



HAL
open science

A global test of Allen's rule in rodents

Bader Alhajeri, Yoan Fourcade, Nathan Upham, Hasan Alhaddad

► **To cite this version:**

Bader Alhajeri, Yoan Fourcade, Nathan Upham, Hasan Alhaddad. A global test of Allen's rule in rodents. *Global Ecology and Biogeography*, 2020, 29 (12), pp.2248-2260. 10.1111/geb.13198. hal-03820244

HAL Id: hal-03820244

<https://hal.u-pec.fr/hal-03820244v1>

Submitted on 19 Jul 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 RUNNING HEAD: ALLEN'S RULE IN RODENTS

2

3 A GLOBAL TEST OF ALLEN'S RULE IN RODENTS

4

5 BADER H. ALHAJERI^{1,†,*}, YOAN FOURCADE^{2,†}, NATHAN S. UPHAM^{3,4}, HASAN
6 ALHADDAD¹,

7

8 ¹*Department of Biological Sciences, Kuwait University, Safat, 13060, Kuwait*

9 ²*Sorbonne Université, UPEC, CNRS, IRD, INRAE, Institut d'écologie et des sciences de
10 l'environnement, IEES, F-75005 Paris, France*

11 ³*Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, 06511,
12 USA*

13 ⁴*School of Life Sciences, Arizona State University, Tempe, AZ, 85287, USA*

14

15 [†]BHA and YF contributed equally to this work and should be considered as co-first author.

16 ^{*}*Corresponding author: Bader H. Alhajeri (bader.alhajeri@ku.edu.kw)*

17

18 **ACKNOWLEDGMENTS**

19 The authors did not receive any specific financial support for this work. NSU was supported by
20 NSF grant DEB-1441737 and the Biodiversity Knowledge Integration Center at Arizona State
21 University. Some of the morphometric data used in this study were collected by A. Almousawi,
22 M. Alkhudher, F. Almousa, and Z. Almousawi as part of student-led projects under the
23 supervision of BHA and HA. This work relied on data from IUCN, WorldClim, museum
24 databases, and the literature, and as such, we are grateful to everyone who contributed to these
25 sources. This manuscript improved by comments from S. Meiri, M. Symonds, and two
26 anonymous reviewers.

27

28 **FUNDING**

29 The authors did not receive any specific grant funding for this project.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/GEB.13198](https://doi.org/10.1111/GEB.13198)

This article is protected by copyright. All rights reserved

30

31 **AUTHOR CONTRIBUTIONS**

32 BHA conceived and designed the study and wrote the first draft of the manuscript. BHA, YF,
33 NSU, and HA collected the data. BHA, YF, and NSU ran preliminary analyses. YF ran all the
34 final analyses and produced the figures. BHA and YF wrote the final version of the manuscript
35 with input from NSU and HA. All authors read and approved the final manuscript.

36

37 **BIOSKETCH**

38 **BADER H. ALHAJERI** is an Associate Professor of Zoology in the Department of Biological
39 Sciences at Kuwait University. He is interested generally in mammalian evolutionary ecology,
40 and particularly the macroecological causes of morphological variation among species, at very
41 broad spatial and taxonomic scales. Most of his research uses rodents as the study system. More
42 information can be found on his website: <https://sites.google.com/view/alhajeri>.

43 **YOAN FOURCADE** is an Assistant Professor at Université Paris Est Créteil and in the Institute
44 of Ecology and Environmental Sciences of Paris. He is broadly interested in conservation
45 biology and spatial ecology. His current research topics deal with the interaction between local
46 and macroecological processes in the context of climate change.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

DR. BADER H ALHAJERI (Orcid ID : 0000-0002-4071-0301)

DR. YOAN FOURCADE (Orcid ID : 0000-0003-3820-946X)

DR. NATHAN UPHAM (Orcid ID : 0000-0001-5412-9342)

Article type : Research Papers

A GLOBAL TEST OF ALLEN'S RULE IN RODENTS

RUNNING TITLE: ALLEN'S RULE IN RODENTS

Word count (excluding title, abstract, references, and supplementary material): 6374

Number of references: 87

Number of figures: 3

Number of tables: 0 **Abstract**

Aim: We test whether geographic variation in length of rodent species' appendages follows predictions of Allen's rule—a positive relationship between appendage length and temperature—at a broad taxonomic scale (order Rodentia). We also test if the applicability of this rule varies based on the unit of analysis (species or assemblage), examined appendage (tail, hind foot, ear), body size, occupied habitat, geographic range size, life mode, and saltation ability.

Location: Worldwide.

Time period: Current.

Major taxa studied: Rodents (order Rodentia).

Methods: We assembled data on morphology, ecology, and phylogeny for up to 2,212 rodent species—representing ~86% of all the described rodent species and ~95% of the described genera. We tested the predicted Allen's rule associations among size-corrected appendage lengths and both latitude and climatic variables (temperature and precipitation). We applied a cross-species approach based on phylogenetic regressions and a cross-assemblage approach based on spatial regressions in equal-area 1.5-degree grid cells.

32 **Results:** Support for Allen's rule was greatest for the tail and was stronger across assemblages
33 than across species. We detected a negative relationship between tail length and (absolute)
34 latitude, which was accounted for by a positive association between tail length and temperature
35 of the coldest month. This association was greatest in desert species. In addition, we observed a
36 negative relationship between ear length and precipitation.

37 **Main conclusions:** In rodents, Allen's rule is confirmed only for tails, and this association seems
38 to be driven by adaptation to the cold, rather than warm temperatures. Habitat type seems to
39 influence conformity to this rule. Conformity to Allen's rule is likely the result of complex
40 evolutionary trade-offs between temperature regulation and other essential species' traits.

41

42 **KEYWORDS**

43 Allen's rule, body size, ear length, habitat, hind foot length, geographic range, macroecology,
44 rodent, tail length, temperature

45 **1 | INTRODUCTION**

46 Allen's (1877) rule posits that the appendages (e.g., limbs, ears, tail, snout) of endotherms tend to
47 be longer and thinner in warmer environments. This rule is among the most studied
48 biogeographic patterns, perhaps second only to Bergmann's (1847) rule, which also makes a
49 prediction about the adaptive response of endothermic animals to climate. These rules are
50 related, and both are commonly interpreted as reoccurring geographic patterns in morphology
51 shaped by adaptation to climate. More specifically, the modification of surface-area-to-volume
52 ratio aids thermoregulation—its decrease in cold environments reduces heat loss and its increase
53 in warm environments facilitates heat dissipation (Mayr, 1956).

54 Allen's rule has been examined in various endotherms, including birds (e.g., Nudds &
55 Oswald, 2007; Symonds & Tattersall, 2010; McCollin et al., 2015) and mammals (e.g.,
56 lagomorphs: Griffing, 1974; Stevenson, 1986; primates: Fooden & Albrecht, 1999; Tilkens et al.,
57 2007; and rodents: Lindsay, 1987; Bidau et al., 2011; Alhajeri, 2016); it has also been examined
58 in ectotherms (e.g., Ray, 1960). So far, most mammal studies of Allen's rule were conducted at
59 the intraspecific level, while cross-species analyses are often restricted to a few species (often
60 within a taxonomically restricted group). However, recent mammal studies have explored the
61 applicability of this rule to broader taxonomic levels (e.g., Gohli & Voje, 2016; Alroy, 2019),
62 following up on earlier large-scale cross-species bird studies (e.g., Nudds & Oswald, 2007;

63 Symonds & Tattersall, 2010). Furthermore, cross-assemblage investigations of Allen's rule are
64 rare, if they exist at all, even though this approach is commonly used to study other
65 biogeographic trends (e.g., Blackburn & Hawkins, 2004; Olalla-Tárraga et al., 2010; Maestri et
66 al., 2016; Alhajeri et al., 2019). The role of ecological and geographic factors in conformity to
67 this rule is also an understudied topic. Recently, using a sample of 360 New World small
68 mammal species (marsupials, lipotyphlans, rodents), Alroy (2019) found evidence for longer
69 tails in tropical habitats (e.g., rainforests).

70 Here, we assemble an extensive dataset to test the predictions of Allen's rule globally in
71 Rodentia. Rodents are an outstanding system to study morphological responses to climate at the
72 interspecific level, especially since they comprise >2,000 extant recognized species (Mammal
73 Diversity Database, 2019) (leading to increased statistical power), have near-global geographic
74 distributions (IUCN, 2017) (encountering diverse climates), and vary greatly in body size
75 (Nowak, 1999) (facilitating the study of morphological covariation with climate). We aimed to
76 test whether rodents' appendage lengths (tail, hind foot, ear) vary consistently over geography
77 and climate, and whether Allen's rule can be similarly applied across rodent species as to spatial
78 assemblages of those species. We predict that phenotypes coherent with Allen's rule should be
79 more common in species with smaller geographic ranges because they are subject to a narrower
80 range of environmental conditions in which to adapt (see Alhajeri & Fourcade, 2019; Serrat et
81 al., 2008). We also predict a stronger appendage length – temperature association in smaller-
82 sized species—this is because in mammals, the relative effect of size modification on
83 thermoregulation (through changes in the surface-area to volume ratio) is greater in smaller
84 species, while in larger species, pelage modification plays a larger role in temperature control
85 (see Ashton et al., 2000; Alhajeri & Steppan, 2016; and references therein). Furthermore, based
86 on the results of Alhajeri (2016) and Alroy (2019), we expect Allen's rule to manifest most
87 strongly in rodent tails (compared to the hind foot and the ear), at tropical latitudes, and
88 specifically in deserts. The novelty of the present study stems from the near comprehensive (and
89 global) sampling of rodent species, the tests of influence of ecological factors on conformity to
90 this rule, and the comparison of cross-species vs. cross-assemblage analyses. The broad
91 taxonomic scale employed ensures that most of the covariation between appendage size and
92 temperature is a consequence of evolutionary adaptation via genetic selection (the mechanism
93 implied by most studies of Allen's and Bergmann's rules), rather than phenotypic plasticity.

94

95 **2 | METHODS**

96 **2.1 | Morphometric data collection**

97 We first compiled a list of all rodent species with range maps available in the International Union
98 for Conservation of Nature (IUCN, 2017). Using this list, we collected external measurement
99 data for all species available in museum databases and the literature. These data consisted of
100 head and body length (total length minus the tail), tail length, hind foot length, and ear length—
101 all in millimeters (mm). We also collected body weight data in grams (g). The following sources
102 contributed most to this database: Arctos, the Collaborative Collection Management Solution
103 (Arctos, 2018; 47,511 observations), VertNet, a Database of Vertebrate Specimen Records
104 (VertNet, 2019; 15,644 observations), the collections database of the Division of Mammals,
105 Smithsonian National Museum of Natural History (NMNH, 2018; 8,445 observations), iDigBio,
106 Integrated Digitized Biocollections (iDigBio, 2019; 6,667 observations), and the database of the
107 zoological collection of the Museum of Comparative Zoology, Harvard University (MCZbase,
108 2018; 1,113 observations). In total, data was collected from 285 different reference sources,
109 which are listed in Table S1 in the Supporting Information. The museum databases included data
110 from 58 natural history collections (see Table S1).

