1   # Spiders bring new insight into the eco-evolutionary drivers of body size

2   variation and sexual size dimorphism in arthropods

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31

32   Abstract

33   Body size has been used thoroughly in arthropod ecology as a reliable trait to assess fitness

34   responses to changes in environmental factors. Among these, spiders represent a large and

35   diverse group, colonizing almost all terrestrial habitats. Here, we propose a review on

36   intraspecific body size variation in arthropods over two main macroecological spatial

37   gradients—latitude and elevation—both of high interest in a global warming context. We found

38   that more species with a direct than with an indirect development present a converse Bergmann

39   cline along both gradients. Focusing on spiders, we propose that life history traits such as

40   voltinism, mobility, and brood care influence intraspecific body size patterns—potentially hiding

41   large-scale patterns. Further, we assessed interspecific sexual size dimorphism (SSD) in spider

42   species. We found that extreme SSD—the most original feature in spider biometry—is

43   influenced by hunting guild rather than phylogeny of spider families, suggesting that ecological

44   factors prevail over evolutionary drivers in shaping SSD.

45

46   **Keywords**

47   Bergmann's rule, climate change, functional trait, macroecology, Rensch's rule

48

49   Introduction

2

50   Ectotherms account for approximately 99% of all animal species on Earth, and they represent

51   the vast majority of the living biomass (Atkinson and Sibly 1997, Rosenberg et al. 2023). This

52   diversity and preponderance has to be studied to understand organisms' ecological and

53   evolutionary responses to environmental changes, such as climate change (Ohlberger 2013).

54   Among ectotherms, arthropods are known for their phenotypic plasticity in life history traits,

55   when habitats vary (Fox and Czesak 2000, Bonte and Lens 2007). As such, they present an ideal

56   taxon to investigate organisms' responses to environmental changes, which indeed shape

57   morphological and life-history traits expressed in a population (Kingsolver and Pfennig 2007,

58   Nussey et al. 2007). The phenotypic plasticity of arthropods has been demonstrated through

59   variations in life-history traits such as dispersal behavior (Bonte and Lens 2007, Bonte et al.

60   2008), amount and timing of reproduction events, and clutch size (Fox and Czesak 2000). For

61   example, female spiders have been shown to maximize their fitness by allowing less energy to

62   reproduction whilst producing larger eggs (Hendrickx et al. 2003a, Pétillon et al. 2009).

63   Body size variation has been broadly used to measure the organism responses to environmental

64   variations. It is a relatively easy trait to measure interspecifically and intraspecifically in

65   arthropods because of their exoskeleton, the large number of individuals and species, and their

66   easy collection and preservation. The study of body size, sometimes coupled with geometric

67   morphometrics, gives us information about body condition (Jakob et al. 1996), fecundity (Berger

68   et al. 2012), fitness (Brown et al. 2003), dispersion ability (Coyle et al. 1985) and eating habits

69   (Evans and Forsythe 1985, Gavín-Centol et al. 2017). In the present review we focus on

70   structural body size, as opposed to condition-dependent body size (Box 1). The mean structural

71   body size of individuals from a population is the result of evolutionary and ecological constraints

72   (Gaston and Blackburn 2000), while condition-dependent body size is influenced by the

73   environment of an individual during its whole life. Structural body size (henceforth body size) is

74   a labile trait, i.e. a trait that can vary over the course of an organism's ontogeny, until the

75   organism finishes its exoskeleton growth (Nussey et al. 2007). Before structural body size is set

76   (i.e before the last ecdysis takes place), it is influenced by physiological traits (growth rate,

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77 resources availability, duration of important periods during juvenile growth), themselves

78 influenced by environmental factors (Chown and Gaston 2010) and by phylogeny.

79 Body size variations will be different whether we consider intraspecific or interspercific

80 patterns, generalist or specialist species, and large or small species. It has been shown for

81 example that small ectotherms acclimate to ambient temperature almost instantly (Stevenson

82 1985). Considering these differences in body size variations, species will be constrained

83 differentially by distinct ecological factors. Body size varies greatly in arthropods: from the 139

84 µm long male mymarid egg-parasitic wasp *Dicopomorpha echmepterygis* (Mockford 1997,

85 Mymaridae) to the 167 mm long beetle *Titanus giganteus* (Linnaeus 1771, Cerambycidae)

86 (Chown and Gaston 2010). In arthropods, a larger body size can be an asset because it means

87 greater fecundity in females, access to mates for males and resource sequestration advantages

88 (Chown and Gaston 2010, Huang et al. 2017). The benefits of small size may include reduced

89 viability costs of growth and development, enhanced agility and reduced detectability, lowered

90 maintenance energy costs, reduced heat stress, reduced costs of reproduction, and increased

91 scramble competitive ability (Blanckenhorn 2000, Chown and Gaston 2010, Huang et al. 2018).

92 Intraspecific variation of body size and other morphologic traits may ultimately lead to

93 parapatric speciation (Mammola et al. 2018).

94 The most studied environmental factors in "trait-based ecology of terrestrial arthropods" (Wong

95 et al. 2019) are macroecological factors—namely latitude and elevation—and their associated

96 biotic and abiotic environmental variables, e.g. temperature or season length, often in the

97 context of climate change (Høye and Forchhammer 2008, Radchuk et al. 2013). A latitudinal

98 gradient will trigger gradients of abiotic factors such as temperature and growing season length

99 (Conover and Present 1990) while an elevational gradient will trigger gradients of temperature

100 lapse rate, short-wave radiation input, partial pressure of respiratory gases, precipitation (and

101 thus humidity), turbulence and wind speed (Hodkinson 2005). Biotic factors that vary along

102 these gradients are life history traits such as density, sex ratio (Lee et al. 2012), fecundity

103 (Bowden et al. 2013), dispersal ability, prey availability and sociality (Guevara and Avilés 2007),

104 wing size, color, absorbance and spectral reflectance, body size, thermal tolerance, diapause and

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105 fecundity (Hodkinson 2005). Elevational and latitudinal gradients also trigger biotic differences

106 in population density or community composition, themselves having an impact on interactions

107 between organisms and resource acquisition. For example, a higher population density can lead

108 to higher intraspecific competition, leading to a longer development period and a decreased

109 body mass (Begon et al. 1986). Longitudinal gradients are understudied in insects, although they

110 correlate to climatic variables (Jego et al. 2023). Species Abundance and Distribution (SAD) is

111 commonly studied along with body size (Gutiérrez and Menéndez 1997, Gaston 2003, Ulrich

112 2008, King 2010) and sometimes along with macroecological factors (Ciplak et al. 2008, Bowden

113 et al. 2013). For example, larger repartition area have been shown to positively correlate to body

114 size, showing a direct implication of the study of body size in conservation (Gaston and

115 Blackburn 1996).

116 Several theories have been proposed to explain the patterns of body size variation along

117 macroecological gradients. The main theory was the Bergmann's rule which proposes that body

118 size increases with latitude (Atkinson and Sibly 1997), while the converse Bergmann's rule

119 states that body size should decrease with latitude (Sheridan and Bickford 2011). We present

120 the most studied theories and hypotheses about the role of temperature in Boxes 2 and 3.

121 Along latitudinal gradients, there is a variety of body size responses in arthropods. In a review

122 on 47 species, (Blanckenhorn and Demont 2004) found that, intraspecifically, around 20% of

123 species did not show any pattern, while among the rest, about half followed the Bergmann's rule,

124 and the other half followed the converse rule. In insects, (Shelomi 2012) found that on a total of

125 779 intra- and interspecific studies, 30% of the groups followed the Bergmann's rule while

126 another 30% followed the converse rule and 40% did not follow any trend. If we take some

127 examples, several species of Diptera follow the Bergmann's rule, while for a lot of Coleoptera,

128 Orthoptera and Lepidoptera (Blanckenhorn and Demont 2004), some spiders (Entling et al.

129 2010) or univoltine insects (Mousseau 1997), the converse rule has been demonstrated.

