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1   # Evolution of morphological allometry

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23 Abstract

24 Allometry refers to the power-law relationship that often occurs between body parts and total

25 body size. Whether measured during growth (ontogenetic allometry), among individuals at

26 similar developmental stage (static allometry) or among populations or species (evolutionary

27 allometry), allometric relationships are often surprisingly tight, and relatively invariant.

28 Consequently, it has been suggested that allometry could constrain phenotypic evolution, that

29 is, force evolving species along fixed trajectories. Alternatively allometric relationship may

30 result from selection. Despite nearly a century of active research on allometry, distinguishing

31 between these two alternatives remains difficult partly due to the use of a broad sense

32 definition of allometry where the meaning of relative growth was lost. Focusing on the

33 original narrow-sense definition of allometry, we review evidence for and against the

34 "allometry as a constraint" hypothesis. Although the low evolvability of the static allometric

35 slopes observed in some studies suggests a possible constraining effect of this parameter on

36 phenotypic evolution, the nearly complete absence of knowledge about selection on allometry

37 prevents any firm conclusion.

38

39 **Keywords**: adaptation, microevolution, macroevolution, evolutionary constraint

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41   Abstract: 166 words; Main text: 5565 words ; 1 table; 5 figures; 2 boxes

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42   Introduction

43   Allometry is the study of the relationship between body size and other organismal traits.

44   Allometry is important because variation in a wide variety of morphological, physiological

45   and life history traits are highly correlated with organism size [1,2,3]. These relationships

46   generate intuitive hypotheses for understanding trait variation; for example, the fact that

47   humans are larger than mice can be used to explain why the basal metabolic rate of a human

48   is much higher than the basal metabolic rate of a mouse. In most cases, traits show a non-

49   linear relationship with size that is accurately captured by a power relationship of the form $z =$

50   ax^b, where the trait value is z, the organism size is x, and a and b are parameters of the

51   relationship. If $b = 1$, the relationship between the trait and size is linear, a condition referred

52   to as isometry. When $b \neq 1$, the relationship is non-linear on the arithmetic scale. For

53   example, the basal metabolic rate in mammals scales with body mass with a coefficient $b \approx$

54   0.71 [4]; as a result, for every unit increase in mass, a larger organism will have a smaller

55   increase in basal metabolic rate than a smaller organism. Consequently, humans have a basal

56   metabolic rate 5 to 10 times smaller than a mouse when corrected for body size. The ubiquity

57   of these power-law relationships has led biologists to refer to them as allometric relationships.

58   Analyzed on log-transformed data these relationships become linear: $\log(z) = \log(a) +$

59    $b \times \log(x)$, where $\log(a)$ and b represent the allometric intercept and slope, respectively.

60   Because size varies during growth, among individuals of similar age, or among populations or

61   species, three types of allometry have been defined. Ontogenetic allometry refers to the

62   allometric relationship when size varies during growth. Static allometry refers to the

63   relationship when size varies among individuals measured at a similar developmental stage

64   and evolutionary allometry refers to the allometric relationship when size varies among

65   population or species means.

66   Allometric relationships often fit very precisely when the range of sizes is large, which

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67   is usually the case at the ontogenetic and evolutionary levels. Furthermore, ontogenetic and

68   static allometric slopes usually vary little among closely related species. These observations

69   have led several authors to suggest that allometric slopes most likely reflect strong physical,

70   physiological or biological mechanisms that somehow constrain the rate and direction of

71   evolution [5,6,7]. For example, the scaling of metabolism with body size, referred to above,

72   may be explained by the limits of diffusion through the limited surface area per volume of the

73   larger human than the smaller mouse [8]. Accordingly, allometric relationships have been

74   taken as prime evidence against the dominance of natural selection as an evolutionary force

75   [9]. This constraint hypothesis has been widely accepted for physiological and life history

76   traits [10,11], but has become more controversial for morphological traits.

77   The alternative to the constraint hypothesis of allometry is that natural selection

78   persistently favors the particular power relationships between traits and size that are observed.

