1　**Applying generalised allometric regressions to predict live body mass of**

2　**tropical and temperate arthropods**

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4　Running Head: Predicting live arthropod body mass

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22   **Abstract**

23   1. The ecological implications of body size extend from the biology of individual organisms

24   to ecosystem–level processes. Measuring body mass for high numbers of invertebrates can be

25   logistically challenging, making length-mass regressions useful for predicting body mass

26   with minimal effort. However, standardised sets of scaling relationships covering a large

27   range in body length, taxonomic groups, and multiple geographical regions are scarce.

28   2. We collected 6293 arthropods from 19 higher-level taxa in both temperate and tropical

29   locations to compile a comprehensive set of linear models relating live body mass to a range

30   of predictor variables. For each individual, we measured live weight (hereafter, body mass),

31   body length and width, and conducted linear regressions to predict body mass using body

32   length, body width, taxonomic group and geographic region. Additionally, we quantified

33   prediction error when using parameters from arthropods of a different geographic region.

34   3. Incorporating body width into taxon- and region-specific length-mass regressions yielded

35   the highest prediction accuracy for body mass. Using regression parameters from a different

36   geographic location increased prediction error, causing over- or underestimation of body

37   mass depending on geographical origin and whether body width was included.

38   4. We present a comprehensive range of parameters for predicting arthropod body mass and

39   provide guidance for selecting optimal scaling relationships. Given the importance of body

40   mass for functional invertebrate ecology and a paucity of adequate regressions to predict

41   arthropod body mass from different geographical regions, our study provides a long-needed

42   resource for quantifying live body mass in invertebrate ecology research.

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44   Keywords: allometric scaling, body size, insects, invertebrates, length-mass regression

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Introduction

Body size is one of the most fundamental traits of living organisms (Peters, 1983). From the individual to the community level, a vast range of ecosystem properties scale with arthropod body size. Body size determines various aspects of an organism's individual biology, such as life-history, behaviour, range size, movement and physiology (Bekoff *et al.*, 1981; Woodward *et al.*, 2005; White *et al.*, 2007; Hirt *et al.*, 2017). Aspects shaping arthropod communities such as species abundance, biomass production, trophic link structure, and interaction strengths are also related to the body size of constituent individuals and populations (Boudreau *et al.*, 1991; Belgrano *et al.*, 2002; Brose *et al.*, 2006; Riede *et al.*, 2011; Rall *et al.*, 2012; Kalinkat *et al.*, 2013). As a result, arthropod body size determines how individuals and communities carry out functions, making it a powerful predictor of ecosystem performance (Barnes *et al.*, 2018).

Most biological rates scale with body size following a power-law relationship (Peters, 1983; White *et al.*, 2007), which has important implications for individual and community ecology. In the early 1930s, Kleiber (1932) proposed an allometric scaling relationship of metabolism with body mass following a ¾ power law function, though this has been extensively debated (see Brown *et al.*, 2004; Kolokotrones *et al.*, 2010; Ehnes *et al.*, 2011).This power-law scaling means that smaller animals have a lower per capita metabolic rate than larger ones, though their mass-specific metabolic rate is higher, yielding distinct patterns of energy demand in populations and communities depending on the relationship between body size and total biomass (Reichle, 1968). Additionally, home- and foraging ranges of animals increase with body size, which has been demonstrated for a wide range of organisms, from small invertebrates to large mammals (Lindstedt *et al.*, 1986; Swihart *et al.*, 1988; Jetz *et al.*, 2004; Greenleaf *et al.*, 2007). Due to the allometric scaling of a large range

71   of physiological and ecological properties, one can utilise general scaling relationships to

72   predict ecological properties from measured values of organism body size.

73   While body size is highly useful as a predictive trait for both the response of

74   arthropods to environmental change and also their effects on ecosystem processes, ecologists

75   face many logistic challenges when collecting body size data. Firstly, measurement of

76   arthropod body mass is particularly challenging due to their small body size and typically

77   high abundance. As a consequence, researchers might measure a few individuals of each

78   species and apply an average of these values to the remaining individuals. This practice

79   eliminates intraspecific variation that occurs among sampling sites, especially when the sites

80   are distributed along ecological gradients (Violle *et al.*, 2012). However, in large field

81   sampling campaigns, collecting individual body mass data across all samples is often

82   infeasible due to the logistic difficulties of weighing large numbers of individual organisms.

83   Furthermore, data on live—rather than dry—body mass is often required to accurately relate

84   body size to a range of ecological attributes. For example, physiological rates (such as

85   metabolism), species interactions (e.g., pollination and predation), and behavioural patterns

86   are directly dependent on the body mass of an animal while it is alive, as opposed to its dry

87   mass which serves only as a proxy for live mass. However, dry mass is far more frequently

88   measured as it is extremely difficult to take live body mass measurements of arthropods,

89   particularly in large sampling campaigns. This limitation calls for the provision of practical

90   and accurate tools to acquire individual-level, live arthropod body mass data in order to

91   assess population and community responses in arthropod size structure and investigate

92   corresponding ecosystem processes.