130 Elevational gradients have been used as a proxy for latitudinal gradient and climatic changes.

131 Along elevational gradients, body size shows a variety of responses in arthropods, similar to

132 what is observed along latitudinal gradients. Some species show a positive correlation between

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133   body size and elevation (Bergmann's rule) while some others show a negative one (converse

134   Bergmann's rule) (Hodkinson 2005).

135   In contrast with arthropods in general, and notably insects, body size variation in spiders is

136   much less known, although they are used in many studies because of their high global and local

137   diversity (see Dimitrov and Hormiga 2021 for a recent review). Like other arthropods, spiders

138   show a very wide size range: the smallest one is thought to be *Patu digua* (Forster and Platnick

139   1977) from the Symphytognathidae family, and whose body length is 0.37 mm, whilst the largest

140   ones occur among tarantulas (Theraphosidae) and can have body lengths up to 90 mm and leg

141   spans up to 250 mm (Mammola et al. 2017). Gigantism can also be observed on islands in spider

142   taxa such as the *Orsonwelles* genus (Hormiga 2002). As generalist predators, spiders can be used

143   for pest control (Toft 2005). They are good bioindicators (Marc et al. 1999, Rainio and Niemelä

144   2003) and represent a diverse and abundant group within the arthropods in various habitats

145   (Wise 2006, Lafage and Pétillon 2014). Species with a direct development such as Orthopterans

146   (hemimetabolous insects), and the majority of spiders, have their body size controlled by

147   feeding while ecdysis still takes place; unlike holometabolous insects (with indirect

148   development) such as ground beetles whose imaginal body size is governed only by larval stages

149   (complete metamorphosis). Spiders body size and shape have been shown to vary across

150   behavioral guilds (Wolff et al. 2022). Along macroecological gradients, we hypothesize that

151   wanderers and web-building species might present different patterns of body size variation.

152   In spiders, males are typically smaller than females and present one of the greatest sexual size

153   dimorphisms (SSD) in animals (Kuntner and Coddington 2020) (Figure 1). Only in rare cases is

154   the male larger than the female (Aisenberg et al. 2007). Across the animal kingdom, SSD tends to

155   increase with mean body size when the male is the larger sex; while the opposite tends to arise

156   when the female is the larger sex. This is known as the Rensch's rule (Rensch 1950, Bidau and

157   Martí 2008) and has also been studied intraspecifically and along latitudinal gradients

158   (Blanckenhorn et al. 2006, Høye and Hammel 2010, Bowden et al. 2013, Laiolo et al. 2013).

159   While most arthropod species follow the Rensch's rule—with some notable exceptions (Bidau et

160   al. 2016, García-Navas et al. 2017, Rossi and Haga 2019)—spiders do not follow it (see e.g.

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161 Figure 1c in Kuntner and Coddington 2020). Several hypotheses have been advocated to explain

162 extreme SSD in spiders (summarized in Foellmer & Moya-Laraño, (2007)). Selection may favor

163 smaller males because (i) being mature earlier than the females (protandry) is advantageous,

164 (ii) larger specimens are eaten by the females (cannibalism) (although this hypothesis has been

165 refuted multiple times, see Foellmer & Moya-Laraño, (2007)), and (iii) a smaller body size allows

166 males to more easily climb to high habitat patches where females are located (gravity

167 hypothesis) and thus win the scramble competition, the race for reaching mates by the time they

168 are receptive (Moya-Laraño et al. 2002). Selection may in parallel favor larger females because

169 (i) they have higher fitness, (ii) they get predated less (predation release (Hormiga et al. 2000,

170 Higgins 2002)), and (iii) they profit from larger prey availability (Foellmer and Moya-Laraño

171 2007). Overall, extreme SSD in spiders is likely due to divergent selective directions on males

172 and females (Kuntner and Coddington 2020). As in spiders, extreme female-biased SSD is found

173 in mantis, where it has been shown that female body size was related to prey size, fecundity, and

174 emergence, and not related to cannibalism or male attraction (Maxwell and Frinchaboy 2014).

175 Yet, most studies assessing processes driving SSD considered single spider species, or reviewed

176 species in local parts of the world (Foellmer and Moya-Laraño 2007).

177 In this work, we review field studies on intraspecific variation of structural body size along

178 macroecological gradients in spiders and other arthropods. We extend the analysis from

179 (Foellmer and Moya-Laraño 2007)—using a large database of 1822 worldwide species

180 synthetizing spider traits and phylogeny—to test hypotheses on both ecological and

181 evolutionary drivers of spider SSD. We address the following three questions: (1) How do body

182 size and SSD of spiders vary along macroecological factors? (2) Is this variation different from

183 other arthropods and among taxa with distinct development (direct vs. indirect)? (3) How do

184 biotic (including life history traits) and abiotic factors interact with body size and SSD, to

185 possibly explain larger spatial scale patterns? We further discuss the implications of monitoring

186 spider body size and SSD in a changing world.

187

Methods

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189   (1) Macroecological patterns in arthropods and spiders

190   We searched for reviews and articles using the search engine 'Google Scholar' until September

191   2024 with the following key words: 'body size' + 'macroecological' / 'altitude'/ 'latitude' /

192   'elevation' + 'ectotherm' / 'Arthropod' / 'insect' / 'spider'/ 'Hexapoda' / 'Chelicerata' / 'Arachnid'

193   / 'Araneae' / 'Myriapoda' / 'Crustacea'. This resulted in 40 combinations of searches.

194   Specifically for spiders, we report studies that we found on other microecological patterns

195   (urbanization and habitat quality) as a non-exhaustive list.

196   (2) Sexual size dimorphism

197   Data on species mean body size were extracted from the betsi database

198   (https://portail.betsi.cnrs.fr/). Data on species substrate were extracted from the Spider and

199   Harvestman Recording Scheme website (http://srs.britishspiders.org.uk/). To avoid a possible

200   size effect due to varying species richness in families we only used families with at least ten

201   species, resulting in a total of 48 families (432 genus, 1822 species). Each family was attributed a

202   guild, either web-builders or non web-builders, based on (Cardoso et al. 2011). Correlation

203   between female body size and female/male body size ratio was estimated in a Bayesian

204   framework with a Student's t distribution with the brms package (Bürkner 2018). We used 2000

205   iterations on four chains. Model convergence was checked by visually inspecting diagnostic

206   plots. The link between female body size and female/male body size ratio was estimated using

207   models built within a Bayesian framework using brms (Bürkner 2018) with two chains and

208   default priors (except for intercept which was set as normal (1,1)). The models included female

209   body size only, female body size and family, female body size, family and guild, guild and size as

210   predictors. Family was included as a random factor. Model convergence was checked by visually

211   inspecting diagnostic plots and using Rhat value. Parameter selection was based on "HDI+ROPE

212   decision rule" with a range value determined as -0.1 * sd(y), 0.1 * sd(y) (Kruschke and Liddell

213   2018) and was performed using bayestestR (Makowski et al. 2019). The best model was selected

214   based on LOO comparison.

215

216   Definitions and concepts

217   Box 1. Body size

218   It is important to differentiate structural body size (SBS, usually called body size indicator (BSI)

219   in vertebrates) from condition-dependent body size (CDBS). Structural body size was defined by

220   (Moya-Laraño et al. 2008a) as a '*measure of body size that does not change with additional*

221   *nutrient acquisition once an animal has discontinued growth, and thus SBS is not directly affected*

222   *by current condition*', while CDBS is '*any measure of body size that changes with current condition*

223   *(i.e. covaries with nutrient storage)*'. Body condition (i.e. body mass corrected for size

224   differences) is a proxy of fitness and reflects nutrient storage and habitat quality (Jakob et al.

225   1996, Moya-Laraño et al. 2008a, Peig and Green 2009, Knapp and Knappová 2013, Labocha et al.

226   2014). Structural body size, on the other hand, is not affected by condition and will thus reflect

227   evolutionary and ecological constraints. In arthropods, the confusion is sometimes made

228   between CDBS and SBS when body condition traits are measured and considered as 'body size'

229   such as mass, density, or abdomen size (Chown and Gaston 2010).