111 Our final database consists of measurement data for 81,880 observations, with the
112 number of observations per species ranging from 6,647 (*Mus musculus*) to several species with a
113 single observation (Table S1). In total, data was collected for 2,212 species (head and body
114 length: $n = 2,212$; tail length: $n = 2,188$; hind foot length: $n = 2,160$; ear length: $n = 1,911$; body
115 weight: $n = 1,191$), belonging to 490 genera (Table S2). According to the Mammal Diversity
116 Database (Burgin et al., 2018), the number of rodent species currently described is 2,552,
117 belonging to 513 genera, indicating that we sampled ~86% of the rodent species and ~95% of
118 their genera. Further details about the process of data collection, processing, cleanup, and quality
119 control can be found in Appendix S1. We used our database to calculate the species means
120 (Table S2) and standard deviations for each measurement. Because the length of species'
121 appendages is correlated to their body size, we need to size-correct each measurement. One
122 option is to calculate the relative length of each appendage by dividing it by body length (e.g.
123 Coetzee, 1970; Fooden & Albrecht, 1999; Bidau et al., 2011; Alhajeri, 2016). Appendage lengths
124 could alternatively be size corrected by computing the residuals of regressions of each species

125 mean appendage value (tail length, hind foot length, ear length) against the species mean value
126 of head and body length (used as an estimate of body size) (e.g., Alroy, 2019). Here, however,
127 we accounted for the relationship between appendage length and body size by including head
128 and body length as an additional predictor in all statistical models (see section 2.3 and 2.4 below)
129 (see Freckleton, 2002).

130

131 **2.2 | Environmental data collection**

132 We extracted distributional data for all 2,212 rodent species from IUCN (2017). These data
133 consist of polygons depicting each species' known global range based on a combination of
134 empirical records, knowledge of elevational and habitat requirements, and expert assessment.
135 Although these range maps may not accurately represent the exact locations where species are
136 present, they are currently the best global assessment of species' distributions at a large
137 taxonomic scale (Schipper et al., 2008). We downloaded IUCN range maps as Environmental
138 Systems Research Institute (Esri) shapefiles from [www.iucnredlist.org/resources/spatial-data-](http://www.iucnredlist.org/resources/spatial-data-download)
139 [download](http://www.iucnredlist.org/resources/spatial-data-download). We kept all polygon subsets, including invasive ranges, as they represent evidence of
140 the adaptation of species to local climates, whether they occur naturally or not. The IUCN
141 shapefiles (polygons) were loaded into R (R Development Core Team, 2019) and manipulated
142 therein using the following libraries: SF (Pebesma, 2018), RGDAL (Bivand et al., 2018),
143 RGEOS (Bivand & Rundel, 2018), and EXACTEXTRACTR (Baston 2020). We used the R
144 library LETSR (Vilela & Villalobos, 2015) to extract the range size of each species (in
145 kilometers squared) based on the IUCN polygons.

146 In addition, we used the RREDLIST R library (Chamberlain, 2018) to obtain a list of
147 habitats used by each species using the highest hierarchical level of habitat classification in
148 IUCN. We considered all categories of polygons (extant, extinct, introduced) as they represent
149 environmental conditions in which species are able to survive and reproduce, and hence are all
150 representative of their climatic niche. Out of 2,212 species, 1,257 had more than one habitat type
151 in the IUCN classification. In order to reduce habitat to one type only for each species, we
152 downloaded a global map of terrestrial habitats that uses the same IUCN classification (Jung et
153 al, 2020), and extracted the area of all habitat types within each species' range, and then
154 classified these 1,257 species according to the most common habitat. For the remaining 955
155 species, we kept the habitat type provided by the IUCN red list (Table S2). Several habitat types

156 are represented by a few species and their inclusion caused multivariate models to crash;
157 therefore, these analyses only included the six main habitat types represented by most species
158 (forest, savanna, shrubland, grassland, rocky areas desert).

159 Species were divided into one of four life modes which roughly correspond to
160 microhabitat use (arboreal [n=307], scansorial [n=173], subterranean [n=125], terrestrial
161 [n=1565]) (Table S2)—these data were downloaded from www.vertlife.org/data (Wilman et al.,
162 2014; Upham et al., 2020). These life modes are associated with consistent modifications in the
163 appendages that could influence conformity to Allen's rule. A total of 42 species in our dataset
164 did not have life mode data, and thus were not used in multivariate models that use these data.

165 Saltatorial (i.e., ricochetel) and a semi-saltatorial locomotory modes are associated with
166 consistent modifications to the appendages, which in turn could influence conformity to Allen's
167 rule. The literature was used to assign terrestrial species, based on morphological modifications
168 to saltation, into those that are fully saltatorial, semi-saltatorial, and those with no information on
169 saltation ability (Table S2). The first category (fully saltatorial [n=65]) includes such species as
170 jerboas and kangaroo rats that are extremely specialized for leaping and commonly employ a
171 bipedal hopping gait almost exclusively as their primary mode of locomotion. The second
172 category (semi-saltatorial [n=281]) is much less specialized for leaping (e.g., gerbils and pocket
173 mice) which often use other locomotory modes (e.g., ambulatory or cursorial locomotion), but
174 assume a (quadrupedal) jumping gait on occasion, such as when alarmed to escape predators
175 (i.e., as a secondary mode of locomotion). All other species are included in the third category (no
176 information [n=1866]), which are species for which we could not find any strong evidence in the
177 literature for specialization to saltation (see Table S2 for details).

178 Allen's rule is commonly explained in terms of the thermoregulation hypothesis, and thus
179 mainly makes predictions about appendage lengths relative to environmental temperature.
180 However, as both temperature and precipitation exhibit strong latitudinal variation, we aimed to
181 disentangle the role of several climate variables in driving the latitudinal patterns in
182 morphological variation. To test which variable contributes to explaining Allen's rule, we used
183 six bioclimatic variables depicting both average annual and maximum and minimum temperature
184 (in °C) and precipitation (in millimeters): BIO1 (annual mean temperature), BIO5 (maximum
185 temperature of the warmest month), BIO6 (minimum temperature of the coldest month), BIO12
186 (annual precipitation), BIO13 (precipitation of the wettest month), and BIO14 (precipitation of

187 the driest month) (for details, see Busby, 1991). These bioclimatic variables were downloaded as
188 raster files from WorldClim (version 2), at a resolution of 2.5 arc-min
189 (<http://worldclim.org/version2>, Fick & Hijmans, 2017), and processed using the R library
190 RASTER (Hijmans, 2017). Version 2 of the WorldClim dataset is based on average temperature
191 and precipitation interpolated from a global database of weather stations, spanning the years
192 1970 to 2000 (Hijmans, 2017).

193 Among rodent species, the latitudinal midpoint of geographic ranges — based on the
194 centroid of IUCN range maps — is positively correlated to annual mean temperature (Pearson's r
195 = 0.743, $p < 0.050$) and negatively to annual precipitation (Pearson's $r = -0.633$, $p < 0.050$). In
196 addition, high pairwise correlations exist among the temperature variables (Pearson's $r = 0.480$ –
197 0.942, all $p < 0.050$) and precipitation variables (Pearson's $r = 0.490$ –0.886, all $p < 0.050$).

198

199 **2.3 | Data analysis**

200 We analyzed the effect of climate on rodents' appendage length both across species and across
201 assemblages. For each type of analysis and for each appendage, we followed the same analytical
202 steps. First, we examined geographical patterns of appendage length by testing the association
203 between appendage length and the absolute value of latitude. Second, we assessed how this
204 pattern could be explained by climatic factors by testing the effect of each of the six bioclimatic
205 variables on the appendage lengths. We selected the best fitting variable among them—the one
206 that leads to the model with the lowest Akaike information criterion score, corrected for small
207 sample size (AICc; Akaike, 1974; Burnham & Anderson, 2002). In all models, we included as
208 explanatory variables both the climate variable to be tested and head and body length to control
209 for the effect of body size on appendage length. An additional null model was computed,
210 excluding climate from the explanatory variables. Third, we computed multivariate models with
211 interactions to test for the effect of various species' characteristics (body size, habitat type, range
212 size, life mode, and saltation ability) on the relationship between appendage length and the
213 selected climate variable.

214 To account for intraspecific phenotypic variability that may bias comparative analyses
215 across multiple species (Garamszegi & Møller, 2010; Silvestro et al., 2015), we repeated all
216 statistical models 100 times, each time sampling a random value of appendage length and head
217 and body length, following a truncated normal distribution (so that sampled values remain > 0)

218 with the mean and standard deviation obtained from the observed distribution of values in our
219 database of morphological measurements. Note that for species where measures originated from
220 one single individual, standard deviation = 0 and the same value was sampled at each repetition.
221 Similarly, there may exist large intraspecific variation in the environmental conditions
222 experienced by a species, especially if it is distributed across a large geographical range. To
223 account for this source of uncertainty we also sampled at each iteration, in the cross-species
224 analyses, a random value of the climate variable following a normal distribution with the mean
225 and standard deviation of the observed climate within the species' range.

226 In all analyses, climate variables, as well as each morphological measurement (tail
227 length, hind foot length, ear length), were scaled and centered to allow post-hoc comparisons of
228 effect sizes (the standardized beta slope coefficients [cross-species: β_{CS} ; cross-assemblage: β_{CA}]).
229 Appendage lengths, as well as head and body lengths, were also log-transformed before scaling
230 to linearize the relationships and to reduce the influence of outliers. Plots were generated using
231 the R base library and/or the following libraries: GGLOT2 (Wickham, 2016), PATCHWORK
232 (Pedersen, 2017), VIRIDIS (Garnier, 2018), and GGTREE (Yu et al., 2017). For all analyses, the
233 significance level (p) was set at $\alpha = 0.05$. All 'log' transformation applied in this paper are
234 natural logarithms. Unless otherwise stated, all other analyses and visualizations were carried out
235 using the R base library. Visual inspections of residual plots (residuals vs. predicted values) and
236 Q-Q (quantile-quantile) plots generally lend support to the distributional assumptions of the
237 residuals of all the linear regression models described below. The complete R script used to
238 perform the phylogenetic and spatial regression analyses can be found in Appendix S2.

240 **2.3.1 | Cross-species analysis**

241 We first examined the association between appendage length and climate across species, using
242 morphological, geographical, and climatic data obtained at the species-level. From the IUCN
243 range maps, we extracted the mean and standard deviation of the latitudinal coordinates of each
244 species' range. Then, combining range maps with bioclimatic variables (raster files), we
245 extracted for each species the mean and standard deviation of each of the abovementioned six
246 bioclimatic variables across locations of its entire range (for details, see Alhajeri et al., 2015).

247 Because species are not independent and because there is evidence of phylogenetic
248 conservatism for all studied morphological traits (see Figures 1a, 2a, 3a), we used phylogenetic

249 regressions to correct for relatedness among species. For this purpose, we used a sample of 100
250 trees from Upham et al. (2019), the most complete mammalian phylogeny to date. This source
251 had two alternative forms of the phylogenetic trees: (1) ‘DNA-only’ trees, which only contain
252 the species for which DNA data was available; and (2) ‘completed’ trees, which also include
253 species missing DNA data that are imputed with birth-death branch lengths within genus- or
254 family-level taxonomic constraints (family if no congeners were sampled for DNA) (for details,
255 see Upham et al., 2019). The reason for analyzing a sample of 100 trees (for both the DNA-only
256 and completed trees) was to consider the uncertainty in phylogenetic placements and node ages.

