial variation of geographic range sizes much better than longer-term variation as captured by CCV
266 since the LGM or mid-Holocene. Available land area and elevation range proved important covariates in
267 the system, whereas Pleistocene ice extent had relatively low impact across the research region and
268 precipitation seasonality apparently played no role.

269

270 **Temperature seasonality fits better than CCV**

271 Unlike earlier studies (e.g., Sandel *et al.* 2011), we did not investigate the CCV-range size link in
272 isolation. If we had, we would have concluded a moderately positive effect (Table 1). By comparing CCV
273 against effects of other hypothetical drivers of range size variation, in univariate and multivariate models,
274 we can evaluate more fully the empirical support for CCV as a mechanism shaping range size
275 distributions. Even though broad spatial patterns of temperature seasonality and CCV resemble each other
276 (Fig. 2), collinearity should not have seriously biased analyses (e.g., T_{seas} vs. CCV21, Pearson's $r = 0.382$).
277 Our data suggest that hypothetical mechanisms acting through adaptations to current climates (i.e.,
278 seasonality, Janzen 1967) are better-supported explanations of range size patterns than those that invoke
279 climatic dynamics of the past (i.e., CVV). This view is also suggested by the inconsistent direction of
280 effects of LGM- and mid-Holocene CCV in our models (but see discussion below). However, our analyses
281 carry the caveat that current temperature seasonality may be correlated to climate variation (hence, CVV)
282 at an unspecified point in the past. Thus, statistical support for seasonality does not rule out more complex
283 causal pathways – it only rejects CCV effects as tested (i.e., temperature during the two tested time
284 periods).

285 Temperature variation between the LGM and the present is one of the strongest climatic changes
286 of the Quaternary (Ruddiman, 2001). However, temperatures did not change linearly (as implied by CCV

287 calculations), but included many smaller shifts and oscillations, as evident from locally studied stable
288 isotopes from ice cores, or from pollen records (Thompson, 1998; Claussen *et al.*, 1999; Davis *et al.*,
289 2003). During the mid-Holocene, temperatures in some areas (e.g., northern Europe) were higher than
290 today (Davis *et al.*, 2003). We would have expected that CCV calculations of both time periods should
291 have similar effects on range sizes if the velocity, not the direction, of climate change mattered. However,
292 we found inconsistent signs of effects (Tables 1 & 2). Negative links indicate that high velocity regions
293 are associated with small range size. In the absence of reasonable ecological interpretation, this is possibly
294 a spurious finding. Model misspecification is always a possibility with messy ecological data (in this study
295 and others). Furthermore, climatic variation since the Holocene was of smaller magnitude than that since
296 the Pleistocene, so CCV21 effects may have overridden CCV6 effects in some parts of the world, leading
297 to unclear patterns. Univariate models (Table 1) showed that CCV since the mid-Holocene had only a very
298 low explanatory power as a single variable. This supports the assessment that temperature change velocity
299 since the mid-Holocene did not influence species range sizes. We had also considered CCV effects from
300 the LGM to the mid-Holocene (not shown), which did not lead to further insights. In conclusion, finding
301 consistent effects of CCV21 and CCV6 would have strengthened the case for the proposed mechanism of
302 CCV acting through selection of species' migration speed and mobility, or their niche breadth. Not finding
303 them in our analyses, however, may be due to a range of methodological issues that do not allow clear
304 inference.

305 The correlation with current seasonality, however, does not rule out the possibility that seasonality
306 patterns of past times shaped range sizes (as the seasonal pattern did not change much through time; e.g.,
307 WorldClim LGM seasonality vs. current seasonality, Pearson's $r = 0.999$). However, we find it intriguing
308 that range size effects of long-term climatic variability can be theoretically explained in an elegant manner
309 as the outcome of selection for mobile, wide-niched taxa (Dynesius & Jansson, 2002; Sandel *et al.*, 2011),
310 while the exact mechanism behind a seasonality effect, which we support here empirically, is somewhat
311 unclear (Janzen, 1967; Stevens, 1998, 1992; McCain & Bracy Knight, 2011). A combination of
312 physiological niche measures and spatially explicit evolutionary modelling may be useful to disentangle

313 the various pathways of how adaptation to high local, or range-wide, climate variability may lead to wider
314 niches and larger geographic ranges (Gaston, 2003).