230   Structural body size can be measured in multiple ways within and across taxa, considering

231   distinct ways to store energy. For example, the whole body of a ground beetle is covered with

232   chitin, which prevents it from storing much energy while a spider's abdomen can grow larger to

233   store energy. It will then be more adapted to measure a sclerotized body part such as the head

234   or the pronotum to measure SBS. Measures of structural body size in spiders include:

235   cephalothorax (carapace) length (Petersen 1950) and width (Høye and Hammel 2010, Bowden

236   et al. 2013) illustrated in Figure 2A: *Pardosa furcifera*, from Ameline *et al.*, (2017), first femur

237   length (Opell et al. 2007) (illustrated in Figure 2B), and tibia-patella length (Skow and Jakob

238   2003). There needs to be a consensus on which body size measures to use in order to allow

239   comparison (Gallagher et al. 2020). Indeed, interspecific meta-analyses using average figures

240   from taxonomic literature (Ulrich 2007, Entling et al. 2010, Ulrich and Fiera 2010, Fattorini et al.

241   2013, 2014) can only do so if the same measures are used. Similarly, intraspecific studies should

242   be comparable among one another. In most recent studies, several measures of sclerotized body

243   parts are correlated (Knapp and Knappová 2013, Puzin et al. 2014, Ameline et al. 2018, Lowe et

244   al. 2020). In the present study, we are interested in evolutionary and ecological constraints, thus

245   focusing on structural body size, henceforth body size throughout this article.

246

247   Box 2. Rules of body size variation along macroecological gradients.

248   Body size has been used interspecifically in allometric studies to try and understand general

249   biological laws (Norris 1998, Raerinne 2013). At the interspecific level, the *Metabolic Theory of*

250   *Ecology* proposes that (i) there are more species at low latitudes than at high latitudes, (ii) there

251   are more small species, (iii) so there are consequently more small species at low latitudes and

252   they show greater diversity (Brown et al. 2004). The most famous body size variation theory is

253   the *Bergmann's rule* which proposes that body size increases with latitude (Bergmann 1848,

254   Atkinson and Sibly 1997). This rule states that a larger organism provides a reduced surface per

255   volume ratio which minimizes the heat loss (Blackburn et al. 1999). The rule was originally

256   thought to apply interspecifically to endotherms, but an intraspecific version has been proposed

257   as *James' rule* or *neo-Bergmann's rule* (Chown and Gaston 2010, Vinarski 2014), and it has been

258   tested in all taxa (Blanckenhorn and Demont 2004, Chown and Gaston 2010, Entling et al. 2010,

259   Meiri 2011, Shelomi 2012). As the opposite pattern has been observed in arthropods (Sheridan

260   and Bickford 2011) and spiders (Puzin et al. 2014), a *converse Bergmann's rule* has then been

261   proposed which postulates that decreasing season length causes smaller body size at higher

262   latitude (Blanckenhorn and Demont 2004). This rule supposes that shorter seasons at higher

263   latitudes reduce the foraging period, hence resulting in reduced growth and development

264   period. A gradient of decreasing body size towards the poles should then be observed

265   (Blanckenhorn and Demont 2004). The *countergradient variation* announces that growth rate

266   increases with latitude, because the growing season is shorter, resulting in a homogenous

267   distribution of body size along latitudinal gradients (Conover and Present 1990). Different

268   intraspecific patterns of body size variation across macroecological gradients are usually

269   reported, including linear and non-linear clines. Linear clines can be *positive* (Bergmann's rule)

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270 or *negative* (converse Bergmann's rule) showing increase or decrease of body size across the

271 range, respectively. Non-linear clines include *sawtooth* and *stepwise* clines (Figure 3A and B,

272 from Shelomi, (2012), which can still show an overall positive or negative cline, *U-shaped* or

273 *hump-shaped* clines, which occur when an increase or decrease is reversed gradually over a

274 single point in the entire range (Figure 3C and D), while *curvilinear* clines occur when increase

275 or decrease is reversed gradually over several points across the range (Shelomi 2012).

276 The *Rapoport's rule* says that the size of a species distribution range increases with latitude, but

277 it is used interspecifically (Gaston and Blackburn 1996). The *Cope's rule* supposes a

278 macroevolutionary trend towards increased size (Kingsolver and Pfennig 2004). The *seasonality*

279 *hypothesis* states that climates characterized by long annual cycles select for large body sizes.

280 This hypothesis was confirmed by (Troost et al. 2009) who proposed that both longer

281 productivity and seasonality may lead to larger body sizes. Although many hypotheses were

282 proposed, the mechanisms underlying these body size patterns are still rarely investigated

283 (Blanckenhorn and Demont 2004).

284

285 Box 3. Body size variation linked to temperature variation.

286 Rules laid down are often thought to be linked to temperature. However, it is still a controversial

287 subject and there is no clear explanation on why body size increases or decreases when the

288 organism is exposed to low temperatures (Atkinson and Sibly 1997). Indeed, 83% of 109 studies

289 on ectotherms showed an increased growth rate and consequently, an increased body size at

290 lower rearing temperatures, although individual growth rates were expected to decrease at

291 lower temperatures. This phenomenon is explained by the *'developmental temperature-size rule'*

292 or *TSR* (Atkinson 1994, Atkinson and Sibly 1997). The organism can 'choose' to trade-off for a

293 delayed maturity which would lead to a larger body size if the increase of fecundity exceeds the

294 loss of fitness caused by delayed maturity. Another hypothesis is that higher temperatures may

295 cause limited resource availability. In response to that limitation, body size is smaller due to the

296 lack of resource acquisition or due to an adaptive response to reduce size at maturity. From a

297 cellular point of view, the TSR argues that cellular differentiation which leads to sexual maturity

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298   is limited by diffusion at low temperatures, thus maturity would be delayed. Consequently, cell

299   size would become larger at lower temperatures (Arendt 2007). The Bergmann's rule has been

300   attributed to the TSR theory (temperature variation) while the converse Bergmann's rule was

301   attributed to a resource limitation, due to season length variation (Hodkinson 2005). This has

302   been shown, for example, by an experiment along a thousand meters elevational gradient on

303   weevils in subantarctic islands by (Chown and Klok 2003).

304   Kingsolver and Huey (2008) summarized the rules linked to temperature as three rules. The first

305   one is "*bigger is better*" (red in Figure 4, adapted from Kingsolver & Huey, (2008)). A larger body

306   size is thought to bring a higher fitness via better performance and dominance. But a larger body

307   size can also be costly and risky because of delayed maturation and increased energy demand.

308   Hence, intermediate sizes are also thought to be optimal. As a counter-example of this first rule,

309   (Moya-Laraño et al. 2007) showed that smaller males are better scramble competitors. Smaller

310   is also generally better in the case of parasites and parasitoids (Blanckenhorn 2000). The second

311   rule is "*hotter is smaller*" (green in Figure 4). It corresponds to the TSR, which takes in account

312   the effect of temperature on the organism during development. Counter-examples exist, e.g. in

313   the case of Orthoptera and Lepidoptera, hotter is bigger (Mousseau 1997, Walters and Hassall

314   2006). '*Ectotherms that obey the temperature size rule are identified as having a higher*

315   *temperature threshold for development rate than for growth rate; exceptions are identified as*

316   *having a lower temperature threshold for development rate than for growth rate*' (Walters and

317   Hassall 2006). The third rule, "*hotter is better*" (blue in Figure 4), proposes that organisms with a

318   high optimal temperature will also have high maximal performance and fitness, according to

319   thermodynamics laws. We chose not to present body size variations in response to temperature

320   because most of the studies consider growth rate and growth efficiency but not directly body

321   size (Angilletta and Dunham 2003).

322

323   Results and discussion

324   (1) Body size and sexual size dimorphism (SSD) along macroecological gradients

325   We found a total of 146 studies reporting intraspecific body size variation of 240 arthropod

326   species along latitudinal and elevational gradients (Figure 5, Supplementary Table S1). We did

327   not find an overall tendency towards positive (Bergmann's rule) or negative (converse

328   Bergmann's rule) variation of body size across elevation or latitude. We found that species with

329   a direct development presented a larger proportion of negative clines than species with an

330   indirect development, both along elevational (Z-test, X-squared = 4.1, df = 1, p-value = 0.02, 42%

331   vs. 23%, Figure 5) and latitudinal clines (Z-test, X-squared = 8.2, df = 1, p-value = 0.002, 74% vs.