93   Length-mass regressions have proven to be a powerful tool to predict body mass

94   based on body length measurements (Rogers *et al.*, 1977; Schoener, 1980; Benke *et al.*, 1999;

95   Johnston & Cunjak, 1999; Gruner, 2003; Wardhaugh, 2013) which are much easier to obtain

96   than measurements of body mass. This approach relies on regression parameters estimated

97   for length-mass relationships, which can be used to predict body mass when only body length

98   data are available. However, finding suitable regression parameters for a given dataset (for

99   example, where parameters are from the same taxonomic group and geographical region) is

100   often not possible. This limitation can be problematic because scaling relationships—and

101   thus, their regression parameters—are likely to vary substantially among taxonomic groups

102   and geographic regions; a discrepancy that has been shown to be especially distinct between

103   tropical and temperate regions (Schoener, 1980; Gruner, 2003; Wardhaugh, 2013). Thus,

104   using length–mass regression parameters from a different geographical region is likely to

105   increase the error in predictions of body mass. Finally, to our knowledge there are no

106   regressions available in the literature that are based on live body-mass measurements and that

107   cover a large range of taxa and multiple geographic regions. Therefore, researchers are

108   typically constrained to using rough conversion factors (Peters, 1983) or more elaborate dry

109   mass–fresh mass regressions (e.g. Mercer *et al.*, 2001), which add further error to body mass

110   predictions due to the very same sources of variation in length-mass scaling relationships

111   (geographic origin, taxon-specificity, etc.). Considering the broad application of body-size

112   data in ecological research, there are surprisingly few studies that provide length-mass

113   regression parameters for terrestrial arthropods, and these are generally restricted to one of

114   either temperate or tropical animals, or to only a few taxonomic groups (Schoener, 1980;

115   Burgherr & Meyer, 1997; Benke *et al.*, 1999; Gruner, 2003; Wardhaugh, 2013).

116   In this paper, we provide an unprecedented dataset of length–mass scaling

117   relationships based on measurements of live body mass and body length of 6293 terrestrial

118   arthropods from both tropical and temperate geographical regions. We measured body mass

119   while the animals were still alive. As such, our regressions will be particularly useful for

120   researchers interested in the physiology, behavior or interaction ecology of their target

121   organisms. We performed length–mass regressions for arthropods, including various

122   combinations of body width, taxonomic group and geographic origin as additional co-

123   variables, and compared the accuracy in predicting body mass among these various models.

124   We hypothesised that prediction accuracy improves with an increasing number of additional

125   predictors (e.g., including body width, taxonomic group and geographic region), as opposed

126   to using only body length as a sole predictor of body mass. Additionally, we expected a

127   higher prediction accuracy when using regression parameters taken from the same geographic

128   region, as opposed to using regression parameters of arthropods from a different geographic

129   region (hereafter, geographically-disjunct regression parameters). Our study thus provides a

130   generalised resource for predicting live body mass across an unprecedented range of

131   terrestrial arthropod groups (including 19 orders of Arachnida, Myriapoda, Crustacea and

132   Insecta), as well as guidance for deciding which scaling relationships to use for predicting

133   arthropod body mass depending on the dataset at hand.

134

135   **Materials and Methods**

136   *Study sites and sampling techniques*

137   To account for different scaling relationships in temperate versus tropical geographical

138   regions, we chose two sampling locations: one temperate location in Germany and one

139   tropical location in Indonesia. Temperate sites were located near Göttingen, Germany

140   (51°32′02″N, 09°56′08″E) at an altitude of around 150 m asl, with a mean annual air

141   temperature of 7.4 °C, mean annual precipitation of 700 mm (Heinrichs *et al.*, 2014) and a

142   vegetation growth period from May to September. Tropical sites were located near Jambi

143   City in Sumatra, Indonesia (1°35′24″S 103°36′36″E), at an altitude around 20 m asl. Jambi

144   City has a mean annual air temperature of 25 °C and a mean annual precipitation of 2100 to

145   2800 mm (Ishizuka *et al.*, 2002). The sampling sites in both regions included wayside

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146   vegetation, open grassland areas and forest strips. Sampling sites were chosen due to their

147   proximity to the laboratory in both regions to ensure a fast and simple work flow, since

148   animals had to be kept alive after collection and living animals could not be stored for more

149   than eight hours to avoid increased body mass-loss.

150   Three standard sampling techniques were used in order to cover a broad variety of

151   arthropod taxa and to achieve a sufficient overlap of taxonomic groups from both sampling

152   regions. For active and fast moving ground animals, as well as nocturnal species, live pitfall

153   traps (diameter of 11 cm and height of 12 cm) were used within forest and grassland sites.

154   Pitfall traps were closed with a funnel-shaped lid to prevent animals from escaping. Pitfall

155   traps were buried so the opening of the pitfall was flush with the surface of the ground. They

156   were installed in the morning and animals were collected after 24 hours to avoid loss of

157   individuals due to predation, drowning, or desiccation. Sweep nets were used in open

158   grassland and wayside vegetation plots to collect animals from within low vegetation, shrubs

159   and small trees to sample stationary, as well as fast-moving and flying animals. At the forest

160   sites, less mobile animals from within the litter layer were collected via leaf-litter sieving.