257 A total of 98 species in our morphometric data set were not found in Upham et al.’s
258 (2019) trees (Table S3). For these species, we used taxonomic information from both IUCN
259 (2017) and the Integrated Taxonomic Information System (ITIS, 2018) to find synonyms to
260 match the species names from our dataset to those in the phylogenetic tree. We were able to find
261 synonyms for 56 species; the remaining 42 species were not found (Table S3), and thus were not
262 included in the cross-species analyses (but are included in the cross-assemblage analyses; see
263 below). As such, the cross-species analyses are based on 2,170 species for the completed sample
264 of trees and 1,466 species for the DNA-only trees.

265 We ran phylogenetic regressions with the length of each of the three appendages as
266 response variable and, as explanatory variables, either latitude or one of the six bioclimatic
267 variables, along with the head and body length always included as a covariable (to account for
268 size). Using the selected climatic variable (the one which leads to the lowest AICc), we
269 computed models where explanatory variables were the interactions between climate and: head
270 and body length, habitat type, range size, life mode, saltation ability as well as all main effects.
271 The significance of these interactions was assessed by likelihood-ratio tests comparing a model
272 with and without the interaction. The whole approach was repeated 100 times (because we use a
273 sample of 100 phylogenetic trees) for each of the completed and the DNA-only sample of trees.
274 In addition, for each tree, analyses were repeated 100 times (because we sampled 100 values of
275 morphology and climate), resulting in a total of 540,000 phylogenetic regressions computed (3
276 $\text{appendages [tail, ear, hind foot]} \times 2 \text{ types of phylogenies [DNA-only + completed]} \times 100 \text{ trees} \times$
277 $100 \text{ random sampling} \times 9 \text{ sets of variables [latitude + null model + 6 bioclimatic variables +}$
278 $\text{interaction model}]$).

279 Phylogenetic linear regressions were computed using the R library PHYLLOM (Ho &
280 Ane, 2014), assuming a Pagel's lambda (λ) phylogenetic model (Pagel, 1999). Out of 100 trees
281 and 100 sampled values, we report for each climate variable and for the null model the mean
282 AICc weight of the corresponding model. We report the mean estimate of the slope of the
283 relationship between appendage length and climate, and the mean coefficient of interactions
284 between climate and continuous variables across 100 trees and 100 sampled values. For all the
285 above estimates, we also report 95% confidence intervals based on the distribution of these
286 coefficients across the 100 trees and 100 sampled values, as well as the proportion of
287 significantly positive or negative coefficients. Significance of interactions are reported as the
288 proportion of cases with p-value < 0.05. Finally, we extracted the mean estimate of the
289 relationship between appendage length and climate (i.e., the selected bioclimatic variable) for
290 each habitat type, life mode and saltation ability.

291 Phylogenetic trees were loaded into R and manipulated therein using the following
292 libraries: GEIGER (Harmon et al., 2008), TREEIO (Yu, 2019), and PHYTOOLS (Revell, 2012).
293 The latter R library was also used to estimate ancestral values of appendage lengths using a re-
294 rooting maximum-likelihood method implemented in order to visualize trait evolution within
295 rodent phylogeny.

296

297 **2.3.2 | Cross-assembly analysis**

298 In addition to species-level analyses, we also examined variation in appendage lengths at the
299 level of rodent species assemblages—this entailed considering a summary value of the traits of
300 all rodent species that co-occur in a given location (i.e., assemblage). We define assemblages as
301 1.5-degree equal-area grid cells globally, following the best practice recommendations of
302 Hurlbert and Jetz (2007). This assemblage-based approach is commonly used to test
303 macroecological patterns (e.g., Meiri, 2011; Maestri et al., 2016; Alhajeri et al., 2019), and can
304 reveal different insights than the species-based approach, such as community assembly in the
305 former and trait evolution in the latter (Feldman & Meiri, 2014). We first converted IUCN range
306 polygons to presence-absence raster maps at 10 arc-min resolution using LETSR, and then
307 aggregated the maps to a resolution of 1.5 degrees (this also had the effect of reducing
308 computation time). A species was considered present in a grid cell if its distribution overlapped
309 any surface of it, ensuring that all 2,212 species (those in Table S2) were included, even those

310 with a distributional range smaller than the maps' resolution. Using the associated morphological
311 traits, we summarized in each grid cell the tail length, hind foot length, or ear length of all
312 species present in the grid cell, by the median as well as by both the 10th and 90th percentile
313 length of each appendage (see Alhajeri et al., 2019 for details). We chose the median to obtain a
314 general perspective on species' appendages within an assemblage, without resorting to the mean
315 that may be uninformative in case of highly skewed traits' distributions. In addition,
316 summarizing assemblages by the 10th and 90th percentile value of appendages' length was
317 necessary to be able to detect an effect of climate if selection acts mostly on species with
318 unusually long or short appendages.

319 To control for the effects of spatial autocorrelation, we performed spatial regressions with
320 eigenvector spatial filtering. In this procedure, we computed Moran's eigenvectors (Dray et al.,
321 2006) that describe the spatial configuration of the grid cells and included them as additional
322 predictors in the linear regressions. This ensures that the resulting β estimates and associated p-
323 values for the variables of interest (here latitude or bioclimatic variables) are free from the effect
324 of spatial autocorrelation. To prevent overfitting, we selected a set of Moran's eigenvectors via
325 forward selection by permutation, according to the following criteria: all Moran's eigenvectors
326 are significant at the 0.05 level, the difference in model R^2 with the previous step is higher than
327 0.005, and the whole set of Moran's eigenvectors does not account for more than 95% of total
328 variation. The calculation of Moran's eigenvectors and the spatial regressions were performed
329 using the SPMORAN R library (Murakami & Griffith, 2019), and their selection was performed
330 using the ADESPATIAL R library (Dray et al, 2020). Because species richness is unequal across
331 assemblages, we included as a weight in the models the number of species in each assemblage.

332 Spatial regressions were run with either the median, 10th percentile, or 90th percentile
333 length of each of the three appendages in each grid cell (= assemblages) as the response variable;
334 while in all models, head and body length (median, 10th percentile, or 10th percentile value to
335 match the response variable) as well as the selected Moran's eigenvectors were used as
336 explanatory variables. Other used explanatory variables were, sequentially, either the average
337 latitude or climate (defined as each of the six bioclimatic variables) of each grid cell. When
338 assessing the effect of species' characteristics on the relationship between appendage length and
339 the selected climate (the one which leads to the model with the lowest AICc), we could not test
340 the effect of species-specific categorical variables such as life mode and saltation ability because

341 they could not be averaged at the scale of whole assemblages. However, we included the
 342 interaction between climate and each of head and body length and range size (averaged within
 343 species' assemblages). The interaction between climate and habitat type was also included using
 344 the main habitat of each grid cell, based on the IUCN habitat map described above; this was
 345 computed as the habitat type that covers the most area in each grid cell, while only retaining grid
 346 cells with a habitat type corresponding to the six dominant types described above for the cross-
 347 species analysis.

348 All analyses were repeated 100 times, corresponding to 100 sampled values of
 349 morphological measurements. In total, 8,100 spatial regressions were computed (3 appendages
 350 [tail, ear, hind foot] \times 3 types of assemblage-level summaries [median, 10th, and 90th percentiles]
 351 \times 100 random samples \times 9 sets of variables [latitude + null model + 6 bioclimatic variables +
 352 interaction model]). Significance of interactions were tested using analysis of variance
 353 (ANOVA) based on type-III (partial) sums of squares as implemented in the CAR library (Fox &
 354 Weisberg, 2019). The mean estimate of the relationship between appendage length and climate
 355 for each habitat type was extracted using the EMMEANS R library (Lenth, 2020). We report for
 356 each coefficient the mean and 95% confidence intervals based on the 100 repetitions, along with
 357 the number of significantly positive and negative results.

359 **3 | RESULTS**

360 **3.1 | Latitudinal patterns**

361 Across assemblages, when appendage size was summarized by the median, we detected a clear
 362 negative relationship between all appendages' length and absolute latitude, which was strongest
 363 for tail length (average $\beta_{CA(\text{median})} = -0.509$) and weak for hind foot length and ear length
 364 (average $\beta_{CA(\text{median})} = -0.197$ and -0.140 , respectively; Figure S1; Table S4). This relationship
 365 was also detected when using the 10th percentile of appendage size, but only for hind foot length
 366 and ear length. We found no evidence for any significant latitudinal pattern when considering the
 367 90th percentile of appendage size. Across species, we observed a negative relationship between
 368 latitude and tail length only (Figure S1; Table S4), although the evidence remains scarce (95%
 369 confidence intervals slightly span 0 for completed trees and only ca. 60% of phylogenetic
 370 regressions were significant). This relationship was also weaker than across assemblages
 371 (average $\beta_{CS(\text{DNA-only})} = -0.060$; average $\beta_{CS(\text{completed})} = -0.056$). In all relationships between

372 appendage length and climatic variables described below, we similarly observed that the
373 standardized effect sizes of regression estimates were of smaller magnitude in cross-species than
374 cross-assembly analyses.

375

376 **3.2 | Climatic patterns**

377 **3.2.1 | Tail length**

378 Both cross-assembly and cross-species analyses found strong support for a positive
379 relationship between tail length and temperature, although the selected variable varied depending
380 on the type of analysis, from BIO6 for cross-species analyses (average $\beta_{CS(DNA-only)} = 0.106$;
381 average $\beta_{CS(completed)} = 0.103$) to BIO1 (median and 10th percentile length; average $\beta_{CA(median)} =$
382 0.472 ; average $\beta_{CA(10thperc)} = 0.280$) and BIO5 (90th percentile length; average $\beta_{CA(90thperc)} =$
383 0.106) for cross-assembly analyses (Table S5 and Figure 1c-d). In addition to these best fit
384 variables, we observed significant relationships between tail length and BIO1 for cross-species
385 analyses, and with all other temperature variables for the cross-assembly analyses (except
386 BIO6 that was not significant when using 90th percentile length). Moreover, there was also a
387 positive relationship between tail length and precipitation variables, especially BIO12 and BIO13
388 in the cross-species analyses. This relationship differed depending on the species' habitat type in
389 all cases (Table S6), although differences between habitats were not constant between analyses.
390 In the cross-species analyses, desert and forest species exhibited the strongest relationship
391 between tail length and BIO6, while shrubland species had the weakest relationship, even
392 negative on average (Figure 1d). In contrast, cross-assembly analyses pointed to different
393 effects of habitat depending on the type of summary statistics we used, and no clear pattern
394 emerged. The median and the 10th percentile of tail length, which were both mainly determined
395 by BIO1, had the lowest relationship with BIO1 in the forest habitat; the habitats with the
396 strongest relationship differed though (median: rocky areas and grassland; 10th percentile: rocky
397 areas and desert). Using the 90th percentile of tail length, we found that shrubland and savanna
398 exhibited a lower relationship between tail length and BIO5 than that of all other habitats (Figure
399 1e). Overall, there was no other evidence of interaction with species' traits in the cross-species
400 analyses, since no more than 58% of models showed a significant interaction with life mode or
401 saltation (Table S6). However, we note that marginal slopes indicate a clearly significantly
402 positive relationship between BIO6 and tail length in subterranean and non-saltating species,

403 while confidence intervals cross 0 in the other species' categories (Figure 1e). In the cross-
 404 assemblage analyses, the effect of temperature on tail length increased in assemblages composed
 405 of species with a small range and, only for the 90th percentile, in assemblages composed of
 406 small-sized species (Figure 1e).