79   This hypothesis is at least implicitly widely accepted in the traditional studies of functional

80   allometry [2]. For example, the relationship between the cross-sectional area of the skeleton

81   with body mass may be explained in terms of optimal allocation, balancing the chances of

82   breakage – favoring a robust skeleton – with the costs of locomotion – favoring a lighter

83   skeleton. Accordingly, several authors have suggested that allometric slope could evolve

84   under selection [12,13,14,15]. In this context, the evolution of the static allometry of sexually

85   selected traits has been a particularly popular topic. Secondary sexual displays have been

86   predicted to evolve particularly steep slopes (i.e. positive allometry: $b>1$) under handicap

87   models [12,13,16,17,18], while genitalia are expected to show negative allometry ($b < 1$) due

88   to stabilizing selection on trait size [14, 19, 20].

89   Optimally, it should be possible to distinguish between the constraint and selective

90   explanations for allometry by quantifying both the selection forces and the evolvability of

91   allometry (i.e. its capacity to evolve) and compare the predicted and observed patterns of

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92   evolution in allometry. The general prediction is that a constrained slope will either be

93   incapable of evolving (an absolute constraint, [21]), or that fitness will decrease so rapidly

94   when moved away from the optimal value that the possible advantages of the altered slope

95   would not outweigh the fitness costs. Unfortunately, despite renewed interest in allometry in

96   the last two decades, progress in understanding the evolution of morphological allometry has

97   been slow. A key reason for this is the rise of a 'broad sense' definition of allometry as any

98   monotonic relationship between trait size and body size [22, 23] (Box 1). This divorces the

99   study of scaling from the prevalence of power relationships (Box 2), and in particular from

100   the centrality of the slope as the essence of allometry [24]. The result is a body of literature

101   that has measured quantities that cannot be interpreted as parameters of a power relationship.

102   Our aim in the current contribution is therefore to define clear predictions concerning

103   the constraint and selection hypotheses on morphological allometries and review the recent

104   literature in the light of these predictions.

105

Evolutionary constraint and allometry

107   Evolutionary constraints are defined as any processes that preclude a trait from reaching a

108   phenotypic optimum, or slow down its evolution towards this optimum [25]. Depending on

109   the perspective and processes involved, many types of constraint have been defined [25,26].

110   Initially, allometry has been classified as developmental constraint, that is, constraint imposed

111   by the developmental architecture in the production of variant phenotypes [27]. Although

112   developmental constraints may themselves result from selection [28,29], they may still limit

113   the direction of phenotypic evolution. Such perspective of allometry as developmental

114   constraint corresponds to the view defended by early students of allometry and heterochrony

115   [5, 6, 7, 30, 31], who explained patterns of species divergence by changes in timing or rate of

116   development along constant ontogenetic processes.

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117   The introduction of the quantitative genetics framework in the study of allometry [32,

118   33, 34, 35] has shifted the hypothesis of allometry as a constraint from a developmental to a

119   genetic perspective. Genetic constraints occur when the amount or pattern of genetic variation

120   limits or channels the response to selection. Although these two perspectives are intimately

121   linked because genetic constraints often result from developmental constraints, this change in

122   perspective may have weakened the constraint hypothesis, given the ubiquity of genetic

123   variation generally found [36]. But more recently, the hypothesis of constraint due to low

124   genetic variation has been refueled by the realization that genetic correlations among traits

125   due to pleiotropy could seriously influence the direction of phenotypic evolution [21, 37, 38,

126   39, 40 , 41, 42, 43], allometry being a perfect example of such a constraint.

127   Importantly, the quantitative genetics approach of allometry underlines the fact that

128   understanding the evolution of allometry, and testing whether allometry represents an

129   evolutionary constraint requires quantifying the evolvability of allometry and comparing the

130   observed evolutionary patterns with those patterns expected under specific selection

131   pressures. If we are to test the "allometry as a constraint" hypothesis, we should therefore

132   answer the following questions; 1) Is allometry evolvable? 2) Does allometry constrains

133   patterns of phenotypic evolution? Static allometry represents the pivotal level at which these

134   questions should be asked. Indeed, it is the level at which developmental constraints will be

135   expressed, and patterns of static allometry will allow us to make predictions about phenotypic

136   evolution.

137

Is static allometry evolvable?

139   Testing whether a trait is evolvable or not may be achieved by quantifying either its

140   propensity to vary (i.e. its evolvability; [44]), or its evolution, that is, quantifying the changes

141   in the trait when selected. In the following, after considering the possible sources of constraint

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142   and selection acting on static allometry, we review evidence for both the evolution of static

143   allometry at the microevolutionary scale and its evolvability.