161   Material from the loose leaf litter (F-Layer) on top of the humus layer was collected and

162   sieved with a coarse-meshed grid (2×2 cm). Animals that fell through the mesh were hand-

163   collected from a collecting tray and stored in individual vials for further processing.

164

165   ***Morphological measurements and data collection***

166   Arthropods were stored in a refrigerator at 10 °C for a maximum of 8 hours after collection to

167   slow down their metabolism and reduce body mass loss. In order to maximise accuracy in

168   live body mass measurements, we conducted preliminary tests of body mass-loss following

169   live capture, comparing live to recently killed arthropods to establish whether specimens

170   should be weighed when alive or dead. As we found considerable variation in body mass

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171   between live and dead animals, we weighed all arthropods whilst still alive on a precision

172   scale (to the nearest 0.01 mg) and subsequently stored them in ethanol (75 %). For

173   measurements of length and maximum width (to the nearest 0.01 mm), pictures of the dorsal

174   or ventral and lateral view were taken with a Dino-Lite Digital Microscope (Dino-Lite Edge;

175   AnMo Electronics Corporation). Afterwards, each individual was measured using ImageJ

176   (Version 1.48k or newer), leaving out appendages to generalize the process. Finally, every

177   individual was identified to family level using 'Insects of Australia' (Commonwealth

178   Scientific and Industrial Research Organization (Australia), 1991), 'Spider Families of the

179   World' (Jocqué & Dippenaar-Schoeman, 2007) and the identification keys of 'Brohmer –

180   Fauna von Deutschland'(Schaefer, 2009). All underlying data can be found online in the

181   Supporting Information (Supporting Data S1).

182

183   *Statistical analysis*

184   All statistical analyses were performed using R Version 3.4.0 (R Core Team, 2015). Prior to

185   the analysis, raw data of body length, mass and width were $\log_{10}$-transformed. Taxa without

186   width measurements were excluded from the main analysis. However, length-mass

187   regressions for these taxonomic groups, along with a range of regressions for higher-

188   resolution taxonomic groups, were carried out separately and results are presented in the

189   Supporting Information (i.e., regressions for selected taxa based on morphology, taxonomy or

190   behaviour; Table S1).

191   We performed linear models to test the relationship between body mass and length

192   (L) alone, and with the co-variables width (W), taxonomic group (T) and geographical region

193   (R) in all possible combinations, yielding eight linear models in total (Table 1). For models

194   that included taxonomic group and geographical region, these two factors were combined and

195   treated as a single factor (e.g. temperate Araneae or tropical Araneae to account for the

196   uneven distribution of some taxonomic groups across geographical regions. The most

197   complex model included length, width, taxonomic group and geographic region (model

198   LWTR) and the least complex model included only length as a single independent variable

199   (model L) (see Supporting Methods S1 for a worked example of body mass predictions using

200   each model type). Finally, model fits were then compared using Akaike's Information

201   Criterion (AIC).

202   Because we hypothesised that using regression parameters from different geographic

203   regions likely increases error in predictions of arthropod body mass, we assessed this

204   prediction error by quantifying the proportional difference between predicted and observed

205   body mass using geographically-disjunct and geographically non-disjunct regression

206   parameters for the two all-taxa models (models LWR and LR). Specifically, body mass

207   prediction accuracy of regression parameters was calculated as the log-response ratio

208     $y = log_{10}\left(\frac{a}{b}\right),$

209   where *y* is the prediction error of body mass, *a* is the predicted body mass using length-mass

210   regressions and *b* is observed body mass. We then assessed how prediction accuracy varied

211   across the range of body length to ascertain if there might be systematic error in body mass

212   predictions depending on arthropod body size.

213

214   **Results**

215   In total, 6293 individuals from 19 arthropod higher-order taxa were collected, weighed while

216   alive, and measured for body length and width across the Indonesian and German sites

217   (hereafter, tropical and temperate geographic regions). Body length of collected arthropods

218   ranged from 0.60 mm to 68.12 mm and body mass ranged from 0.01 mg to 5108.57 mg

219   (Table 2). As expected, we found a consistent positive scaling relationship for body mas with

220   body length across all collected arthropods.

221   The most complex model (Model LWTR, including body length, body width,

222   taxonomic group and geographic region as predictors) best explained variation in body mass

223   according to AIC selection and r^2 (Table 3). The consistently positive slope in the relationship

224   between body length and body mass (for all arthropod taxa except for Odonata and

225   Neuroptera) was significantly influenced by body width, taxonomic group and geographic

226   region that the arthropods originated from (Table 3, Figure 1). Thus, the slope of the length-

227   mass relationship varied with body width, taxonomic group and geographic region (e.g. the

228   slope of the length-mass relationship differed between spiders and beetles as well as between

229   temperate and tropical spiders).