407

408 **3.2.1 | Hind-foot length**

409 There was no evidence of a relationship between hind-foot length and climate in the cross-
 410 species analyses, as the null model generally had the lowest AICc (Table S5 and Figure 2b).
 411 Cross-assemblage analyses revealed opposite trends depending on the summary statistics (Table
 412 S5 and Figure 2b-c). Using the median or 10th percentile of hind-foot length, a temperature
 413 variable had the best fit overall (BIO1 and BIO6 respectively), and there was generally a positive
 414 relationship between hind-foot length and all bioclimatic variables, temperature and precipitation
 415 included. However, temperature had no effect on the 90th percentile of assemblage-level hind-
 416 foot length, but we observed a negative correlation with all precipitation variables (BIO12 had
 417 the best fit on average). Although the effect of climate alone appeared similar, the effect of range
 418 size had an opposite effect on the relationship between the median (positive) and 10th percentile
 419 (negative) hindfoot length (Table S6 and Figure 2e). Using the 10th percentile, there was also a
 420 negative interaction between BIO6 and body size, and a significant effect of habitat type (Table
 421 S6) in which BIO6 and hindfoot length show a reduced relationship in savannas, shrublands, and
 422 rocky areas compared to other habitats (Figure 2e).

423

424 **3.2.3 | Ear length**

425 Cross-species variation in ear length appeared to be associated with precipitation, as there was
 426 strong support for a negative relationship between ear length and BIO14 (precipitation of the
 427 driest month) (average $\beta_{CS}(\text{completed}) = -0.063$; average $\beta_{CS}(\text{DNA-only}) = -0.050$; Figure 3c; Table S5).
 428 Cross-assemblage results were largely similar to those observed for hindfoot length (Table S5
 429 and Figure 3): the median or 10th percentile of ear length were mostly determined by BIO1
 430 (average $\beta_{CA}(\text{median}) = 0.195$) and BIO6 (average $\beta_{CA}(10\text{th perc}) = 0.230$) respectively, and were
 431 positively related to both temperature and precipitation variables. In contrast, the 90th percentile
 432 of assemblage-level ear length was better explained by precipitation (BIO14, average $\beta_{CA}(90\text{th perc})$
 433 $= -0.070$) and we observed a negative correlation with all precipitation variables (we note,

434 though, that there is also evidence for a positive relationship with BIO5). There was an effect of
435 habitat type in cross-assembly analyses only (Table S6), that showed desert habitat to have the
436 lowest relationship between the 90th percentile ear length and precipitation, and the highest
437 relationship between median or the 10th percentile ear length and temperature (Figure 3e).

438

439 **4 | DISCUSSION**

440 We assembled for this study an unprecedentedly large database of rodents' morphological
441 measurements, which, coupled with up-to-date phylogenetic, climatic, and distributional data,
442 allowed us to investigate variation in appendage size in relation to climate at broader spatial
443 scale and taxonomic level than previous works (see Alroy, 2019 for a recent example). We also
444 accounted for intraspecific variation in morphology and in the climatic conditions encountered
445 across the range, which improves the robustness of our conclusions relative to those based on
446 species averages (Ives et al., 2007; Des Roches et al., 2018). At the global scale of order
447 Rodentia, we observed that Allen's rule seems to apply mostly for tails, as this is the only
448 appendage whose size exhibits relatively strong latitudinal variation and a relationship with
449 temperature in both cross-species and cross-assembly analyses. Generally, the association
450 between appendage lengths and climate appeared to be more clearly detected among units of
451 assemblages than species. Part of this outcome could be driven by the conservative nature of
452 integrating both phylogenetic uncertainty and intra-specific trait variation in the cross-species
453 approach, the former of which is not considered in cross-assembly analyses. Alternatively, we
454 hypothesize that stronger effect sizes in the cross-assembly analyses could be caused by
455 geographically widespread species, which may disproportionately contribute to global
456 morphological gradients. If this were the case, cross-species analyses would provide a better
457 assessment of the true dynamics of Allen's rule; therefore, we will mostly focus our
458 interpretation on results that were consistently supported by both cross-species and cross-
459 assembly analyses.

460 We found that tail lengths seem to increase toward the equator and with increasing
461 temperature. This result is partly in accordance with the desert rodent study of Alhajeri (2016) in
462 that relative tail length was associated with temperature variables (but not hind-foot length nor
463 ear length). Alroy (2019) also detected an increase in relative tail lengths in small mammals in
464 the tropics (and no increase in the size of hind feet or ears); however, in that study, increased tail

465 length was not associated with increasing temperature, as our analyses suggest. Furthermore, our
466 cross-species analyses suggest that the variation in tail length is driven by BIO6 (minimum
467 temperature of the coldest month) rather than BIO1 (mean annual temperature) or BIO5
468 (maximum temperature of the warmest month). This can be explained in terms of this association
469 being adaptive for heat conservation in cold environments (by having relatively shorter tails)
470 rather than heat dissipation in warmer environments (by having relatively longer tails). A similar
471 interpretation was proposed in birds, where appendage size (bill and tarsus lengths) was found to
472 be mostly associated with winter temperature (Nudds & Oswald, 2007; Danner & Greenberg,
473 2015; Friedman et al., 2017; Fan et al., 2019; Romano et al., 2020). Cold temperatures appear to
474 be a greater evolutionary constraint than warm ones.

475 We also found evidence that conformity to Allen's rule (in tail length) varies depending
476 on the habitat type—more specifically, a stronger pattern is observed in desert and forest species.
477 For the former, this may indicate that variation in tail length is driven by thermoregulatory
478 pressures. However, it has also been previously suggested (e.g., Alroy, 2019) that the increase in
479 tail lengths with decreasing latitude is caused by increased tropical arboreality. However, we did
480 not find an effect of life mode on the strength of the relationship between tail length and BIO6.
481 Moreover, the greater tail length increase in some deserts (e.g., Sahara, Arabia, central Asia,
482 western Australia, and to a lesser degree Mexico; Figure 1b) could be driven by increased
483 saltatorial ability in such habitats, where a longer tail aids in aerial balance (see Alhajeri, 2016).
484 Thus, convergence toward longer tails could have been driven by extreme selective pressures in
485 desert environments, as is the case in other morphological traits in desert rodents (Mares, 1975;
486 Kotler et al., 1994; Alhajeri et al., 2016; Alhajeri, 2016, 2018; Alhajeri & Steppan, 2018a, b).
487 We could not, however, test the effect of saltation ability at the scale of assemblages, and
488 analyses conducted across species did not show a significant interaction of this variable on the
489 relationship between tail length and temperature, although some results (see Figure 1e) may
490 point to a stronger relationship in non-saltating species, contradicting the hypothesis above.

491 For the 90th percentile, Allen's rule seems to more strongly apply in assemblages
492 composed of small-sized species, and weakly to assemblages of large-sized species. This could
493 be explained by the fact that a modification in tail length would have a disproportionately
494 stronger effect on the surface-area to volume ratio (and thus thermoregulation) in smaller rodent
495 species (see Introduction). The stronger effect of temperature on tail length in assemblages

496 composed of small-ranged species could be driven by the fact that these species are subjected to
497 a narrower range of environmental conditions for which to adapt.

498 In addition, we also observed that the variation of ear length (across species) could be
499 explained by a negative relationship between ear length and the precipitation variable BIO14
500 (precipitation of driest month). In birds, there is evidence of the opposite (positive) relationship
501 between appendage length and precipitation/humidity. Indeed, longer bills have been found to be
502 associated with higher humidity, a pattern that was attributed to the need of more efficient heat
503 dissipation at high humidity during summer, because humidity reduces evaporative cooling at
504 high temperature (Gardner et al., 2016). Here, a possible explanation for the tendency for ear
505 length to decrease with increasing precipitation could be that this pattern is adaptive in dry and
506 hot environments, where longer appendage sizes help heat dissipation as per the prediction of
507 Allen's rule. In addition, desert habitats had a strongly negative relationship between the 90th
508 percentile ear length and precipitation, which suggests that rodents in the driest desert habitats
509 have the longest ears. Although there is no clear prediction of the role precipitation may have in
510 driving appendage length variation in mammals, our results suggest that such a relationship
511 exists. More thorough investigations of the complex link between inter- or intra-specific
512 variation in appendage size and precipitation, such as non-linear relationships or interactions
513 with temperature, may help to more fully decipher the underlying mechanisms.

514 In conclusion, Allen's rule is observed at the global scale in rodents but can only be
515 confidently asserted for tails. The length of hind feet shows no relationship with climatic
516 variables in cross-species, phylogenetically informed analyses. The case of ear length is
517 somewhat intermediate: measured across species, it does not show latitudinal variation nor a
518 relationship with temperature, but it appeared to be associated with global variation in
519 precipitation. Furthermore, it seems that certain species characteristics either promote or hinder
520 the observance of this rule, while others have no effect upon it. Therefore, we provide evidence
521 here of a strong departure from the global expectations of Allen's rule, i.e. a general increase in
522 the length of all appendages with increasing temperature. Most likely, this pattern reflects trade-
523 offs between selection for thermoregulation and for alternative traits (locomotion, in the case of
524 tails and hind feet). Additional studies on other taxa, conducted at the same global spatial scale
525 and high taxonomic resolution, would help assess whether conformity to Allen's rule can be

526 considered a general, widespread pattern, or is a more idiosyncratic pattern restricted to a few
527 species groups and specific appendages.

528

529 **DATA ACCESSIBILITY**

530 All data and R code generated in this study are available in the supporting information.

531

532 ACKNOWLEDGMENTS -.

533 FUNDING -.

534 AUTHOR CONTRIBUTIONS -.

535

536 **REFERENCES**

537 Akaike, H. (1974) A new look at the statistical model identification. *IEEE Transactions on*
538 *Automatic Control*, 19, 716–723.

539 Alhajeri, B. H., Hunt, O. J., & Steppan, S. J. (2015). Molecular systematics of gerbils and
540 deomyines (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the
541 tympanic bulla. *Journal of Zoological Systematics and Evolutionary Research*, 53, 312–
542 330.

543 Alhajeri, B. H. (2016). A phylogenetic test of the relationship between saltation and habitat
544 openness in gerbils (Gerbillinae, Rodentia). *Mammal Research*, 61, 1–11.

545 Alhajeri, B. H., & Steppan, S. J. (2016). Association between climate and body size in rodents: A
546 phylogenetic test of Bergmann's rule. *Mammalian Biology*, 81, 219–225.

547 Alhajeri, B. H. (2018). Craniomandibular variation in the taxonomically problematic gerbil
548 genus *Gerbillus* (Gerbillinae, Rodentia): Assessing the influence of climate, geography,
549 phylogeny, and size. *Journal of Mammalian Evolution*, 25, 261–276.