144

145   *Sources of constraint*

146   Evolution of static allometry depends on the evolution of the static allometric slopes and

147   intercepts. One key challenge is that an individual organism expresses neither a slope nor an

148   intercept. Therefore, if these parameters represent quantitative traits, estimating their genetic

149   variation requires clonal organisms where genetically similar organisms of different size can

150   be measured, measurement of "allometries" across relatives in family groups, or across

151   modules in modular organisms. Alternatively, because ontogenetic, static and evolutionary

152   allometries of morphological traits all result from a single process, namely growth, testing the

153   evolvability of static allometry could be achieved by estimating the evolvability of the growth

154   processes that generate covariance among traits. Several growth models have been suggested

155   to explain how static allometry is generated from simple growth patterns [5, 16, 31, 45, 46].

156   Using these models one can identify possible constraints on the variation of static allometry.

157   From Huxley's (1932) [5] model of relative growth (Box 1), it can be shown that when

158   two traits present an ontogenetic allometry such as $z = a + bx$, with x and z varying during

159   growth, the static allometric slope at any specific time t can be expressed as:

160

161    $$b_s = \bar{b} + \frac{Cov(x_t, a) + \bar{x}_t Cov(x_t, b)}{Var(x)},$$ (1)

162

163   where $\bar{b}$ is the ontogenetic allometric slope averaged across all individuals, (i.e. the mean

164   ontogenetic allometry of the population), and $\bar{x}_t$, the mean body size at time t [47]. This

165   shows that the static allometric slope is affected by both the average slope of the ontogenetic

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166 allometry and the covariance between the parameters of the ontogenetic allometry (slope and

167 intercept) and body size. Similarly, parameters of the ontogenetic allometry will affect the

168 average value of the trait over the entire range of sizes. This effect can be expressed in terms

169 of the mean trait at the population mean body size, $\overline{x}_t$, in the following way:

170

171 $$\overline{z}_t = \overline{a} + E(bx_t) = \overline{a} + \overline{b}\overline{x}_t + \sigma(b, x_t),\qquad(2)$$

172

173 where $\overline{a}$ is the average ontogenetic intercept across all individuals. Therefore a positive

174 covariance between the ontogenetic slope and body size at stage t will increase the mean

175 value, while a negative covariance will decrease it. This model illustrates how variation in the

176 static allometric slope and intercept can be generated by variation of the ontogenetic

177 parameters. Importantly, it also shows that when ontogenetic and static allometries are

178 different ($Cov(x_t, b) \neq 0$ or $Cov(x_t, a) \neq 0$), invariance of static allometry across populations

179 with different mean body size implies changes in the ontogenetic parameters. Comparing

180 ontogenetic and static allometries and estimating the variation of the ontogenetic parameters

181 should therefore provide valuable insight in the possibility for static allometry to evolve.

182 Different body parts do not always grow simultaneously; some traits grow most

183 rapidly early in development (e.g. mammalian brain, [48]) while others continue to grow after

184 body mass has stopped increasing (e.g. appendages in holometabolous insects, secondary

185 sexual traits in vertebrates [49], and see [50] for the special case of deer antlers). Ontogenetic

186 allometry resulting from this type of growth pattern is necessarily non-linear [e.g. 45, 46], and

187 sometimes the link between ontogenetic and static allometry can be difficult to establish.

188 Nevertheless, even in such cases the overall growth of the trait may be coordinated with the

189 expected body size, despite the difference in the timing of growth. Static allometry could then

190 be interpreted as the reaction norm of a trait to changes in body size which represents the

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191   growth environment (see [16] for such a model). Variation in the allometric slope could then

192   have a component due to variation in the trait sensitivity to the growth state of the whole

193   organism. Lack of genetic variance in trait growth sensitivity to the size of the body or the

194   sharing of a large proportion of the developmental pathway therefore seem the most likely

195   sources of constraint on changes in static allometry. Importantly, such constraints would

196   affect the allometric slope, but not necessarily the intercept.