230   The eight different models explained between 81.4 % (model L, least complex model)

231   and 98.6 % (model LWTR, most complex model) of the total variance in body mass (Table

232   1). According to AIC comparisons, the four models that included body width as a co-variate

233   explained more variation in body mass than models that only included body length as a

234   predictor. In contrast to the results from AIC comparisons, however, r^{2}-values suggested that

235   the model including taxonomic group but not body width (model LTR and model LT, Table

236   1) explained marginally more variance in body mass than the model including body width but

237   not taxonomic group or geographic region (model LW, Table 1).

238   Finally, to test if the application of geographically-disjunct regression parameters (i.e.,

239   where regression parameters obtained from one geographic region are used to predict body

240   mass of arthropods in a different geographic region) increases error in body mass predictions,

241   we calculated body mass using geographically-disjunct and geographically non-disjunct

242   regression parameters and quantified the difference from observed body mass. In general, we

243   found that the application of geographically-disjunct parameters for whole-fauna regressions

244   led to increased prediction error of body mass when compared to using non-disjunct

245   regression parameters (Figure 2). Whether this prediction error leads to an under- or over-

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246   estimation of body mass depended on the geographic region and the morphological traits

247   used to predict body mass. With only body length included as a predictor (Model LR), body

248   mass of temperate arthropods was underestimated on average by 33 % (geometric-mean ratio

249   = 0.77) using tropical regression parameters (Figure 2a), whereas tropical arthropod body

250   mass was overestimated on average by 29 % (geometric-mean ratio = 1.29) when using

251   temperate regression parameters (Figure 2b). Interestingly, when using model LR, prediction

252   error increased with increasing body length for both temperate and tropical arthropods using

253   geographically-disjunct regression parameters (Figure 2a, b). In contrast, when body width

254   was included in the model, the geographically-disjunct regression prediction error shifted

255   between overestimation and underestimation with increasing body length. For temperate

256   arthropods, the models tended to underestimate predicted body mass at small body lengths

257   and overestimate predicted body mass at large body lengths, with an average underestimation

258   of 8% (geometric-mean ratio = 0.92) (Figure 2c). In contrast, body mass of tropical

259   arthropods was overestimated at smaller body lengths and underestimated at larger body

260   lengths when using geographically-disjunct regression parameters in model LWR, with an

261   average overestimation of 10 % (geometric-mean ratio = 1.10) (Figure 2d).

262

263   **Discussion**

264   A wide range of individual- to community-level characteristics are influenced by body size,

265   including abundance, metabolic rate, movement speed or growth rate (Gillooly *et al.*, 2001;

266   White *et al.*, 2007; Hirt *et al.*, 2017). In order to make realistic predictions of these measures,

267   it is essential to have reliable body mass data of target organisms. In our dataset consisting of

268   6293 organisms spanning 19 higher order taxa from both tropical and temperate geographic

269   regions, we found an overall positive power law relationship between body mass and body

270   length across taxonomic groups and the tropical and temperate geographic regions. The only

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271 exception to this universal trend was for Odonata and Neuroptera, which showed a negative

272 relationship between body mass and body length in a subset of models.

273   The slope of the relationship between body length and mass depended on taxonomic

274 group and geographic region of arthropods. Furthermore, adding body width as an additional

275 morphological predictor strongly improved body mass prediction accuracy. This is probably

276 due to certain groups where the body length-to-width ratio is considerably different to the

277 average of all taxonomic groups (e.g., Staphyilinid beetles have a higher body length-to-

278 width ratio than other beetle families). Thus, using body length as the only predictor of body

279 mass is almost certainly insufficient to capture the morphological variation present within

280 taxonomic groups. Therefore, we expected that the incorporation of body width as an

281 additional predictor in our models should increase the accuracy of body mass predictions.

282 Consistent with our expectations, we found that including body width into the estimation of

283 body mass resulted in a strong improvement of prediction accuracy, in comparison to using

284 body length, alone, as a single predictor of body mass. Moreover, incorporating only body

285 width as an additional predictor yielded higher prediction accuracy than incorporating

286 taxonomic group and geographic region into the models. Body mass is related to the volume

287 of an organism, which can be described by length, width and height. Hence, adding height to

288 predict body mass could lead to more accurate body mass estimations than using only body

289 length and width. Measuring another morphological trait of an organism, however, increases

290 time needed for processing samples, presenting a trade-off between maximising prediction

291 accuracy and minimising time spent measuring traits. As more than 98 % of variance in body

292 mass was described by length, width, taxonomic group and geographic region, the benefit of

293 adding body height would unlikely outweigh the added workload. Indeed, previous studies

294 have shown that including body shape (i.e. body length and width) instead of taxonomy lead

295 to more accurate body mass estimates at the order level, but not at higher taxonomic

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296   resolution (Gruner, 2003; Wardhaugh, 2013). Our results strongly support the finding that the

297   accuracy in predicting body mass improves with additional morphological traits in addition to

298   body length for scaling relationships conducted at the order level.