332   40%, Figure 5). This result suggests that the growth of species with a direct development might

333   be restricted by the environmental changes caused by increasing latitude or elevation—notably

334   the shorter season length. Because species with an indirect development go through

335   metamorphosis between the larval and the adult stages, they may dispose from more

336   possibilities to increase their growing season. In spiders, we found that 11 out of 18 species

337   showed no body size trend along elevational gradients (61 %, Figure 5). This proportion was

338   higher than in other arthropod species (Z-test, X-squared = 8.2, df = 2, p-value = 0.02, 61% vs.

339   22% and 33% in species with direct and indirect development, respectively). This result may be

340   caused by the high dispersal of spiders which would hide existing body size variations along

341   elevational gradients. It is important to note that most studies have been performed on a limited

342   number of populations and have not been repeated, which may result in a low statistical power

343   to detect overall patterns (Gienger et al. 2019).

344   Sexual Size Dimorphism (SSD) has been shown to vary across macroecological gradients in

345   arthropods interspecifically (Blanckenhorn et al. 2006, Laiolo et al. 2013) and intraspecifically,

346   e.g. in beetles (Baranovská et al. 2019) and spiders (Høye et al. 2009, Høye and Hammel 2010,

347   Bowden et al. 2013, Laiolo et al. 2013). A meta-analysis on SSD variation across macroecological

348   gradients in arthropods revealed that, on average, males body size varied more than females

349   (Horne et al. 2019, Kojima 2019). In spider species this was found to be the opposite, as female

350   body size varied more across elevation gradients (Horne et al. 2019). This study suggests that

351   SSD variation is constrained by evolutionary forces rather than environmental ones (Horne et al.

352   2019). They also found no relationship between SSD variation and varied tested factors like

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353   environment type (aquatic or terrestrial), voltinism, mean body size, degree of SSD and gradient

354   direction. Conversely, it was found in grasshoppers that female body size varied more across an

355   elevational gradient and the authors hypothesized that female body size might be more plastic

356   or evolve faster in harsh environments (Laiolo et al. 2013).

357   In contrast with sexual *size* dimorphism, sexual *shape* dimorphism is studied in other arthropods

358   (Vujić et al. 2020) and might be relevant in further, spider-focused, studies.

359   In the context of anthropic impacts, macroecological gradients have been studied in spiders,

360   such as urbanization and land use. It was shown for one species of orb-weaver spider

361   (Araneidae) that body size increased in an urbanized habitat (Lowe et al. 2014), while another

362   species was shown to decrease body size in highly urbanized habitats (Dahirel et al. 2019).

363   Interspecifically, urbanization and fragmentation have been shown to cause body size decrease

364   (Merckx et al. 2018, Piano et al. 2020). High habitat quality, determined by more rocks,

365   precipitation and duration of snow coverage, was shown to intraspecifically increase body size

366   and eggcase size (Mammola et al. 2019). Corroborating this result, (Bowden et al. 2018)

367   observed a decline in spider abundance correlated to snowmelt timing and moisture availability.

368   In an agricultural context, (Plath et al. 2021) revealed that mean body size of spider community

369   decreased with intensive agriculture. On the other hand, (Pinto et al. 2021) observed no

370   difference in body size in spider communities across different land uses, and hypothesized that

371   microhabitat rather than global land use influenced the observed interspecific body size pattern.

372   In the following, we pinpoint several factors that could explain variability of intraspecific body

373   size responses along macroecological gradients among taxa and even species, focusing on

374   spiders.

375

376   (2) Biotic and abiotic factors driving local changes in body size and SSD

377   (a) Biotic factors

378   Diet quality has been correlated to body size variation across latitudinal gradients (Ho et al.

379   2010). Higher competition and variation in prey availability might also lead to fewer resources

380   and explain a lack of overall body size variation along environmental gradients (Beckers et al.

381   2020).

382   Among life history traits, the degree of voltinism—i.e. how many reproduction events occur

383   during the year—may influence body size (of both male and female) response to

384   macroecological gradients. Shifts in voltinism across elevational or latitudinal gradients—due to

385   changing seasonality—might cause body size variation along these gradients (Beckers et al.

386   2020). (Cabon et al. 2024) showed that temperature had an effect on the body size of univoltine,

387   but not bivoltine species. A sawtooth cline is typically interpreted as the result of a shift in

388   voltinism (Shelomi 2012). The level of voltinism is known to change interspecifically with

389   latitude and hence temperature (Kivelä et al. 2011, Zeuss et al. 2017). Voltinism is less studied

390   across populations and along elevational gradients, as these gradients are usually smaller than

391   latitudinal ones. A shorter generation time in multivoltine species would provide a longer

392   growing season for earlier clutches of offspring (Chown and Klok 2003). A different degree of

393   voltinism would then mean a different resource allocation strategy and the underlying

394   mechanisms of body size variation would differ. In the present study, we could not consider

395   voltinism *a priori*, as it may vary within species and populations.

396   Brood care is common in spiders and may provide them with a lower susceptibility to

397   unfavorable conditions in comparison with insect species with stationary larval stages (Beckers

398   et al. 2020). Body size might then be less influenced by environmental conditions during

399   development and show no trend across an environmental gradient.

400   Mobility and dispersal are important factors that could influence the degree of body size

401   variation across gradients. In (Cabon et al. 2024), only species with a low ballooning capacity

402   showed body size variation across a temperature gradient. Species with low mobility may be

403   split in subpopulations that would induce body size variation across gradients (Beckers et al.

404   2020). A higher mobility may thus cause a species to show variation induced by large-scale

405   rather than fine-scale environmental factors (Hein et al. 2019). For example, body size variation

406   has been linked to foraging ability in bees (Gathmann and Tscharntke 2002). Here we want to

407   emphasize the role of body size particularly in spider dispersion. Long-distance dispersal in

15

408   spiders will be passive via ballooning and favored by a small body size or mass while short-

409   distance dispersal will be active via walking on the ground and favored by a large size or

410   amplitude. Ideal Free Distribution (IFD) is expected to homogenize body sizes among habitats

411   (Fretwell and Lucas 1970, Hendrickx et al. 2003b, Yip et al. 2008), while disturbances may select

412   for increased dispersal propensities: smaller body size in ballooning species or individuals,

413   mostly web-building spiders (Coyle et al. 1985, Blandenier 2009, Blandenier et al. 2013,

414   Simonneau et al. 2016) or longer legs in runners, i.e. ground-dwelling spiders (Lafage et al.

415   2015). Selection for relatively longer legs was previously reported in web-building (mate search:

416   Foellmer and Fairbairn 2005), free-running (mate search: Framenau 2005) and cave-living

417   species (cave adaptation: Miller 2005). Longer legs have also been proved to increase speed in

418   steep ground (Prenter et al. 2012), and in suspensory locomotion (Moya-Laraño et al. 2008b).

419   Although we do not present an exhaustive list of such results, traits linked to body size have

420   been shown to vary across macroecological gradients: sexual size dimorphism (SSD), growth

421   rate⸻related to temperature in (Angilletta, Jr., and Dunham 2003), or fecundity (Reed and

422   Nicholas 2008, Berger et al. 2012, Bowden et al. 2013, Marshall et al. 2013).

423   Body size in spider offspring is typically measured to reveal reproduction trade-offs (Petersen

424   1950, Brown et al. 2003, Skow and Jakob 2003, Walker et al. 2003, Pétillon et al. 2009, Ameline

425   et al. 2017), and these reproductive trade-offs have been revealed along macroecological

426   gradients (elevation: Ameline et al. 2018).

427   (b) Abiotic factors

428   Habitat has been shown to be an important factor in spider communities distribution (Koponen

429   2002, Entling et al. 2007). At a local spatial scale (m^2), habitats can shape body size patterns

430   (Brown et al. 2003, Hendrickx et al. 2003a, Pétillon et al. 2009, Puzin et al. 2011). After finding

431   no overall body size patterns along elevational gradients, studies suggested that microhabitats

432   played a more important role than the large-scale landscape (Hein et al. 2015, Ameline et al.