550 Alhajeri, B. H., & Steppan, S. J. (2018a). A phylogenetic test of adaptation to deserts and aridity
551 in skull and dental morphology across rodents. *Journal of Mammalogy*, 99, 1197–1216.

552 Alhajeri, B. H., & Steppan, S. J. (2018b). Community structure in ecological assemblages of
553 desert rodents. *Biological Journal of the Linnean Society*, 124, 308–318.

554 Alhajeri, B. H., & Fourcade, Y. (2019). High correlation between species-level environmental
555 data estimates extracted from IUCN expert range maps and from GBIF occurrence data.
556 *Journal of Biogeography*, 46, 1329–1341.

- 557 Alhajeri, B. H., Porto, L. M. V., & Maestri, R. (2019). Habitat productivity is a poor predictor of
558 body size in rodents. *Current Zoology*, zoz037. <https://doi.org/10.1093/cz/zoz037>
- 559 Allen, J. A. (1877). The influence of physical conditions in the genesis of species. *Radical*
560 *Review*, 1, 108–140.
- 561 Alroy, J. (2019). Small mammals have big tails in the tropics. *Global Ecology and*
562 *Biogeography*, 28, 1042–1050.
- 563 Arctos (2018). Arctos, Collaborative Collection Management Solution. Downloaded on 2018
564 September 18. <http://arctos.database.museum>
- 565 Ashton, K. G., Tracy, M. C., Queiroz, A. (2000). Is Bergmann's Rule Valid for Mammals? *The*
566 *American Naturalist*, 156, 390–415.
- 567 Daniel Baston. (2020). exactextractr: Fast Extraction from Raster Datasets using Polygons. R
568 package version 0.4.0. <https://CRAN.R-project.org/package=exactextractr>
- 569 Bergmann, C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.
570 *Göttinger Studien*, 3, 595–708.
- 571 Bidau, C., Martí, D., & Medina, A. (2011). A test of Allen's rule in subterranean mammals: The
572 genus *Ctenomys* (Caviomorpha, Ctenomyidae). *Mammalia*, 75, 311–320.
- 573 Bivand, R., & Rundel, C. (2018). rgeos: Interface to Geometry Engine-Open Source (GEOS). R
574 package version 0.3-28. <https://CRAN.R-project.org/package=rgeos>
- 575 Bivand, R., Keitt, T., & Rowlingson, B. (2018). rgdal: Bindings for the 'Geospatial' Data
576 Abstraction Library. R package version 1.3-3. <https://CRAN.R-project.org/package=rgdal>
- 577 Blackburn, T. M., & Hawkins, B. A. (2004). Bergmann's rule and the mammal fauna of northern
578 North America. *Ecography*, 27, 715–724.
- 579 Blix, A. S., (2016). Adaptations to polar life in mammals and birds. *Journal of Experimental*
580 *Biology*, 219, 1093–1105.
- 581 Burgin, C. J., Colella, J. P., Kahn, P. L., & Upham, N. S. (2018). How many species of mammals
582 are there? *Journal of Mammalogy*, 99, 1–14.
- 583 Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multi-Model Inference: A*
584 *Practical Information-Theoretic Approach*. Springer-Verlag, New-York.
- 585 Busby, J. R. (1991). BIOCLIM: a bioclimate analysis and prediction system. *Plant Protection*
586 *Quarterly*, 61, 8–9.

- 587 Chamberlain, S. (2018). rredlist: 'IUCN' Red List Client. R package version 0.5.0.
 588 <https://CRAN.R-project.org/package=rredlist>
- 589 Coetsee, C. G. (1970). The Relative Tail-Length of Striped Mice *Rhabdomys pumilio* Sparrman
 590 1784 in Relation to Climate. *Zoologica Africana*, 5, 1–6.
- 591 Danner, R. M., & Greenberg, R. (2015). A critical season approach to Allen's rule: bill size
 592 declines with winter temperature in a cold temperate environment. *Journal of*
 593 *Biogeography*, 42, 114–120.
- 594 Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T.,
 595 Schweitzer, J.A. & Palkovacs, E.P. (2018) The ecological importance of intraspecific
 596 variation. *Nature Ecology & Evolution*, 2, 57–64.
- 597 Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive
 598 framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological*
 599 *Modelling*, 196, 483–493.
- 600 Dray, S., Blanchet, G., Borcard, D., Guenard, G., Jombart, T., Larocque, G., Legendre, P., &
 601 Wagner, H. H. (2020). adespatial: Multivariate Multiscale Spatial Analysis. R package
 602 version 0.3-8. [https://CRAN.R-project.org/package= adespatial](https://CRAN.R-project.org/package=adespatial)
- 603 Fan, L., Cai, T., Xiong, Y., Song, G., & Lei, F. (2019). Bergmann's rule and Allen's rule in two
 604 passerine birds in China. *Avian Research*, 10, 34.
- 605 Feldman, A., & Meiri, S. (2014). Australian Snakes Do Not Follow Bergmann's Rule.
 606 *Evolutionary Biology*, 41, 327–335.
- 607 Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces
 608 for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- 609 Fooden, J., & Albrecht, G. H. (1999). Tail-Length Evolution in Fascicularis-Group Macaques
 610 (*Cercopithecidae*: *Macaca*). *International Journal of Primatology*, 20, 431–440.
- 611 Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression*. Third edition. Thousand
 612 Oaks, CA: Sage.
- 613 Freckleton, R.P. (2002) On the misuse of residuals in ecology: Regression of residuals vs.
 614 multiple regression. *Journal of Animal Ecology*, 71, 542–545.
- 615 Friedman, N. R., Harmácková, L., Economo, E. P., & Remeš, V. (2017). Smaller beaks for
 616 colder winters: Thermoregulation drives beak size evolution in Australasian songbirds.
 617 *Evolution*, 71, 2120–2129.

- 618 Garamszegi, L. Z., & Møller, A. P. (2010). Effects of sample size and intraspecific variation in
 619 phylogenetic comparative studies: A meta-analytic review. *Biological Reviews*, 85,
 620 797-805.
- 621 Gardner, J. L., Symonds, M. R. E., Joseph, L., Ikin, K., Stein, J., & Kruuk, L. E. B. (2016).
 622 Spatial variation in avian bill size is associated with humidity in summer among Australian
 623 passerines. *Climate Change Responses*, 3, 11.
- 624 Garnier, S. (2018). *viridis*: Default Color Maps from 'matplotlib'. R package version 0.5.1.
 625 <https://CRAN.R-project.org/package=viridis>
- 626 Gohli, J., & Voje, K.L. (2016). An interspecific assessment of Bergmann's rule in 22
 627 mammalian families. *BMC Evolutionary Biology*, 16, 1–12.
- 628 Griffing, J. P. (1974). Body measurements of black-tailed jackrabbits of Southeastern New
 629 Mexico with implications of Allen's rule. *Journal of Mammalogy*, 55, 674–678.
- 630 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014)
 631 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals.
 632 *Ecology*, 95, 2027.
- 633 Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER:
 634 investigating evolutionary radiations. *Bioinformatics*, 24, 129–131.
- 635 Hijmans, R. J. (2017). raster: Geographic Data Analysis and Modeling. R package version 2.2-
 636 12. <https://CRAN.R-project.org/package=raster>
- 637 Ho, L. S. T., & Ane, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait
 638 evolution models. *Systematic Biology*, 63, 397–408.
- 639 Hurlbert, A. H., & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range
 640 maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, 104,
 641 13384–13389.
- 642 iDigBio (2019). iDigBio, Integrated Digitized Biocollections. Downloaded on 2019 July 4.
 643 <https://www.idigbio.org/portal/search>
- 644 ITIS (2019). Integrated Taxonomic Information System. Accessed on 2019 October 6 – 10.
 645 <http://www.itis.gov>
- 646 IUCN (2017). The IUCN Red List of Threatened Species. Version 3. Downloaded on 2019 June
 647 9. <https://www.iucnredlist.org>

- 648 Ives, A.R., Midford, P.E. & Garland, T.J. (2007) Within-species variation and measurement error
649 in phylogenetic comparative methods. *Systematic Biology*, 56, 252–270.
- 650 Jung, M., Dahal, P. R., Butchart, S. H. M., Donald, P. F., De Lamo, X., Lesiv, M., Kapos, V.,
651 Rondinini, C., & Visconti, P. (2020). A global map of terrestrial habitat types [Data set].
652 Zenodo. <https://doi.org/10.5281/zenodo.3816946>
- 653 Kotler, B. P., Brown, J. S., & Mitchell, W. A. (1994). The Role of Predation in Shaping the
654 Behavior, Morphology and Community Organization of Desert Rodents. *Australian Journal*
655 *of Zoology*, 42, 449–466.
- 656 Lenth, R. (2020). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package
657 version 1.4.6. <https://CRAN.R-project.org/package=emmeans>
- 658 Lindsay, S. L. (1987). Geographic size and non-size variation in Rocky Mountain *Tamiasciurus*
659 *hudsonicus*: significance in relation to Allen's rule and vicariant biogeography. *Journal of*
660 *Mammalogy*, 68, 39–48.
- 661 Maestri, R., Luza, A. L., de Barros, L. D., Hartz, S. M., Ferrari, A., de Freitas, T. R. O., &
662 Duarte, L. D. S. (2016). Geographical variation of body size in sigmodontine rodents
663 depends on both environment and phylogenetic composition of communities. *Journal of*
664 *Biogeography*, 43, 1192–1202.
- 665 Mainwaring, M. C., & Street, S. E. (2019). Conformity to Bergmann's rule in birds depends on
666 nest design and migration. *bioRxiv*, 686972. <https://doi.org/10.1101/686972>
- 667 Mammal Diversity Database (2019). American Society of Mammalogists. Accessed on 2019
668 October 4. www.mammaldiversity.org
- 669 Mares, M. A. (1975). South American mammal zoogeography: evidence from convergent
670 evolution in desert rodents. *Proceedings of the National Academy of Sciences*, 72, 1702–
671 1706.
- 672 Mayr, E. (1956). Geographical character gradients and climatic adaptation. *Evolution*, 10, 105–
673 108.
- 674 McCollin, D., Hodgson, J., & Crockett, R. (2015). Do British birds conform to Bergmann's and
675 Allen's rules? An analysis of body size variation with latitude for four species. *Bird Study*,
676 62, 404–410.