299   In addition to body width, taxonomic group and geographic origin of the arthropods

300   also influenced the relationship between body length and body mass. This is likely because

301   variation in arthropod body size is influenced by a range of other factors such as evolutionary

302   history and environmental variation (Chown & Gaston, 2010). For example, Bergmann's rule

303   proposes that body size increases with latitude, though the opposite has been observed for

304   arthropods (Mousseau, 1997). Generally speaking, these concepts suggest that the body size

305   of arthropods depends strongly on their geographic origin, particularly with respect to

306   latitude. Therefore, we expected that the application of geographically-disjunct regression

307   parameters from tropical and temperate regions could lead to significant prediction error in

308   arthropod body mass. If researchers are unable to use regression parameters from data

309   collected in a similar geographic regions to their study site (due to a lack of available scaling

310   relationships), this could have important consequences for the body mass-related results

311   drawn from such studies. Consistent with our expectations, we found that the use of

312   geographically-disjunct length-mass regression parameters led to inaccurate body mass

313   predictions ranging between average prediction-errors of 8 % to 33 %, depending on the

314   model used. Furthermore, when only body length was used as a morphological predictor,

315   body mass prediction accuracy of geographically-disjunct regressions decreased with

316   increasing body length of arthropods. This has important consequences for the quality of

317   body mass data, as our results suggest that body mass of longer arthropods will be more

318   severely over- or underestimated than that of shorter arthropods. Therefore, our results

319   highlight a potential systematic bias of decreasing prediction accuracy with increasing body

320   length when applying regression parameters from different geographical regions. Ultimately,

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321 studies investigating body size responses to environmental conditions and the resulting

322 impacts on ecosystem functioning rely on accurate calculations of body mass. Therefore, it is

323 essential for such studies to use length-mass regression parameters that are obtained from

324 similar geographic origins as the organisms for which body mass is being predicted.

325   Our study provides a highly comprehensive set of regression parameters for

326 predicting live body mass of terrestrial arthropods. This set of regression parameters is useful

327 for researchers wishing to quantify body mass of arthropods across a range of underlying

328 morphological traits, taxonomic identities, and geographical regions. By incorporating all

329 combinations of geographic region, taxonomic group and body width in our allometric

330 models, our results allow investigators to choose length-mass regression parameters for

331 predicting body mass across a broad variety of arthropod datasets. Additionally, we provide

332 an explicit estimation of the prediction error caused by using geographically disjunct

333 regression parameters, to assist in deciding which regression parameters will be the most

334 appropriate for predicting arthropod body mass for a given dataset. In summary, our results

335 will aid future studies in accurately assessing body mass of arthropods, thus increasing our

336 ability to further explore the ecological implications of body size.

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14

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443 **Table 1:** Model comparisons for the eight linear models used to predict live body mass based

444 on different explanatory variables. Models are compared based on AIC and r^2.

Model no.	Model parameters	AIC	Δ AIC	r^2
1 (LWTR)	Length, width, taxa, region	-8551.2011	0	0.9860
2 (LWT)	Length, width, taxa	-8087.7384	463.4627	0.9849
3 (LWR)	Length, width, region	-4377.9316	4173.2695	0.9725
4 (LW)	Length, width	-4267.3045	4283.8966	0.9438
5 (LTR)	Length, taxa, region	-1179.7326	7371,4685	0.9546
6 (LT)	Length, taxa	-793.3381	7757.8630	0.9516
7 (LR)	Length, region	3050.0298	11601.2309	0.9103
8 (L)	Length	3249.5840	11800.7851	0.8143

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447   **Table 2:** Taxonomic groups sampled in the two geographic regions (temperate and tropical), including the number of individuals (n), number of

448   families, length range and mass range (live body mass) per taxon.

Order	n		No. of families		Length range (mm)		Mass range (mg)	
	Temp.	Trop.	Temp.	Trop.	Temp.	Trop.	Temp.	Trop.
Araneae	519	1081	16	27	1.01 - 12.26	0.78 - 25.71	0.15 - 212.78	0.01 - 5108.57
Coleoptera	408	298	15	21	1.66 - 35.10	1.10 - 43.42	0.33 - 1067.93	0.05 - 3698.96
Dermaptera	60	130	2	3	3.00 - 13.96	1.87 - 18.71	2.13 - 72.06	0.01 - 92.57
Dictyoptera	-	247	1	6	-	1.69 - 65.07	-	0.42 - 1060.93
Diptera	504	189	31	28	1.49 – 16.82	1.58 - 23.61	0.07 - 74.50	0.07 - 165.17
Geophilomorpha	-	13	-	2	-	7.47 - 33.54	-	0.29 - 21.03
Hemiptera	598	454	14	35	1.31 - 12.05	0.95 - 23.76	0.27 - 146.90	0.05 - 261.53
Hymenoptera	222	371	14	23	1.70 - 22.26	0.62 - 31.88	0.06- 835.43	0.01 - 1664.61
Isopoda	88	88	6	3	2.45 - 16.16	2.45 - 16.16	0.81-181.27	0.22 - 189.52
Lepidoptera	31	121	4	10	3.56 - 16.23	3.23 - 35.52	1.67-91.02	0.56 - 908.65
Lithobiomorpha	161	60	1	1	2.77 - 23.63	2.22 - 51.21	0.65 - 170.65	0.01- 439.53
Neuroptera	21	18	2	4	3.79 - 11.34	3.26 - 27.29	2.61 - 17.44	1.33 - 144.05
Odonata	-	21	-	4	-	23.37 - 54.83	-	14.24 - 367.32