433   2017). Local environmental conditions such as soil pH, occurrence of ice and abundance have

434   been shown to play a role in species body size distribution (Ornaghi et al. 2023). In spiders,

435   snow cover and habitat type are considered to play a role in body size distribution across

16

436 macrogeographic scales (Hein et al. 2014, Bowden et al. 2015). (Bowden et al. 2015) emphasize

437 that environmental conditions are especially important for small size species with low dispersal

438 ability. Further, models showed that body size was linked to how ectotherms move in

439 microclimatic environments (Woods et al. 2015).

440 Climate has been shown to drive body size patterns in arthropods along macroecological

441 gradients (Hu et al. 2012). Alternatively, little effect of climate change on body size has been

442 observed in herbivorous beetles (Baar et al. 2018). The effect of temperature on body size or

443 related traits is often studied in insects (Opell et al. 2007, Ciplak et al. 2008) and has also been

444 studied along latitudinal and elevational gradients (Koyama et al. 2015, Pérez-Valencia and

445 Moya-Raygoza 2015). In insects, further analysis of the effect of temperature on physiology

446 (growth rate, metabolic rate) has been performed along elevational gradients (Bulgarella et al.

447 2015, Cogo et al. 2020). Dispersal ability, mentioned above, has also been shown to be

448 influenced by temperature in spiders (Bonte et al. 2008). In various arthropods, temperature

449 and season length has been found to influence body size—e.g. in crustaceans (Jaramillo et al.

450 2017) and beetles (Collard et al. 2021). Overall patterns of reduced body size were observed

451 with warming temperatures, likely linked to oxygen lack in aquatic environments (Verberk et al.

452 2021) and heat tolerance in endotherms (Peralta-Maraver and Rezende 2021).

453 Other climatic factors such as photoperiod (Hassall 2013) have been correlated to body size

454 variation along macroecological gradients. We further develop the broader impact of climatic

455 changes on body size variation in the last section of the results.

456 In this review, we collected data about interspecific SSD in spiders, using a large dataset of 48

457 families (432 genus, 1822 species). SSD was previously shown to be positively correlated with

458 female size in spiders (converse Rensch's rule: Foellmer and Moya-Laraño 2007). Using a larger

459 dataset, we confirm this hypothesis (Figure 6). Across spiders species, body size has been shown

460 to be highly phylogenetically conserved (Entling et al. 2007). We thus use mean body size of

461 males and females in spider species to approximate interspecific SSD.

462 The ratio between female and male body size was significantly correlated with female body size

463 ($R^2 = 0.42$, 95%-CI = 0.38 – 0.46). The best model explaining the ratio between female and male

464 body size included female size and family as predictor with a R^2 of 0.327 (95%-CI = 0.289 –

465 0.357). Female size effect on the ratio between female and male body size has a very high

466 probability of existing and being positive (pd = 100%, Median = 0.032, 89% CI [0.028, 0.035])

467 and could be considered as significant (0% in ROPE). Family effect on the ratio between female

468 and male body size has a very high probability of existing and being positive (pd = 100%,

469 Median = 0.21, 89% CI [0.20, 0.22]) and could be considered as significant (0% in ROPE).

470 We found that SSD was less prominent in web-building spider families (Figure 7, Mann-Whitney

471 test, W = 554928, p < 0.0001). We found no curvilinear relationship between ln (males) and ln

472 (females) in either web-building and non web-building spiders (Figure S1) contrary to the

473 expectations regarding the 'gravity hypothesis' made by Foellmer & Moya-Laraño (2007). We

474 found no correlation between SSD and more specific guild categories within web-building and

475 non-web building species (Figure S2, Mixed linear model: ratio~guild+1|family, X^2 = 16.13, df =

476 7, p = 0.024). We then tested whether the position of the species in the substrate (ground,

477 herbaceous, shrub, canopy) was correlated with SSD (Figure 8) and found no correlation (Mixed

478 linear model: ratio~substrate+1|family, X^2 = 13.44, df = 7, p = 0.062). To test the correlation

479 between SSD and the phylogeny of spider families, we projected the mean values of SSD on a

480 phylogenetic tree (based on Macías-Hernández *et al.*, (2020)) for each family containing more

481 than ten species (Figure 9). We did not find that phylogeny influenced SSD in spider families. Our

482 results suggest that ecological rather than evolutionary factors influence SSD in spider species.

483   (3) Perspectives and future research directions in a changing world

484 Latitude and elevation are macroecological factors that are good correlates of temperature

485 variations in a global change context. There is a need to predict how species and populations will

486 adapt to macroecological variations, since global change brings fast and important

487 modifications. Anthropic activity threatens biodiversity and thus stability of ecosystems and

488 biogeological cycles, causing an increase of severe weather events. It has been shown for birds

489 that severe weather events can exert directional selection pressure, favoring larger size

490 (Goodman et al. 2012). Global warming is thought to generally result in an intraspecific decrease

491   in body size, but the underlying mechanisms are not well known and very few studies have

492   focused on endotherms (Sheridan and Bickford 2011). Body size and SSD can also vary with

493   anthropogenic disturbance (Sukhodolskaya and Eremeeva 2013). Intraspecifically, climate

494   change may result in increased SSD at higher elevations due to expanding growing seasons

495   (Høye and Hammel 2010).

496   Thermal tolerance may be studied along with body size variation (Hoffmann et al. 2013),

497   although we assume that it may play a less important role than habitat niches in ectotherms.

498   Sudden environmental changes can lead to niche shifts, thus leading to invasions depending on

499   dispersion ability and range size (Iversen et al. 2013). Climate indeed acts as a major constraint

500   on range boundaries (Thomas 2010). This is a major social issue as invasive species may also be

501   vectors of disease, such as mosquitoes with malaria. Invasions can also inverse the clines

502   brought by climate change (Treasure and Chown 2014). A good example of habitat that is

503   particularly prone to global warming is the arctic habitat; where arthropods rely on snowmelt to

504   emerge. Hence, the predicted variability of snowmelt may affect organisms in areas of late

505   snowmelt most severely (Hein et al. 2014, Bowden et al. 2018, Wehner et al. 2023). Moreover,

506   specialized species that present a narrow phenological range or host specialization like

507   butterflies or parasitoid wasps will possibly be more vulnerable to trophic mismatch (Høye and

508   Forchhammer 2008). As a contrasting example, body size can remain stable over decades (one

509   arctic lycosid population: Høye et al. 2009). Global change may have a bigger impact on tropical

510   insects because they are living close to their optimal temperature and they are relatively

511   sensitive to temperature change (Deutsch et al. 2008). We also know that plasticity increases in

512   an unpredictable environment (Fischer et al. 2011) and this raises again the issue of anthropic

513   disturbance in stable environments.

514   Because of the variety of morphologies in arthropods, studies use diverse measures of body size

515   and often did not compare or repeat their results within the same taxa. The results we present

516   thus offer a rough overview of body size variation in arthropods. Multivariate analyses of body

517   size provide a better approximation of a population's body size (Caldas et al. 1996, Bidau and

518   Martí 2007, Knapp and Knappová 2013). Ratios (Azevedo et al. 1998), allometry (Bidau and

519   Martí 2007) or Geometric Morphometrics (GM) (Hernández et al. 2011) can further take shape

520   into account. These methods require however a large sampling and analyzing effort, difficult to

521   implement in large-scaled analyses. For future meta-analyses to be richer and more precise,

522   open-source databases (Gallagher et al. 2020) and standardized traits measurements in

523   arthropods (Moretti et al. 2017) and spiders (Lowe et al. 2020, Pekár et al. 2021)—including

524   habitat and life-history traits—are essential. We plead for integrating more life history traits in

525   monitoring and predicting research, which is increasingly easy due to the development of

526   worldwide databases and mechanistic species distribution models, respectively.

527

528   Conclusions

529   (1) In arthropods and in spiders specifically, we argue that life-history traits such as

530   voltinism, development, mobility and dispersal ability, guild—e.g. wanderer vs. web-

531   building—are explanatory variables that influence body size patterns along

532   macroecological gradients.

533   (2) Multivariate assessment of body size is often lacking, although essential to grasp its

534   variation across macroecological gradients. As an example, separate measurement of

535   female and male body size can reveal sexual size dimorphism (SSD), an important trait to

536   consider in spiders.

537   (3) Abiotic factors such as microclimate, habitat are also key factors influencing body size

538   variation, although they are not often reported.