- 677 MCZbase (2018). Museum of Comparative Zoology, Harvard University, Database of the
678 Zoological Collections. Accessed on 2018 July 10 – August 8.
679 <https://mczbase.mcz.harvard.edu>
- 680 Meiri, S. (2011). Bergmann's Rule – what's in a name? *Global Ecology and Biogeography*, 20,
681 203–207.
- 682 Murakami, D., & Griffith, D. A. (2019). Eigenvector Spatial Filtering for Large Data Sets: Fixed
683 and Random Effects Approaches. *Geographical Analysis*, 51, 23–49.
- 684 NMNH (2018). Smithsonian National Museum of Natural History, the Division of Mammals
685 Collections Database. Downloaded on 2018 October 8.
686 <https://collections.nmnh.si.edu/search/mammals>
- 687 Nowak, R. M. (1999). *Walker's Mammals of the World. 6th Edition*. Baltimore, MA: Johns
688 Hopkins University Press.
- 689 Nudds, R. L., & Oswald, S. A. (2007). An interspecific test of Allen's rule: Evolutionary
690 implications for endothermic species. *Evolution*, 61, 2839–2848.
- 691 Olalla-Tárraga, M. A., Bini, L. M., Diniz-Filho, J. A. F., & Rodríguez, M. A. (2010). Cross-
692 species and assemblage-based approaches to Bergmann's rule and the biogeography of
693 body size in *Plethodon* salamanders of eastern North America. *Ecography*, 33, 362–368.
- 694 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.
- 695 Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R*
696 *Journal*, 10, 439–446.
- 697 Pedersen, T. L. (2017). patchwork: The Composer of ggplots. R package version 0.0.1.
698 <https://github.com/thomasp85/patchwork>
- 699 R Development Core Team (2019). R: A Language and Environment for Statistical Computing.
700 Vienna, Austria: R Foundation for Statistical Computing. 3.5.3. <http://www.r-project.org>
- 701 Ray, C. (1960). The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of*
702 *Morphology*, 106, 85–108.
- 703 Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other
704 things). *Methods in Ecology and Evolution*, 3 217–223.
- 705 Romano, A., Séchaud, R. & Roulin, A. (2020) Geographical variation in bill size provides
706 evidence for Allen's rule in a cosmopolitan raptor. *Global Ecology and Biogeography*, 29,
707 65–75.

- 708 Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., ... Young, B.
709 E. (2008). The status of the world's land and marine mammals: Diversity, threat, and
710 knowledge. *Science*, 322, 225–30.
- 711 Serrat, M. A., King, D. & Lovejoy, C.O. (2008) Temperature regulates limb length in
712 homeotherms by directly modulating cartilage growth. *Proceedings of the National*
713 *Academy of Sciences*, 105, 19348–19353.
- 714 Silvestro, D., Kostikova, A., Litsios, G., Pearman, P. B., & Salamin, N. (2015). Measurement
715 errors should always be incorporated in phylogenetic comparative analysis. *Methods in*
716 *Ecology and Evolution*, 6, 340–346.
- 717 Stevenson, R. D. (1986). Allen's rule in North American rabbits (*Sylvilagus*) and hares (*Lepus*) is
718 an exception, not a rule. *Journal of Mammalogy*, 67, 312–316.
- 719 Symonds, M. R. E., & Tattersall, G. J. (2010). Geographical variation in bill size across bird
720 species provides evidence for Allen's rule. *The American Naturalist*, 176, 188–197.
- 721 Tilkens, M. J., Wall-Scheffler, C., Weaver, T. D., & Steudel-Numbers, K. (2007). The effects of
722 body proportions on thermoregulation: An experimental assessment of Allen's rule. *Journal*
723 *of Human Evolution*, 53, 286–291.
- 724 Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets
725 of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*, 17,
726 e3000494.
- 727 Upham, N. S., Esselstyn, J. A., & Jetz, W. (2020) Ecological causes of uneven speciation and
728 species richness in mammals. *bioRxiv*, 504803.
- 729 VertNet (2019). VertNet, a Database of Vertebrate Specimen Records. Downloaded on 2019
730 June 29. <http://portal.vertnet.org/search>
- 731 Vilela, B., & Villalobos, F. (2015). letsR: a new R package for data handling and analysis in
732 macroecology. *Methods in Ecology and Evolution*, 6, 1229–1234.
- 733 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag
734 New York. <http://ggplot2.org>
- 735 Yu, G. (2019). treeio: Base Classes and Functions for Phylogenetic Tree Input and Output. R
736 package version 1.6.2. <https://guangchuangyu.github.io/software/treeio>

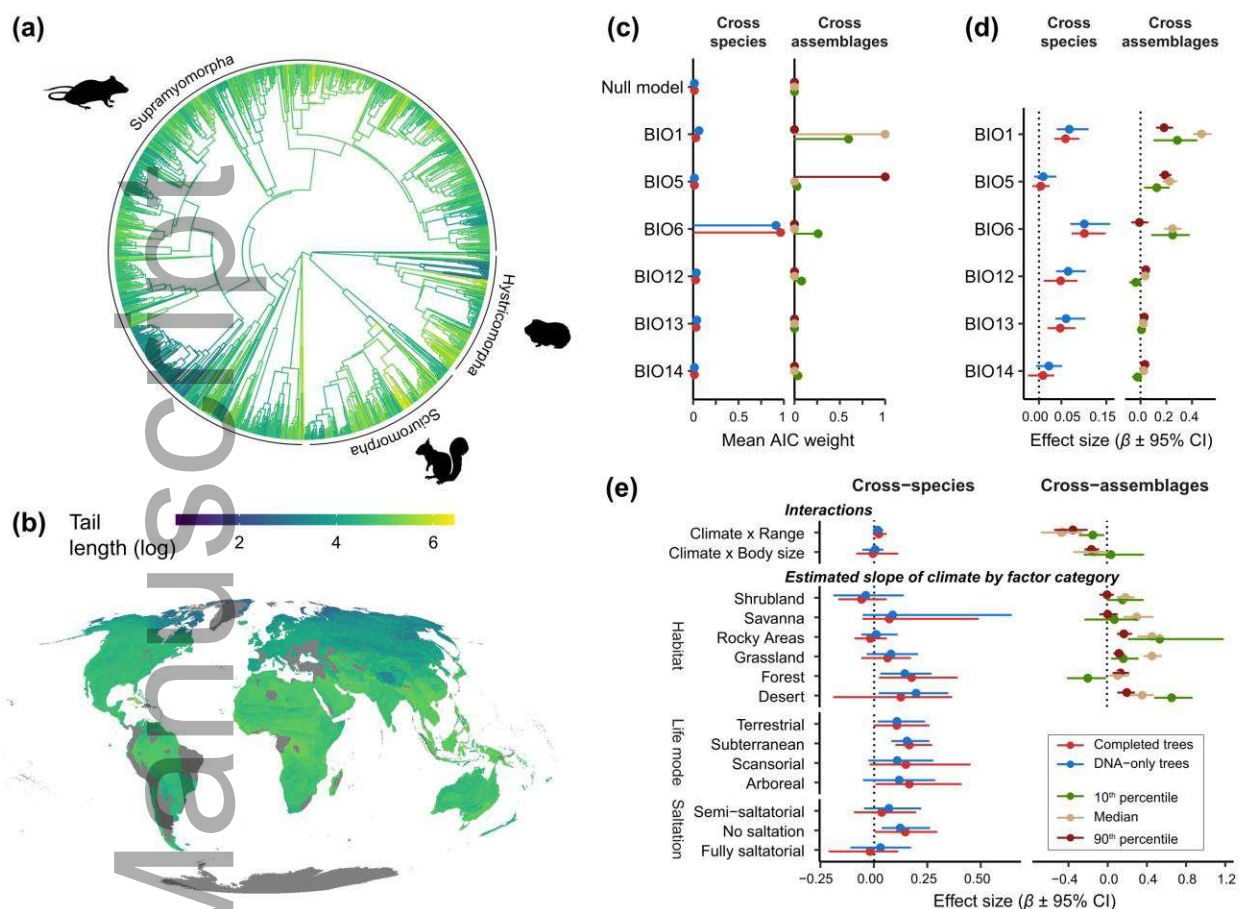
737 Yu, G., Smith, D., Zhu, H., Guan T., & Lam, T. T-Y. (2017). ggtree: an R package for
738 visualization and annotation of phylogenetic trees with their covariates and other associated
739 data. *Methods in Ecology and Evolution*, 8, 28–36.

Author Manuscript

740 **FIGURES**

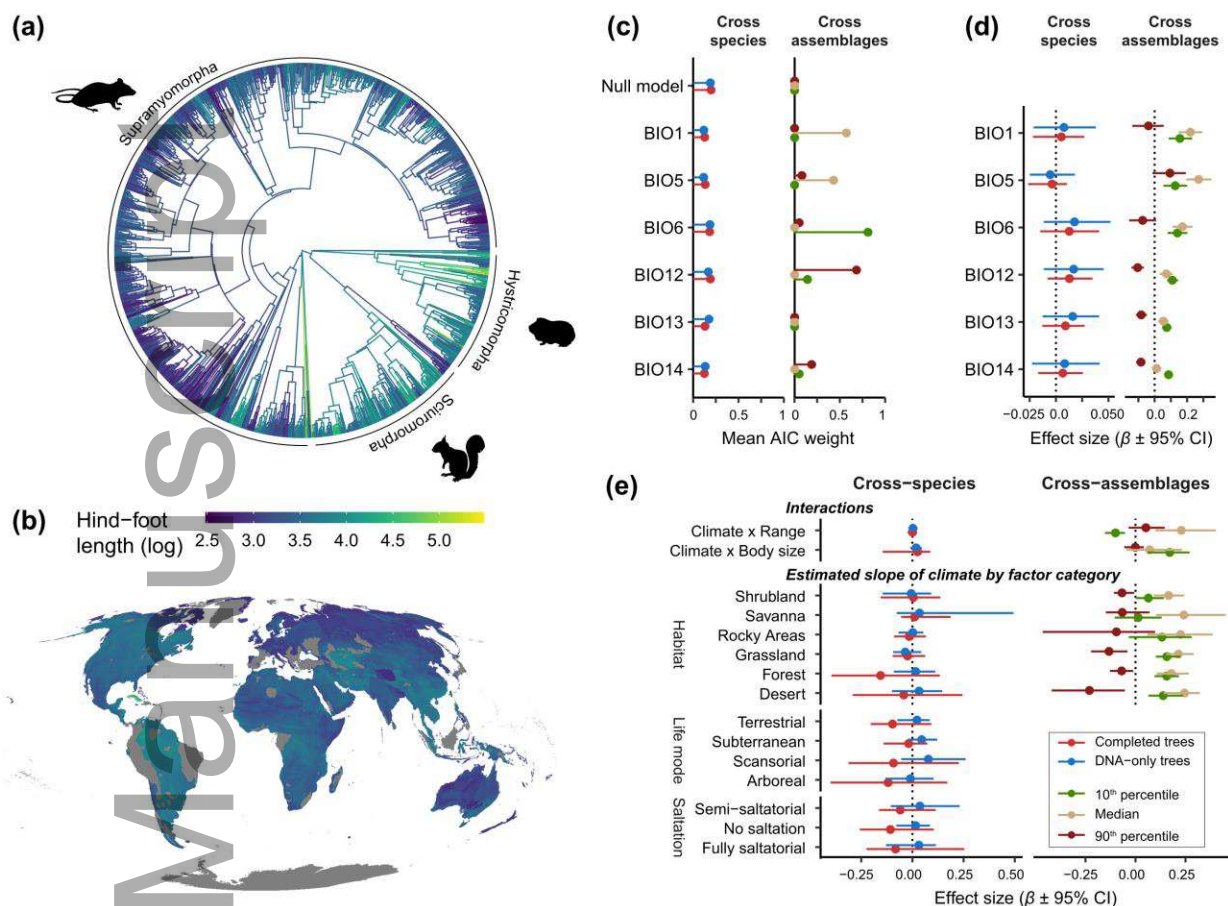
741 **Figure 1.** Relationship between tail length and climatic variables. (a) Example of one of the 100
742 completed phylogenetic trees used in the phylogenetic regressions, with branch colors
743 corresponding to the maximum likelihood estimates of the ancestral states for tail length. (b)
744 Map of assemblage-level mean tail length (log-transformed) values shown at 10 arc-min
745 resolution (note that we aggregated to 1.5-degree grid cells for all assemblage-based analyses).
746 (c) Mean AICc weight of models including each bioclimatic variable or none (i.e. null model) (d)
747 Standardized effect sizes based on coefficient estimates (β) \pm 95% confidence intervals (CI) for
748 the regression between tail length and the climate variables at the level of species (left,
749 phylogenetic regressions) or assemblages (right, spatial regressions). Results shown in (e) are the
750 effect of the interaction between climate [i.e. the climate variable with the highest AICc weight
751 as shown in (c); results are thus averaged across the subset of models for which this variable was
752 selected] and two interacting continuous variables: range size and body size (top), as well as the
753 estimated marginal slope of the relationship between tail length and climate for each level of
754 three interacting factor variables: habitat type, life mode, and saltation ability (bottom). All
755 confidence intervals are drawn from the distribution of coefficient estimates across the 100
756 repetition of random sampling, and additionally across 100 phylogenetic trees for both the DNA-
757 only trees and the completed trees in which DNA-missing species were imputed. Tail length
758 across assemblages was summarized by either the median, the 10th or the 90th percentile value.
759 Climatic variables are defined as follows: BIO1=annual mean temperature, BIO5=maximum
760 temperature of the warmest month, BIO6=minimum temperature of the coldest month,
761 BIO12=annual precipitation, BIO13=precipitation of the wettest month, BIO14=precipitation of
762 the driest month. Results are also reported in Tables S4, S5, and S6. Silhouettes were
763 downloaded from publicdomainpictures.net.