Opiliones	89	24	3	3	0.93 - 7.53	1.09 - 10.09	0.81 - 95.02	0.40 - 165.61
Orthoptera	35	277	2	6	3.79 - 24.28	1.28 - 68.12	3.81 - 417.84	0.14 - 3895.10
Polydesmida	12	80	1	1	9.21 - 19.95	4.02 - 32.55	9.24 - 67.25	0.05 - 205.02
Pseudoscorpionida		36	-	2	-	0.95 - 4.16	1.33 - 19.91	0.16 - 2.12
Psocoptera		26	-	3	-	1.12 - 2.92	0.22 - 0.64	0.11 - 8.00
Scolopendromorpha	-	11	-	2	-	4.83 - 41.84	-	0.88 - 276.18
Total (geogr. region)	2748	3545	122	190	0.930 - 35.1	0.62 - 68.12	0.06 - 1067.93	0.01 - 5108.57
Grand total	**6293**		**246**		**0.60 - 68.10**		**0.01 - 5108.57**	

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450 **Table 3:** Regression parameters for the eight linear models for live body mass prediction in

451 dependence of body length (L, in mm), maximum body width (W, in mm), taxonomic group

452 (T) and geographic region (R, temperate and tropical).

Taxonomic group	Region	Intercept (a_x)	Slope$_{length}$ (b_{length})	Slope$_{width}$ (b_{width})	SD
Model 1: Length-Width-Taxonomic group-Geographic region-Zone (LWTR)					
Araneae	temperate	-0.281	1. 368	1.480	0.100
Coleoptera	temperate	-0.299	0.874	1.920	0.104
Dermaptera	temperate	-0.369	1.180	1.580	0.099
Diptera	temperate	-0.309	0.997	1.595	0.119
Hemiptera	temperate	-0.420	1.177	1.431	0.078
Hymenoptera	temperate	-0.450	1.144	1.724	0.115
Isopoda	temperate	-0.453	0.898	1.756	0.074
Lepidoptera	temperate	-0.442	1.084	1.720	0.102
Lithobiomorpha	temperate	-0.549	1.416	1.543	0.064
Neuroptera	temperate	0.575	-0.042	2.535	0.114
Opiliones	temperate	-0.241	1.353	1.377	0.131
Orthoptera	temperate	0.136	0.823	1.713	0.081
Polydesmida	temperate	-1.400	2.443	0.215	0.035
Araneae	tropical	-0.464	1.539	1.448	0.127
Coleoptera	tropical	-0.545	1.175	1.786	0.164
Dermaptera	tropical	-0.605	1.301	1.704	0.106
Dictyoptera	tropical	-0.326	0.845	1.764	0.180
Diptera	tropical	-0.441	1.199	1.399	0.137
Geophilomorpha	tropical	-0.420	0.964	1.766	0.129
Hemiptera	tropical	-0.529	1.337	1.260	0.120
Hymenoptera	tropical	-0.463	1.070	1.798	0.132

Isopoda	tropical	-0.800	1.646	1.154	0.106
Lepidoptera	tropical	-0.553	1.245	1.667	0.120
Lithobiomorpha	tropical	-1.350	2.112	0.742	0.163
Neuroptera	tropical	-0.727	1.506	1.344	0.146
Odonata	tropical	-0.588	-0.386	4.438	0.181
Opiliones	tropical	-0.384	2.301	0.370	0.128
Orthoptera	tropical	-0.117	1.001	1.673	0.111
Polydesmida	tropical	-0.179	1.012	2.191	0.146
Pseudoscorpionida	tropical	-0.801	1.750	0.300	0.143
Psocoptera	tropical	-0.936	2.294	0.666	0.235
Scolopendromorpha	tropical	-0.962	1.669	1.278	0.051

Model 2: Length-Width-Taxonomic group (LWT)

Araneae	-	-0.410	1.486	1.492	0.129
Coleoptera	-	-0.435	1.039	1.847	0.139
Dermaptera	-	-0.187	0.747	2.228	0.108
Dictyoptera	-	-0.326	0.845	1.764	0.180
Diptera	-	-0.376	1.107	1.498	0.125
Geophilomorpha	-	-0.419	0.964	1.766	0.129
Hemiptera	-	-0.473	1.253	1.362	0.101
Hymenoptera	-	-0.429	1.050	1.801	0.129
Isopoda	-	-0.690	1.387	1.393	0.093
Lepidoptera	-	-0.5539	1.242	1.662	0.117
Lithobiomorpha	-	-0.327	1.083	2.058	0.121
Neuroptera	-	-0.515	1.251	1.533	0.152
Odonata	-	-0588	-0.386	4.438	0.181
Opiliones	-	-0.243	1.442	1.262	0.132
Orthoptera	-	-0.095	0.968	1.729	0.109

Polydesmida	-	-0.417	1.245	1.809	0.141
Pseudoscorpionida	-	-0.801	1.750	0.300	0.142
Psocoptera	-	-0.936	2.294	0.666	0.235
Scolopendromorpha	-	-0.962	1.669	0.300	0.051