539   (4) In addition, we emphasize the need for future studies to use standardized measurements

540   and to publish them in public databases to allow for comparable and more complete

541   analyses.

542   (5) Many rules have been set to fit body size trends, without however explaining the

543   underlying patterns that drive body size clines (Meiri 2011). This review gathers

544   empirical data about body size variation along elevational and latitudinal gradients in

20

545   arthropods, providing a step forward to better understanding of underlying mechanisms

546   driving body size variation.

547   (6) The intraspecific study of body size through space and time is key in ecology, as it is

548   driven by physiological and adaptive mechanisms, and addresses conservation and

549   invasion issues (Violle et al. 2007, Thomas 2010, Wills et al. 2014, Bertelsmeier 2017,

550   Austin and Dunlap 2019). However, most studies solely report correlations of

551   phenotypic variation with macroecological gradients. We found many studies

552   investigating body size variation along macroecological gradients, but we still know little

553   about the causes and consequences of variation in life history trait plasticity in the wild,

554   or how natural selection operates on plasticity (Pigliucci 2005, Stillwell 2010). A few

555   studies combined body size measurements with common-garden experiments or genetic

556   data on arthropods collected on macroecological gradients (Bulgarella et al. 2015,

557   Sandoval-Arango et al. 2020, Yadav et al. 2021), but more of these studies are needed to

558   address the mechanisms underlying body size variation along macroecological gradients.

559

Acknowledgments

563

Supplementary Data

565   Datasets and R scripts used for both body size and SSD reviewing analysis are available in the

566   Figshare repository at https://doi.org/10.6084/m9.figshare.27118986.v2.

567

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1035

1036 **Figures**

1037 **Figure 1** Sexual size dimorphism (SSD) in spiders. A male (above) and a female (below) Golden

1038 Orb-web spider *Nephila pilipes* mating in the Kaeng Krachan National Park, Thailand.

1039 Photograph by Thai National Parks, distributed under a Creative Commons Attribution 2.0

1040 Generic license.

1041 **Figure 2** Structural body size measurement in the wolf spider *Pardosa furcifera* (Araneae,

1042 Lycosidae). From Ameline *et al.*, (2017). **A**: carapace length and width, **B**: first femur length.

1043 **Figure 3** Non-linear clines as described in (Shelomi 2012). Non-linear clines include *sawtooth*

1044 and *stepwise* clines (**A and B**), which can still show an overall positive or negative cline, *U-*

1045 *shaped* or *hump-shaped* clines, which occur when an increase or decrease is reversed gradually

1046 over a single point in the entire range (**C and D**), while *curvilinear* clines occur when increase or

1047 decrease is reversed gradually over several points across the range.

1048 **Figure 4** Body size variation linked to temperature variation. Adapted from Kingsolver & Huey,

1049 (2008). Red: "*bigger is better*", green: "*hotter is smaller*", blue: "*hotter is better*".

1050 **Figure 5** Intraspecific body size response to elevation and latitude in arthropods. We separately

1051 report studies on spider species along elevational gradients. Only two studies were found in

1052 spiders along latitudinal gradients, we included them in the direct development category. We

1053 distinguished taxa with direct from taxa with indirect development (Schäfer 1976).The number

1054 of species is reported below each barplot. Details of the studies are given in Supplementary

1055 Table 1.

1056 **Figure 6** Correlation between sexual size dimorphism (SSD) and mean body size in spider

1057 species.

1058 **Figure 7** Sexual size dimorphism in non web-building and in web-building spiders.

1059 **Figure 8** Sexual size dimorphism in spider species occupying distinct substrates.

1060 **Figure 9** Sexual size dimorphism projected on the phylogenic tree of spider families.
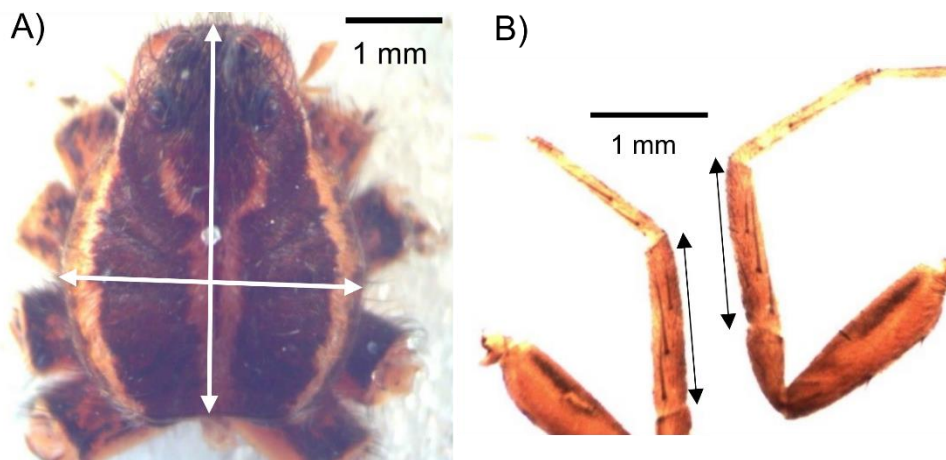
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1065   Figure 1

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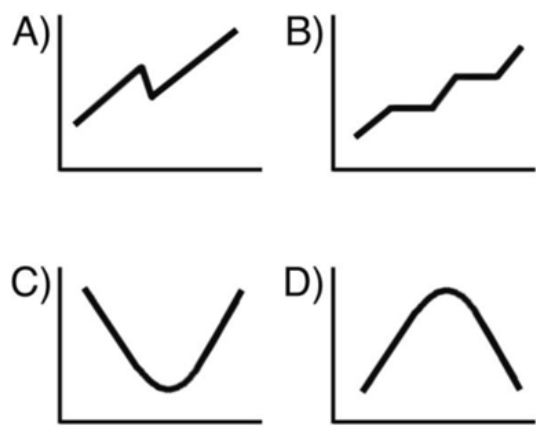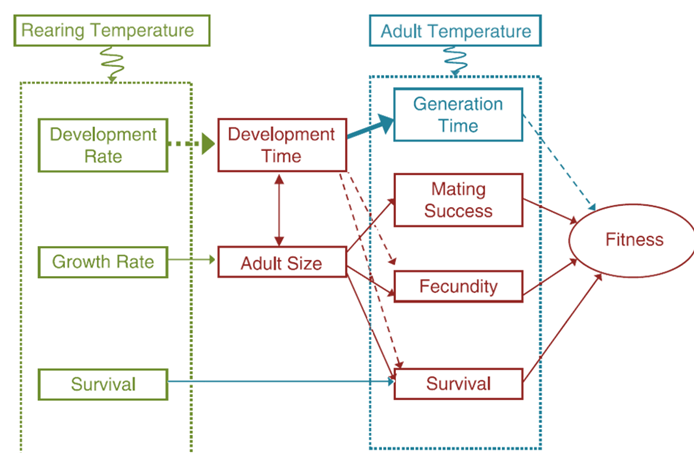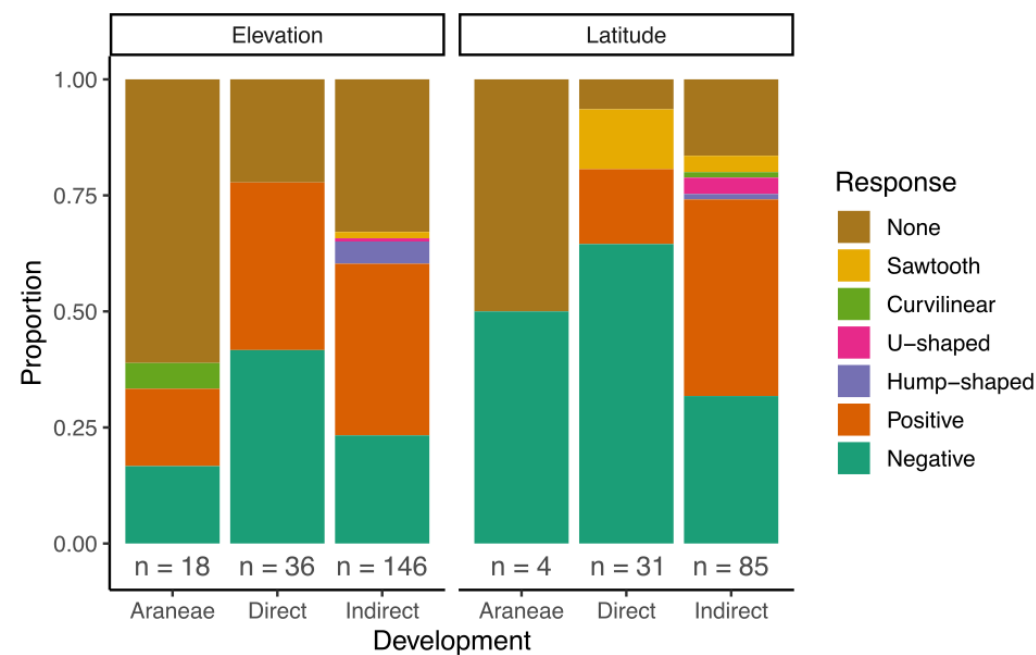1067   Figure 2