315 While the data in this study reject the CCV hypothesis in the tested timeframes, it may be argued
316 that these were not appropriate to the evolutionary history, migration ability, generation length or other
317 biological traits of the studied taxon. For example, high mobility in sphingids may have led to new
318 equilibria much faster after climatic disturbance than, for example, in poorly-dispersing amphibians
319 (Sandel *et al.*, 2011). Thus, our results cannot reject the general idea that CCV at any, unspecified time
320 window had effects on today's range size distribution. However, without an a priori hypothesis on a
321 specific, appropriate time window, rigorous scientific testing is impossible (we are not aware of any
322 specific CCV hypothesis for alternative timeframes, for sphingids or any other taxon). Data-mining for
323 links between any CCV and range size data for a given taxon may give interesting exploratory clues to
324 relevant drivers, but this cannot be viewed as hypothesis testing (see Forstmeier *et al.*, 2016, for a general
325 critique of post-hoc 'testing' in biological science).

326

327 **Available habitat area matters**

328 Habitat area, as pointed out by Morueta-Holme *et al.* (2013), is an important pre-condition for the
329 development of species range sizes. Without land, there is no potential for expansion in terrestrial species.
330 This effect is strong and obvious on small, isolated islands, where many endemics are typically found.
331 However, after excluding these from our analyses we still recovered relatively strong land area effects on
332 median range sizes (Tables 1 & 2). Many small-ranged species in Madagascar, New Guinea and
333 Australia's east, in particular, are associated with small areas of available land in the vicinity. Land area,
334 however, is only a crude proxy for suitable habitat. We can expect that the availability of homogeneous,
335 suitable habitat (e.g., size of biomes or ecoregions; Jetz & Fine 2012) could have an even larger impact on
336 the potential range size of a species. Species adapted to widespread habitats should, all other conditions
337 being equal, have larger ranges. However, in the absence of detailed knowledge of each species'

338 requirements, this is difficult to test in any objective manner.

339 Habitat rarity is also one (of several) potential explanations for the effects of elevation range.
340 Highlands have smaller areas than lowlands and, as there tends to be taxonomic turnover from lowland to
341 highland regions (for sphingids: Beck *et al.*, 2012), highlands will contain species adapted to those rare
342 habitats. Additionally or alternatively, elevation gradients may act as dispersal barriers or ecotones that
343 facilitate speciation (Doebeli & Dieckmann, 2003). Highlands may therefore be associated with the
344 presence of young, yet small-ranged taxa. Furthermore, elevation gradients act as buffers to climatic
345 change (Hawkins & Diniz-Filho, 2006). The latter effect is essentially the suggested mechanism of CCV,
346 as climatic stability (due to easy migration up and down a mountain) would lower extinction rates and
347 gives small-ranged species a higher chance to survive (Burgess *et al.*, 2007). In line with this, in other taxa
348 phylogenies (Smith *et al.*, 2007) and richness patterns (Collwell *et al.*, 2008) on mountains seem to
349 support the idea of highest survivability at mid-elevations on mountains. Elevation range of grid cells was
350 a very weak univariate predictor of range sizes, but had a strong effect in multivariate models. Thus, while
351 an additional effect of mountains on range size is evident (irrespective of the mechanism) it is not a
352 factor that can serve as a main determinant of the global-scale pattern (given that much variability occurs
353 also across lowland regions, Fig. 1).