Model 3: Length-Width-Geographic region (LWR)

-	temperate	-0.281	1.030	1.597	0.149
-	tropical	-0.370	1.086	1.649	0.186

Model 4: Length-Width (LW)

-	-	-0.339	1.066	1.640	0.172

Model 5: Length-Taxonomic group-Geographic region (LTR)

Araneae	temperate	-0.733	2.623	-	0.151
Coleoptera	temperate	-0.935	2.455	-	0.295
Dermaptera	temperate	-0.947	2.337	-	0.114
Diptera	temperate	-1.057	2.489	-	0.182
Hemiptera	temperate	-0.902	2.386	-	0.219
Hymenoptera	temperate	-1.486	3.018	-	0.195
Isopoda	temperate	-1.292	2.950	-	0.110
Lepidoptera	temperate	-1.294	2.493	-	0.194
Lithobiomorpha	temperate	-1.671	2.780	-	0.101
Neuroptera	temperate	0.156	0.889	-	0.169
Opiliones	temperate	-0.364	2.379	-	0.157
Orthoptera	temperate	-0.640	2.267	-	0.158
Polydesmida	temperate	-1.519	2.595	-	0.037
Araneae	tropical	-0.862	2.611	-	0.191
Coleoptera	tropical	-1.104	2.553	-	0.375
Dermaptera	tropical	-1.775	2.929	-	0.135
Dictyoptera	tropical	-0.644	1.913	-	0.303

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Diptera	tropical	-0.973	2.270	-	0.249
Geophilomorpha	tropical	-2.917	2.837	-	0.225
Hemiptera	tropical	-0.813	2.189	-	0.213
Hymenoptera	tropical	-1.422	2.792	-	0.248
Isopoda	tropical	-1.268	2.839	-	0.124
Lepidoptera	tropical	-1.433	2.587	-	0.251
Lithobiomorpha	tropical	-1.884	2.701	-	0.166
Neuroptera	tropical	-0.884	2.112	-	0.197
Odonata	tropical	-0.816	1.856	-	0.300
Opiliones	tropical	-0.453	2.648	-	0.129
Orthoptera	tropical	-0.775	2.205	-	0.192
Polydesmida	tropical	-1.825	2.726	-	0.184
Pseudoscorpionida	tropical	-0.942	2.015	-	0.149
Psocoptera	tropical	-1.154	2.710	-	0.237
Scolopendromorpha	tropical	-2.084	2.702	-	0.116

Model 6: Length-Taxonomic group (LT)

Araneae	-	-0.830	2.637	-	0.190
Coleoptera	-	-1.042	2.537	-	0.334
Dermaptera	-	-1.316	2.529	-	0.206
Dictyoptera	-	-0.644	1.913	-	0.303
Diptera	-	-1.0318	2.430	-	0.205
Geophilomorpha	-	-2.917	2.837	-	0.225
Hemiptera	-	-0.817	2.237	-	0.219
Hymenoptera	-	-1.401	2.809	-	0.235
Isopoda	-	-1.322	2.967	-	0.119
Lepidoptera	-	-1.390	2.554	-	0.24
Lithobiomorpha	-	-1.888	2.934	-	0.169

Neuroptera	-	-0.871	2.010	-	0.217
Odonata	-	-0.816	1.856	-	0.300
Opiliones	-	-0.385	2.439	-	0.154
Orthoptera	-	-0.791	2.245	-	0.199
Polydesmida	-	-1.986	2.944	-	0.175
Psocoptera	-	-1.154	2.710	-	0.237
Pseudoscorpionida	-	-0.942	2.015	-	0.149
Scolopendromorpha		-2.084	2.702	-	0.116
Model 7: Length-Geographic region (LR)					
-	temperate	-0.730	2.175	-	0.283
-	tropical	-0.822	2.146	-	0.327
Model 8: Length (L)					
-	-	-0.786	2.166	-	0.313

453 Regression equations for the eight models:

454 Model 1 (LWTR): $\log_{10}$(body mass) = $a_{\text{taxon region}}$ + $b_{\text{length taxon region}} \times \log_{10}$(body length) + $b_{\text{width taxon region}}$

455 $\times$ $\log_{10}$(body width)

456 Model 2 (LWT): $\log_{10}$(body mass) = a_{taxon} + $b_{\text{length taxon}} \times \log_{10}$(body length $_{\text{taxon}}$) + $b_{\text{width taxon}} \times$

457 $\log_{10}$(body width)

458 Model 3 (LWR): $\log 10$(body mass) = a_{region} + $b_{\text{length region}} \times \log_{10}$(body length) + $b_{\text{width region}} \times \log_{10}$(body

459 width)

460 Model 4 (LW): $\log 10$(body mass) = a + $b_{\text{length}} \times \log_{10}$(body length) + $b_{\text{width}} \times \log_{10}$(body width)

461 Model 5 (LTR): $\log 10$(body mass) = $a_{\text{taxon region}}$ + $b_{\text{taxon region}} \times \log_{10}$(body length)