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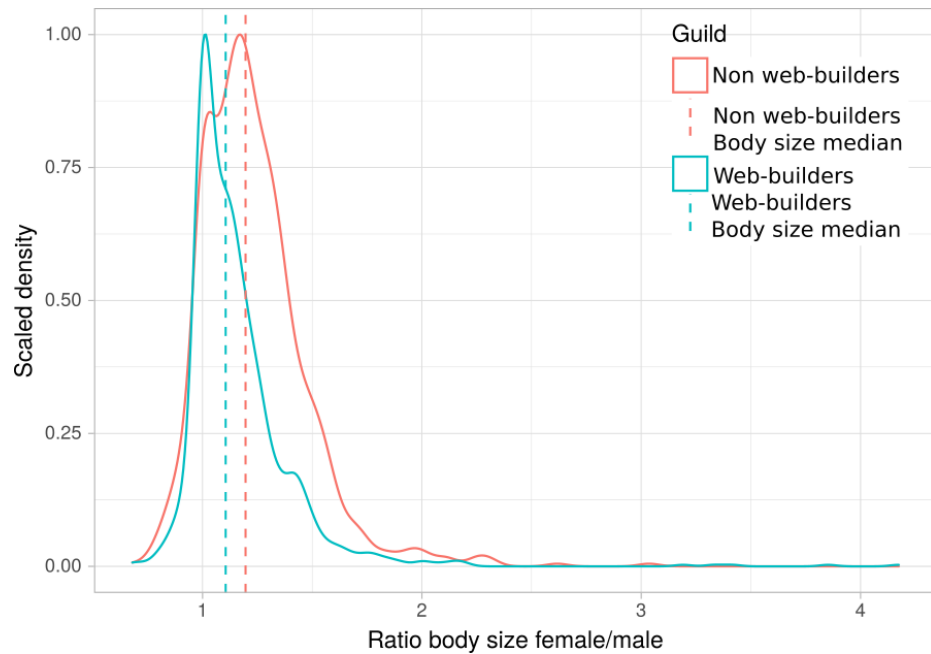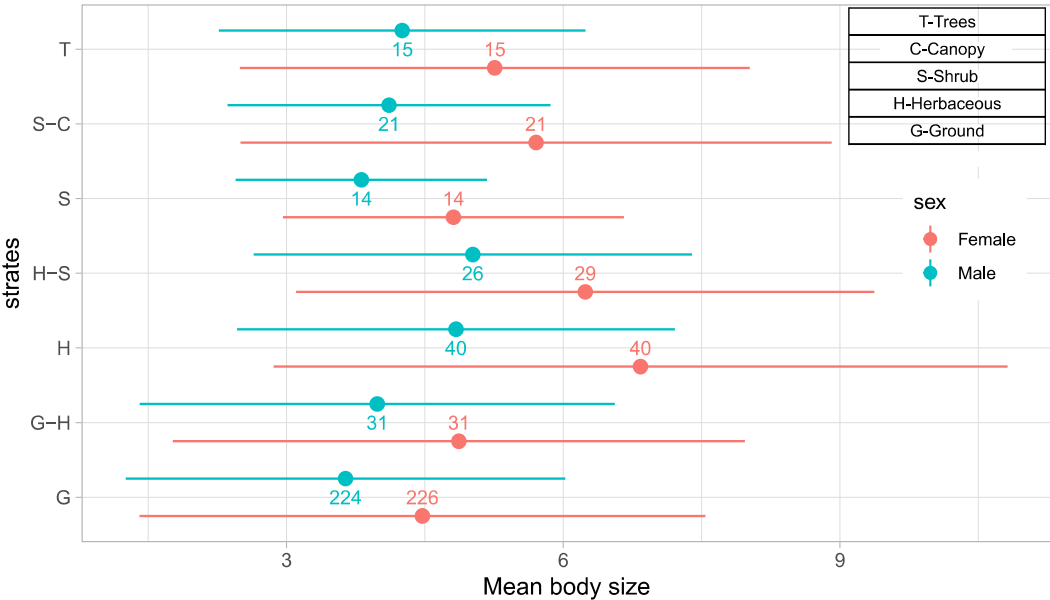1078

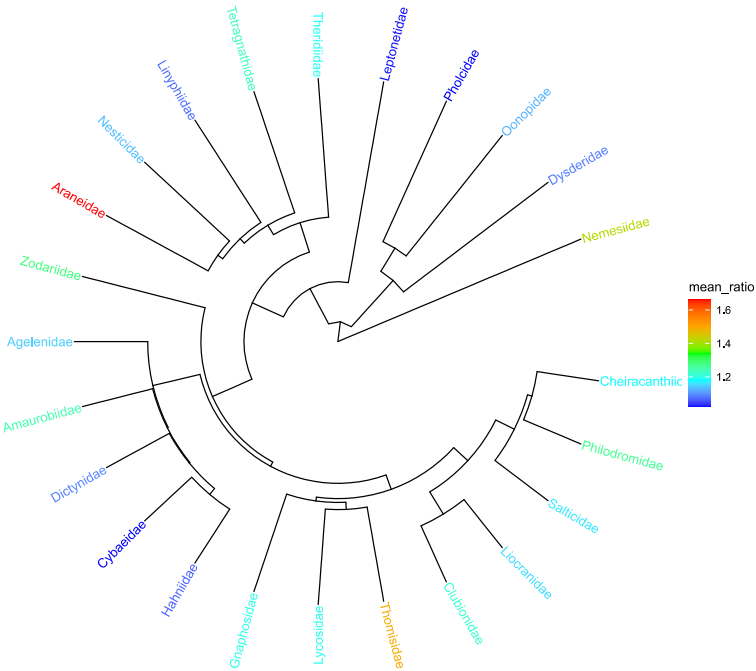1079   Figure 7

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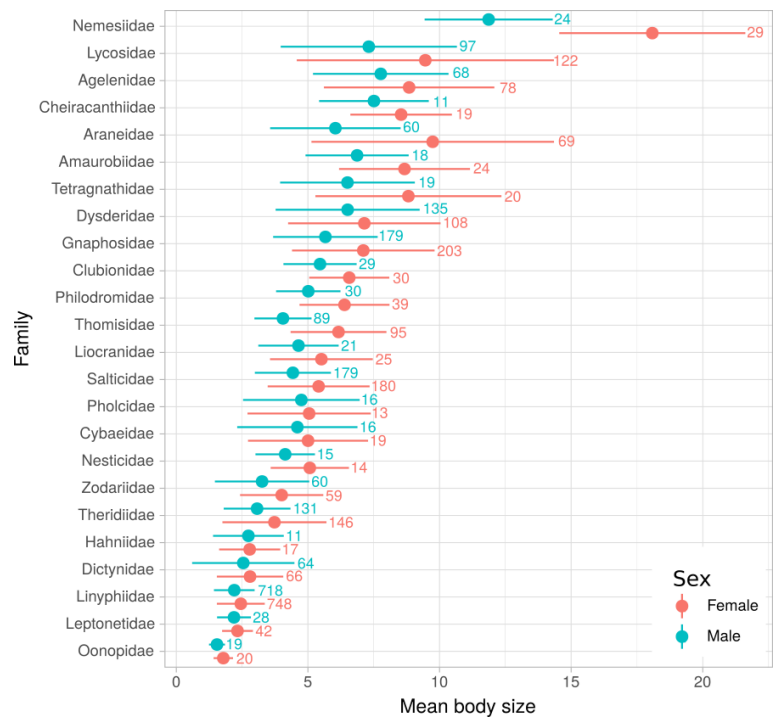
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Figure 9

Tables

1092 **Table 1:** The eight essential dichotomies implied by the study of body size variation in spiders in

1093 ecological and evolutionary research. The choices appear in bold.