764

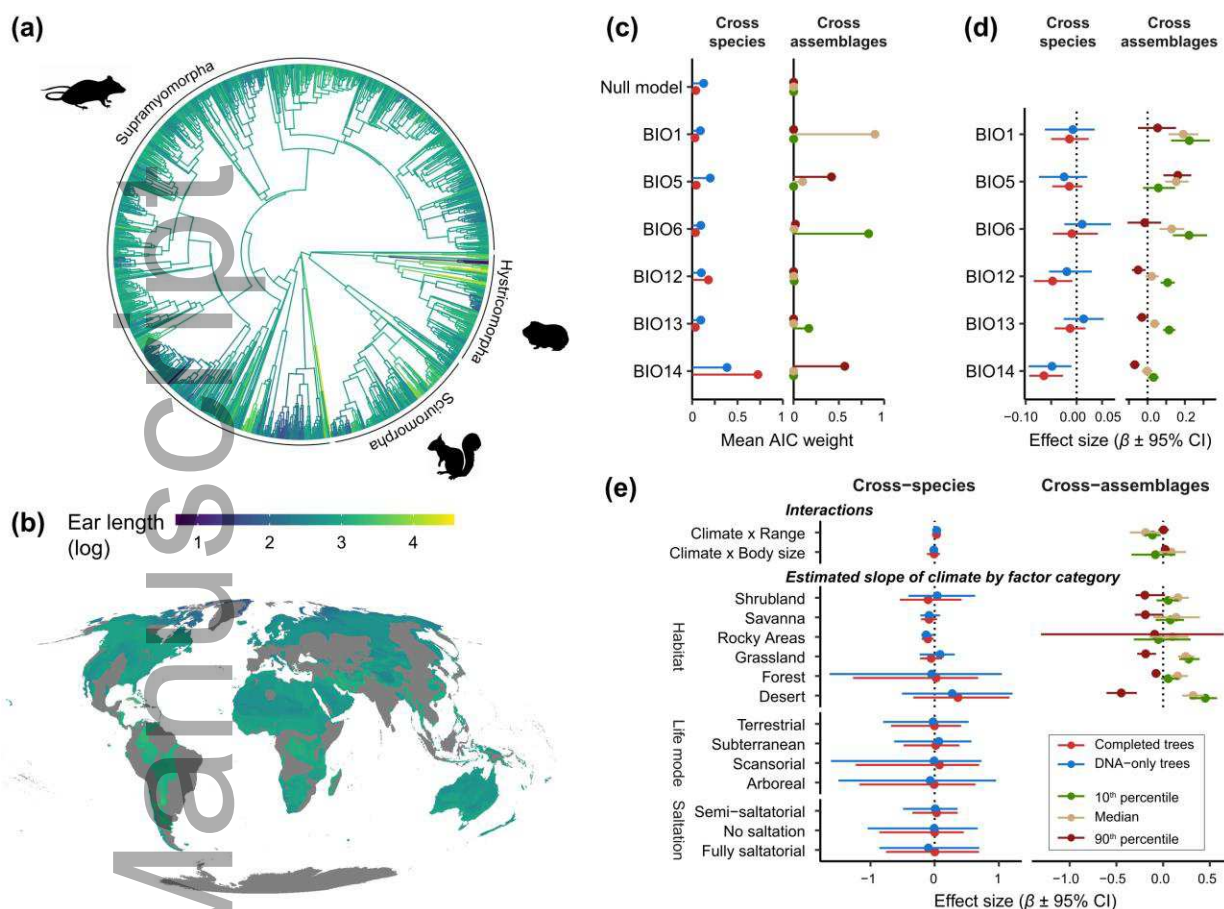
765
766

767 **Figure 2.** Relationship between hind foot length and climatic variables. (a) One of the 100
 768 phylogenetic trees used in the phylogenetic regressions, with branch colors corresponding to the
 769 maximum likelihood estimates of the ancestral states for hind foot length. (b) Map of
 770 assemblage-level mean hind foot length (log-transformed) values shown at 10 arc-min resolution
 771 (assemblage-based analyses were performed in 1.5-degree grid cells). (c) Mean AICc weight of
 772 models including each bioclimatic variable or none (i.e. null model). (d) Standardized effect
 773 sizes based on coefficient estimates (β) \pm 95% confidence intervals (CI) for the regressions
 774 between hind foot length and the climate variables. (e) Interaction between the selected climate
 775 variable and species characteristics. See the Figure 1 legend for more information.

776

777
778

779 **Figure 3.** Relationship between ear length and the climatic variables. (a) One of the 100
 780 phylogenetic trees used in the phylogenetic regressions, with branch colors corresponding to the
 781 maximum likelihood estimates of the ancestral states for ear length. (b) Map of assemblage-level
 782 mean ear length (log-transformed) values shown at 10 arc-min resolution (assemblage-based
 783 analyses were performed in 1.5-degree grid cells). (c) Mean AICc weight of models including
 784 each bioclimatic variable or none (i.e. null model). (d) Standardized effect sizes based on
 785 coefficient estimates (β) \pm 95% confidence intervals (CI) for the regressions between ear length
 786 and the climate variables. (e) Interaction between the selected climate variable and species
 787 characteristics. See the Figure 1 legend for more information.



788

789

790 SUPPORTING INFORMATION

791 **Appendix S1.** Morphometric data collection, processing, cleanup, quality control, and
792 preliminary analyses (supplementary methods).

793 **Appendix S2.** R script used to perform the phylogenetic and spatial regression analyses.

794 **Table S1.** Morphometric data retrieved from museum databases and the literature. The
795 descriptions of the columns and the abbreviations for the collections appear in the “Metadata”
796 sheet. The references appear in the “References” sheet. Observations (rows) lacking head and
797 body length and at least one appendage length (tail length, hind foot length, ear length) were not
798 included in this data set and thus are not used in any of the analyses. All data are untransformed.
799 Blank cells indicate missing data.

800 **Table S2.** Species means for morphometric and environmental data, along with habitat, life
801 mode, and saltation ability. Species means of morphometric data were calculated based on the

802 data shown in Table S1. The descriptions of the columns appear in the “Metadata” sheet. Species
803 with environmental data only (no morphometric data) were not included in this data set and thus
804 are not used in any of the analyses. All data are untransformed. Blank cells indicate missing data.

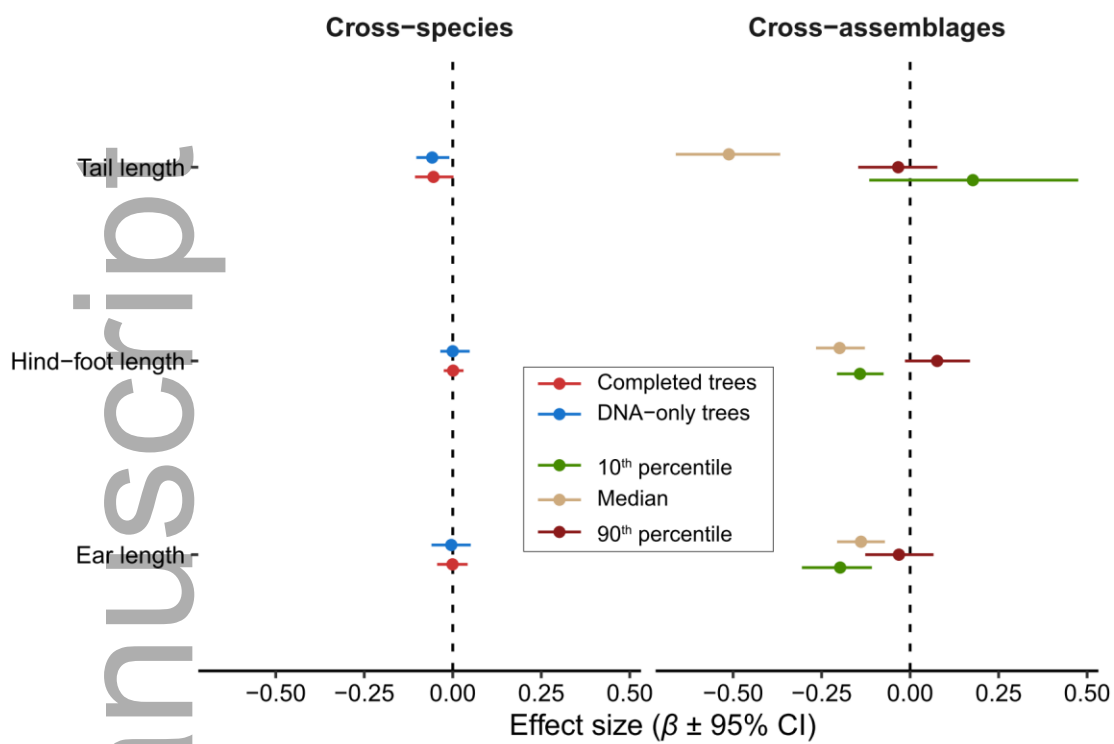
805 **Table S3.** List of species in Table S2 that are not found in the Upham et al. (2019) phylogeny,
806 and their synonyms, when available. Blank cells indicate species with no matching synonyms in
807 the Upham et al. (2019) phylogeny. See the “Metadata” sheet for more details.

808 **Table S4.** Results of the relationship between appendage length and the absolute value of
809 latitude.