462 Model 6 (LT): $\log_{10}$(body mass) = a_{taxon} + $b_{\text{taxon}} \times \log_{10}$(body length)

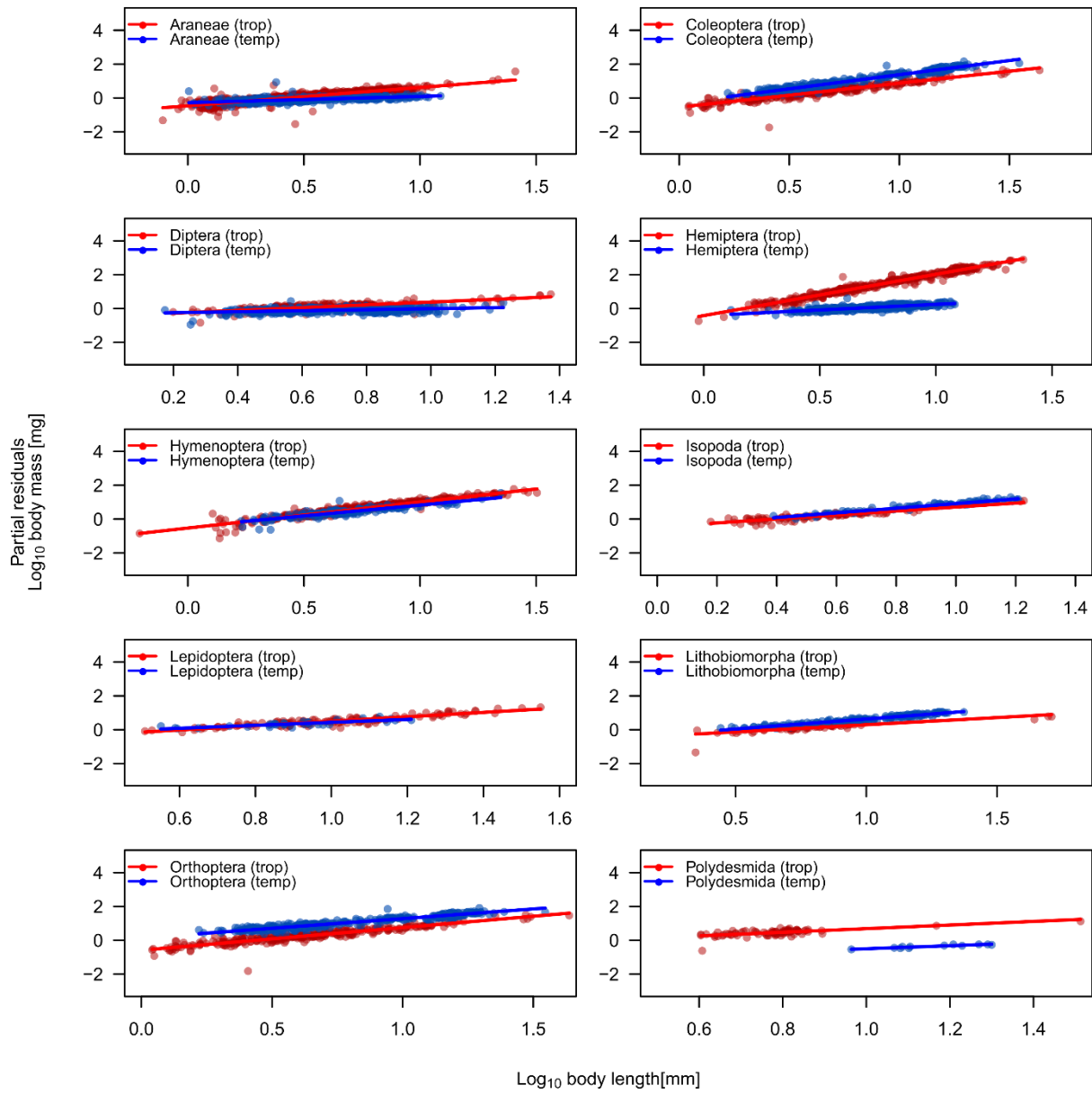463 Model 7 (LR): $\log_{10}$(body mass) = a_{region} + $b_{\text{region}} \times \log_{10}$(body length)

464 Model 8 (L): $\log_{10}$(body mass) = a + $b \times \log_{10}$(body length)

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467   **Figure 1:** Length-mass regressions of the best fit model, which included body length,

468   maximum body width, taxonomy and geographic region (LWTR) to predict body mass for

469   the ten most abundant arthropod groups from the temperate (blue) and tropical (red) study

470   areas. The y-axis displays partial residuals and, therefore, shows the effect of body length

471   after correcting for the other variables.

472

473   **Figure 2:** Prediction error (log response ratio of predicted versus observed body mass values)

474   for temperate (blue lines, panels a and c) and tropical (red lines, panel's b and d) arthropod

475   body mass obtained by using geographically disjunct (dashed lines) and non-disjunct (solid

476   lines) regression parameters for the LR (a and b) and LWR (c and d) models. LR = length +

477   region and LWR = length + width + region models.

478

479   **Figure 1**

480

481

482   **Figure 2**

483

484