354

355 **Ice cover and precipitation**

356 The extent of the glaciation is an effect of Pleistocene history that goes beyond temperature
357 effects, as it determines the available land area for all taxa than depend on plant growth. Glaciation history
358 undoubtedly affects species richness and composition in Europe and in particular in North America, where
359 glaciation was more extensive (Morueta-Holme *et al.*, 2013). By adding Pleistocene ice extent as a
360 separate predictor to our analysis, we recovered consistent, although not particularly strong effects in the
361 multivariate model (Table 2). Given that sphingid moths are generally very mobile, that extensive
362 glaciation was restricted to northern Europe, and that southern European species are also relatively wide-

363 ranging (Fig. 1), it is perhaps not surprising that the ice effect was not overly strong. However, glaciation
364 history, in combination with high CCV, may be a reason for different latitudinal range size clines in
365 Western Europe compared to East Asia (Fig. 1), a pattern also evident in data from Sandel *et al.* (2011).
366 Pleistocene refuge areas, such as Iberia, Italy and the Balkans (Hewitt, 1999; Sommer & Nadachowski,
367 2006), had clearly lower CCV (Fig. 2).

368 A surprising result was the apparent irrelevance of precipitation seasonality in explaining range
369 size variation. The mechanisms suggested for effects of temperature seasonality should also be relevant
370 for precipitation, and the map of range size variation suggests higher values in low-precipitation regions at
371 least in the subtropics and tropics (e.g., fringes of Sahara, Namib, Australian deserts). Although there are
372 options for artefacts – e.g., niche modelling may have an inherent tendency to overestimate the range
373 filling (or occupancy) of desert species (who may be dependent on water sources other than precipitation,
374 unknown to the niche models), and Worldclim precipitation data may lack precision in tropical regions –
375 we find it surprising that this absence of a precipitation effect has so far not been a topic of the scientific
376 discourse.

377 Our multivariate model explained a substantial part of the near-global range size variation studied
378 here (OLS: 57%, SAR: 69%; Table 2) from only a few environmental correlates, and results clearly
379 supported some variables while deeming others irrelevant. Nevertheless, statistical as well as principal
380 issues remain to be solved before we can optimistically claim to understand how climate and other factors
381 shape range sizes and endemism. For example, large-ranged species generally contribute overly to pixel-
382 based analyses (a phenomenon of pseudo-replication; Jetz & Rahbek, 2002), but it is far from trivial to
383 overcome this effect. Sizling *et al.* (2009) pointed out how geometric effects alone can lead to (in parts)
384 counter-intuitive patterns of range size and species richness. Furthermore, phylogeny may link species'
385 occurrences (i.e., closely related taxa tend to occur in nearby regions) with their range sizes (Beck *et al.*,
386 2006; Jablonski, 2008; Cardillo, 2015). It is not straightforward to control analyses simultaneously for
387 spatial and phylogenetic effects of non-independent data. Last, and most important in our view, unclear

388 ideas on mechanisms lead to vague hypothesis predictions, which reduces the inference value of tests.
389 This highlights the need to investigate more thoroughly how seasonality affects niche evolution, and what
390 testable predictions can be derived from that.

391

392 **CONCLUSIONS**

393 We found a distinct spatial pattern of range size variation that does not conform to Rapoport's
394 effect, but showed an across-tropics North-South pattern (cf. Di Marco & Santini, 2015). This fits with the
395 long-standing observation that northern hemisphere studies tend to find support for a Rapoport pattern
396 while southern hemisphere studies do not (Gaston *et al.*, 1998). Our findings confirmed that regions
397 directly or indirectly associated with high climatic instability selected for species with large range sizes.
398 However, among variables of climatic instability, temperature seasonality was the strongest empirical
399 predictor of the range size distribution, while measures of CCV received much weaker support. This
400 illustrates the inference value of testing competing hypotheses in comparison to each other (McGill, 2003).

401 Although our models explained a substantial proportion of the measured range variability across a
402 near-global study extent, we see need for caution. Without deeper insights (e.g., from physiology and
403 evolutionary modelling) into evolutionary mechanisms of how niche evolution responds to climatic
404 variability (e.g., seasonality), it is difficult to move from statistical pattern search towards true testing of
405 mechanistic hypotheses.