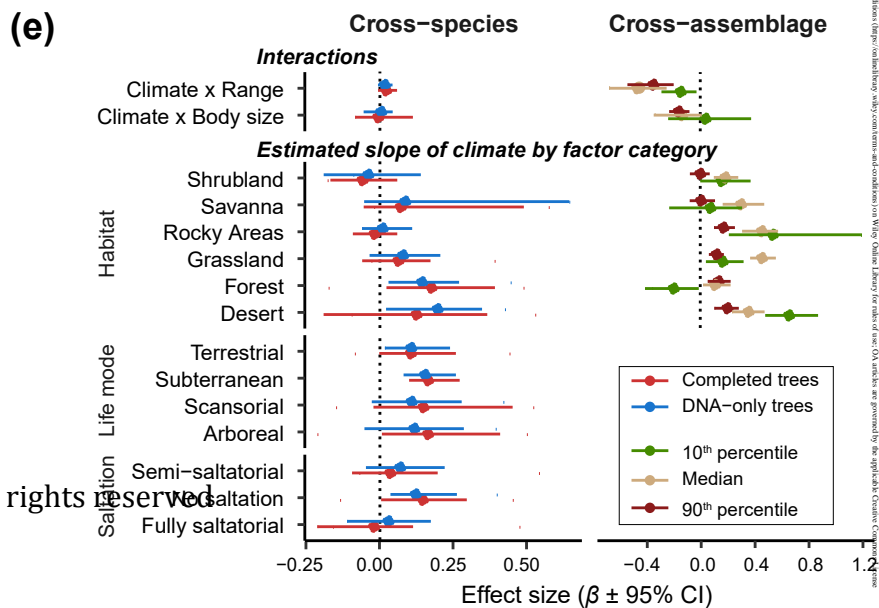
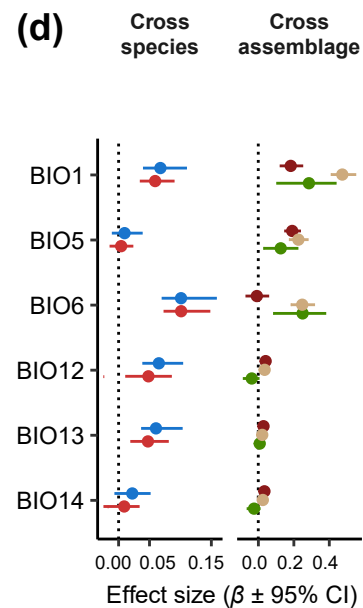
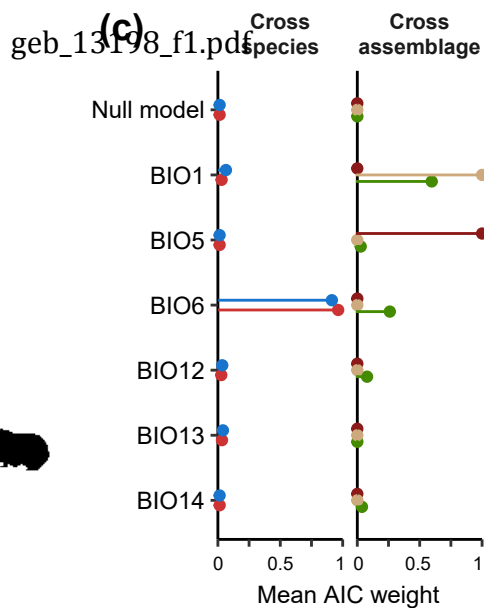
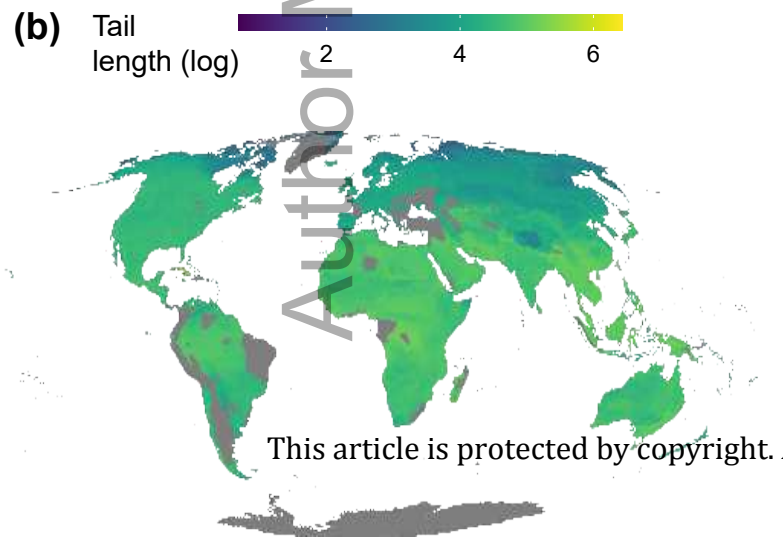
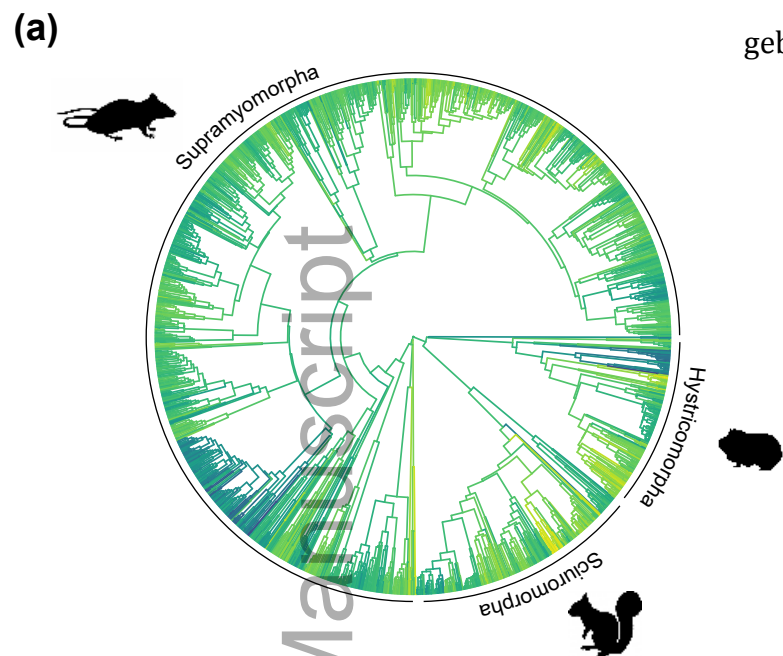
810 **Table S5.** Results of the relationship between appendage length and climate.

811 **Table S6.** Proportion of significant interactions between climate and habitat, body size, range
812 size, life mode, and saltation.

813 **Figure S1.** Relationship between appendage length and latitude (absolute value). Standardized
814 effect sizes are represented as coefficient estimates (β) \pm 95% confidence intervals (CI) for the
815 regressions between tail length, hind foot length, and ear length and the absolute value of
816 latitude, for the cross-species analyses and for the cross-assemblage analyses. Results are based
817 on 100 repetitions of random sampling and, for cross-species analyses, 100 phylogenetic trees.
818 Climatic variables are defined as follows: BIO1=annual mean temperature, BIO5=maximum
819 temperature of the warmest month, BIO6=minimum temperature of the coldest month,
820 BIO12=annual precipitation, BIO13=precipitation of the wettest month, BIO14=precipitation of
821 the driest month.

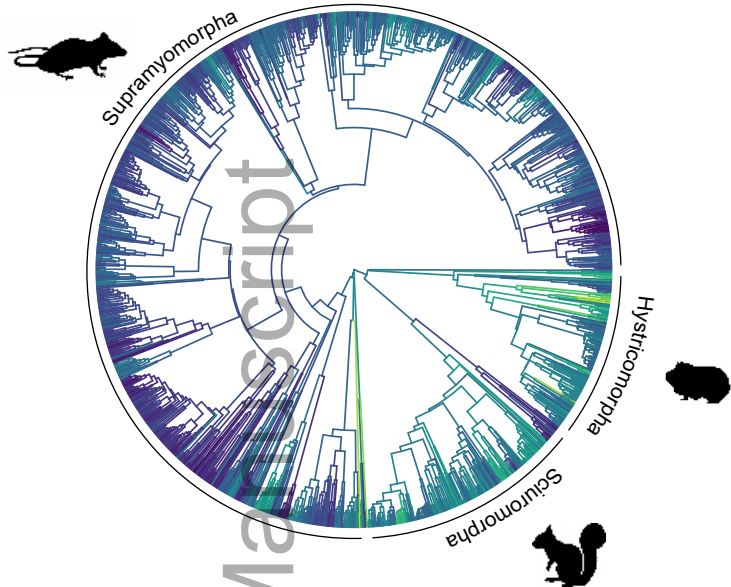


822



This article is protected by copyright. All rights reserved.

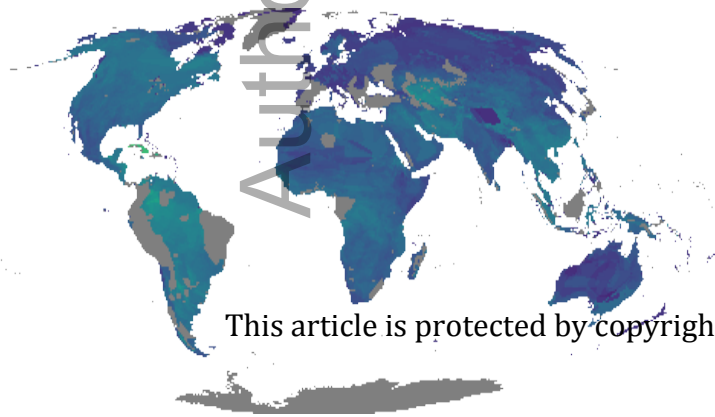
(a)



(b)

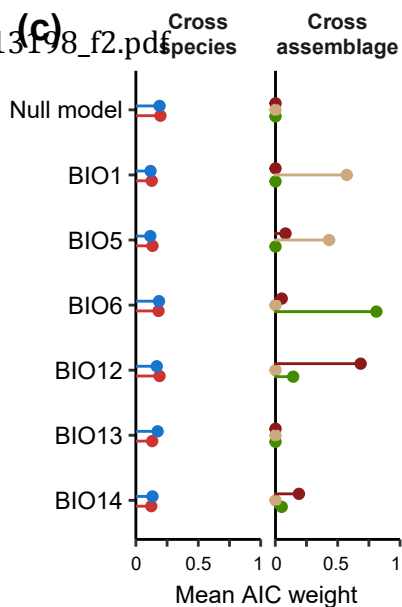
Hind-foot length (log)

2.5 3.0 3.5 4.0 4.5 5.0

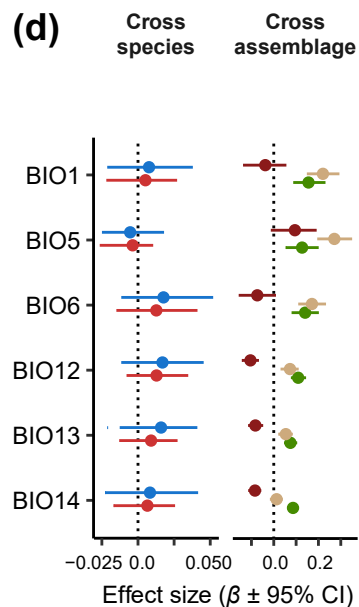


This article is protected by copyright. All rights reserved.

geb_13198_f2.pdf



(d)



(e)