Restrictions for this study
Due to prior choices
1. **Ectotherms** vs. endotherms
2. **Intraspecific** vs interspecific variation
3. **Structural body size** vs. condition-dependent body size (see Box1)
Due to lack of studies
4. **Field** vs. experiments
5. **Bergmann's rule** vs. Temperature-Size Rule
6. **Macro** vs. microecological/spatial gradients
Possible comparisons within our field study
7. Direct vs. indirect development
8. Wandering vs. web-building spiders

1094

1095 **Table 2**: Body size variations in response to macroecological gradients in spiders. Response can

1096 be negative (-), positive (+), curvilinear (C), humped-shaped (H), none (N), sawtooth (S) or U-

1097 shaped (U). The full table of body size variation found in all arthropods is given in

1098 Supplementary Table S1 and at https://doi.org/10.6084/m9.figshare.27118986.v2. References:

1099 (Opell et al. 2007, Høye and Hammel 2010, Lee et al. 2012, Bowden et al. 2013, Lowe et al. 2014,

1100 Puzin et al. 2014, Hein et al. 2015, 2018, 2019, Ameline et al. 2018, Dahirel et al. 2019, Mammola

1101 et al. 2019, Beckers et al. 2020, Wolz et al. 2020, Monsimet et al. 2021, Viel et al. 2022, Cabon et

1102 al. 2024).

Gradient	Species	Family	Guild	Measure	Response	Reference
Latitude						
	Amaurobioides maritima	Anyphaenidae	Orb-weaver	Carapace, abdomen lengths	N	Opell 2007
	Argiope bruennichi	Araneidae	Orb-weaver	Total length of patella + tibia of the first right leg	-	Wolz et al. 2020
	Dolomedes fimbriatus	Pisauridae	Non web-building	Prosoma width and length	N	Monsimet et al. 2021
	Pardosa agrestris purbeckensis	Lycosidae	Non web-building	Carapace length	-	Puzin et al. 2014
Elevation						
	Arctosa insignata	Lycosidae	Non web-building		-	Hoye & Hammel 2010
	Pardosa uintana				-	Bowden et al. 2013
	Pardosa glacialis				N	
	Pardosa hyperborea	Lycosidae	Non web-building	Prosoma width	N	Ameline et al. 2018
	Pardosa hyperborea				+	
	Pardosa palustris				+	
	Pardosa palustris				C	Hein et al. 2019

Gradient	Species	Family	Type	Measure	Response	Reference
	Pardosa palustris				+	Hein et al. 2018
	Pardosa palustris				N	Beckers et al. 2020
	Pardosa palustris				N	
	Pardosa amentata				N	
	Pardosa lugubris				N	Hein et al. 2015
	Pardosa hyperborea				N	
	Pardosa riparia				N	
	Pardosa hyperborea				-	
	Pardosa furcifera				N	Viel et al. 2022
	Myro kerguelensis	Toxopidae		Carapace and sternum width	N	Lee et al. 2012
Urbanization	*Waitkera waitakerensis*	Uloboridae	Orb-weaver	Femur I length	N	Opell et al. 2007
	Nephila plumipes	Araneidae	Orb-weaver	Tibia length of leg I	+	Lowe et al. 2014
	Araneus diadematus			Prosoma width	-	Dahirel et al. 2019
	Pardosa prativaga				+ (temp on females)	
	Pardosa pullata	Lycosidae	Non web-building		+ (local temp on females)	
	Pardosa cf. tenuipes			Prosoma width and right leg IV segments length	N	Cabon et al. 2024
	Bathyphantes gracilis				N	
	Diplostyla concolor				N	
	Erigone dentipalpis	Linyphiidae	Orb-weaver		N	
	Oedothorax fuscus				N	
	Oedothorax retusus				N	
	Tenuiphantes tenuis				N	
	Hahnia nava	Hahniidae	Orb-weaver		N	
	Pachygnatha degeeri	Tetragnathidae	Orb-weaver		N	
Quality (climatic, topographical and geomorphological variables)	*Vesubia jugorum*	Lycosidae	Non web-building	Femur, tibia and metatarsus length, and carapace length and width	+	Mammola et al. 2019

1103

1104 **Table 3**: Sexual size dimorphism (SSD) variation along macroecological gradients in arthropods:

1105 D: direct, I: indirect development. References: (Bidau and Martí 2007, Ciplak et al. 2008, Høye et

1106 al. 2009, Høye and Hammel 2010, Bowden et al. 2013, Laiolo et al. 2013, Marshall et al. 2013,

1107 Yadav et al. 2020, Outomuro et al. 2021, Dudaniec et al. 2022, Jarčuška et al. 2023, Papandreou

1108 et al. 2023, Tanaka 2024).

Gradient	Species	Development	Measure	Response	Reference
Latitude					
	Coleoptera				
	Agrilus planipennis	I	Dorsal length and dry mass	Negative for ♀	Marshall et al. 2013
	Odonata				
	Ischnura elegans	I	PCA with total length, wing length, abdomen length, thorax width and S4 width	Positive for ♂, none for ♀	Dudaniec et al. 2021
	Lestes sponsa	I	Head width, wing centroid size	None	Outomouro et al. 2021
	Orthoptera				
	Dichroplus pratensis	D	Total body length	None	Bidau & Marti 2007

	Locusta migratoria	D	Head width, hind femur length, and forewing length	More positive for ♀	Tanaka 2024
Elevation					
	Araneae				
	Pardosa lapponica	D	Carapace width	More negative for ♀	Bowden et al. 2013
	Alopecosa aculeata	D	Carapace width	Positive for ♂, none for ♀	
	Pardosa glacialis	D	Carapace width	Negative for ♀, none for ♂	Høye & Hammel 2010
	Pardosa groenlandica	D	Carapace width	Negative for ♀, none for ♂	
	Lepidoptera				
	Afrasura cf. *numida*	I		Positive for ♂, none for ♀	
	Asythosia velutina	I		More positive for ♂ than ♀	
	Eilema cf. *fletcheri*	I		Positive for ♂, none for ♀	
	Galtara sp. "1"	I	Right forewing length, from the base of the apex	More positive for ♂ than ♀	Papandreou et al. 2023
	Ligulosia costimaculata	I		Negative for ♂, none for ♀	
	Palaeugoa camerunensis	I		More positive for ♂ than ♀	
	Mylantria xanthospila	I		None for ♂, negative for ♀	
	Orthoptera				
	Chorthippus cazurroi	D	Hind femur length	Negative for ♀, none for ♂	Laiolo et al. 2013
	Dichroplus pratensis	D	Total body length	None	Bidau & Marti 2007
	Chorthippus vagans	D	Tegmina length	Negative for ♂, positive for ♀	Ciplak et al. 2008
	Kosciuscola usitatus	D	Femur length	Negative for both	Yadav et al. 2020
	Kosciuscola tristis	D	Femur length	None in ♂, negative in ♀	Yadav et al. 2020
	Kosciuscola cognatus	D	Femur length	Negative in ♂, none in ♀	Yadav et al. 2020
	Pholidoptera griseoaptera	D	Pronotum width, femur length, tibia length and ovipositor length	None	Jarčuška et al. 2023
Temperature					
	Araneae				
Earlier snowmelt	*Pardosa glacialis*	D	Carapace width	More positive for ♀	Høye et al. 2009
	Orthoptera				
Mean annual temperature	*Chorthippus cazurroi*	D	Hind femur length	More positive for ♀	Laiolo et al. 2013
Mean annual temperature	*Chorthippus parallelus*	D	Hind femur length	More positive for ♀	

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