406

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411

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- 542
- 543

544 **Supporting Information**

545 Additional Supporting Information may be found in the online version of this article:

546 **Appendix S1:** Full range size data per 100 km pixel (tab-delimited text file)

547 **Appendix S2:** Range size data properties (incl. legend for S1) and predictors

548 **Appendix S3:** AIC-based model selection

549 **Appendix S4:** Models accounting for biogeographic region

550 **Appendix S5:** Results for average range size

551 **Appendix S6:** Methods and Results for multivariate CCV

552 **Appendix S7:** Biomes and range sizes

553

554 **Biosketch**

555 Marc Grünig completed his MSc in the research group of Jan Beck, which focusses on insect

556 macroecology. He is interested in GIS analyses of ecological and environmental data, academic or applied.

557 Author contributions: MG & JB designed the study, analysed data and wrote the manuscript, with input

558 from LB-M, NB and IJK. JB, LB-M & IJK provided sphingid range map data.

559

560 Editor: Simone Fattorini

561 **Tables**562 **Table 1** Results of univariate linear models modelling predicting median range size.

	Slope_{OLS}	t_{OLS}	R²_{OLS}	Slope_{SAR}	z_{SAR}	R²_{SAR}	P_{SAR}
CCV21	0.388	35.39	0.150	0.107	11.41	0.564	<0.0001
CCV6	-0.228	-19.75	0.052	-0.046	-5.13	0.565	<0.0001
T _{seas}	0.545	54.72	0.296	0.479	44.94	0.650	<0.0001
Precip _{seas}	-0.143	-12.20	0.020	0.060	6.58	0.572	<0.0001
Elev. range	-0.196	-16.87	0.038	-0.168	-20.07	0.583	<0.0001
Land area	0.566	57.78	0.320	0.296	20.25	0.572	<0.0001
Ice	1.131	14.25	0.028	-0.066	-1.13	0.565	<0.0001

563

564 All modelling was carried out on standardized data (except “Ice”, a binary variable); sample size N =
565 7,108 pixels, grain size = 100 km. All OLS regressions were highly significant (not shown). Spatial
566 autoregressive models (SAR) were used to control for autocorrelation. Pseudo-R² values for SAR were
567 based on a regression of modelled vs. observed data.

568

569 **Table 2** Results of a multivariate model predicting median range size.

	Slope_{OLS}	t_{OLS}	Slope_{SAR}	z_{SAR}	P_{SAR}
CCV21	0.019	1.61	-0.043	-4.14	<0.0001
CCV6	-0.107	-11.32	-0.063	-7.44	<0.0001
T _{seas}	0.308	30.00	0.473	43.49	<0.0001
Precip _{seas}	-0.067	-7.38	-0.021	-2.44	0.015
Elev. range	-0.276	-28.07	-0.176	-20.08	<0.0001
Land area	0.510	59.00	0.371	27.88	<0.0001
Ice	0.844	14.79	0.433	8.56	<0.0001

570

571 All modelling was carried out on standardized data (sample size N = 7,108 pixels, grain size 100 km).

572 OLS model fit was R²_{adj} = 0.571, SAR had a pseudo-R² = 0.691.

573 **Figure legends**

574 **Fig. 1** Median range sizes per 100 km pixel (units: standard deviations, SD). Calculations are based on the
575 962 species occurring in map pixels shown here. Small islands, coastal cells, and pixel with less than five
576 species were excluded.

577

578 **Fig. 2** Maps of predictor variables: (a) climate change velocity since the last glacial maximum (LGM;
579 CCV21), (b) climate change velocity since mid-Holocene (CCV6), (c) elevation range, (d) ice extent
580 during LGM, (e) temperature seasonality, (f) precipitation seasonality, (g) land area, (h) zoogeographic
581 regions (for analysis see Tables S3.2 in Appendix S3, and Appendix S4). (d) and (h) are measured as
582 categorical variables; all others were standardized to a mean of zero and a SD of one.

583

584 **Fig. 3** Effects of temperature seasonality (T_{seas}) and LGM climate change velocity (CCV21) on median
585 range size. *Upper*: Univariate plots of (a) T_{seas} and (b) CCV21. LOESS fits are shown to visualize patterns.
586 *Lower*: Partial effects from a multivariate SAR model for (c) T_{seas} and (d) CCV21. All variables were z-
587 transformed and measured in standard deviations (details in Tables 1 & 2).

588