197

198   *Sources of selection*

199   *Selection on trait and body size* – Change in the allometric slope may occur as a side effect of

200   directional selection on trait or body size. This type of selection probably represents the most

201   common selection in the wild, as demonstrated by variation in size among populations and

202   closely related species. Following the model described above (Eq. 1 and 2), in absence of

203   covariance between body size and the ontogenetic parameters, ontogenetic and static

204   allometry should be similar, and changes in body size should not affect the static allometric

205   slope (Fig. 1; scenario A), except if the ontogenetic allometry is non-linear. If one of the

206   covariance terms between body size and the slope or the intercept of the ontogenetic

207   allometry is different from zero and constant, changes in body size should generate changes in

208   static allometric slope (Fig. 1; scenario D). Finally, changes in the mean trait ($\bar{z}_t$) are

209   expected to affect either the mean ontogenetic intercept ($\bar{a}$, Fig. 1 scenario C), the mean body

210   size ($\bar{x}_t$, Fig. 1 scenario A), the mean ontogenetic slope ($\bar{b}$), the covariance between these

211   last two terms $\sigma(b, x_t)$, or any combination of these parameters. Changes in static allometric

212   slope with increasing body size may also occur if the sensitivity of trait growth to the growth

213   environment is non-linear. In presence of threshold or saturation effects, one can predict that

214   changes in body size may result in changes in the static allometric slope.

215

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216   *Selection on the slope* – Alternatively the static allometric slope can evolve as a result of

217   selection on the slope itself, with no change in $\bar{x}_t$ or $\bar{z}_t$ (Fig. 1, scenario B), which is

218   equivalent to assuming correlated selection on size and the trait. With correlated selection,

219   there will be an adaptive ridge that links the bivariate distribution of the traits to fitness (Fig.

220   2A). We can completely separate selection on the allometric slope from selection on trait

221   means by imagining an adaptive landscape that selects on trait (co)variances but not on trait

222   mean (i.e. no directional selection). We generally expect that trait means will evolve more

223   rapidly than trait variation, so when a change in selection regime affects both means and

224   (co)variances, we will rapidly approach the situation where only the (co)variances continue to

225   be selected. A simple example of such changes would be selection for a decrease in trait

226   variance combined with either an increase or constant variance in body size, which would

227   decrease the allometric slope. Selection for increasing variance in trait size combined with a

228   decreasing variance in body size should generate an increase in the allometric slope. Figure

229   2B shows a case of disruptive selection favoring extreme combinations of trait and body size

230   over those near the means. This type of selection maximizes selection on variances and

231   covariances, and therefore should lead to the maximum rate of response in the allometric

232   slope. Strong disruptive selection balanced precisely to lead to no directional selection is

233   probably an extremely rare event in nature, however. In theory, the presence of a selective

234   ridge should be sufficient to favor a particular slope in the absence of disruptive selection, but

235   the strength of selection on the slope will be quite weak, because many individuals the center

236   of the distribution (i.e. with non-informative genotype) will be selected (Compare Fig. 2A and

237   B).

238   Verbal models of selection on allometric slope have been proposed to explain the

239   positive allometry often observed in sexually selected traits [12,13, 17, 18, 51]. In these

240   models, positive allometry evolves either because large males, presumably in better condition,

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241   are able to invest more in costly traits, or because the benefits of large traits increased with

242   body size. By applying various selection regimes on an allocation model of growth,

243   Bonduriansky and Day (2003) [16] showed that the conditions under which positive allometry

244   evolved were more restrictive than previously thought, but that an increase in the relative

245   fitness gain for larger traits with an increase in body size should select for positive allometry.

246   Canalizing selection on trait size, on the other hand, has also been suggested to affect static

247   allometry by generating negative allometries as for example for male copulatory organs in

248   insects [14, 19].

249   The variational properties that generate variance and covariance among traits are

250   pivotal to the evolution of static allometry. Although selection experiments have suggested

251   that variation may respond to selection [52] it remains unclear how efficiently selection can

252   mold genetic and environmental variation [53, 54, 55, 56]. The evolution of covariance

253   between trait size and body size directly links the evolution of the static allometric slope with

254   the evolution of the phenotypic and genetic covariance matrices (**P** and **G** on log scale). Much

255   theoretical and empirical work shows that genetic covariances do evolve [54, 57, 58, 59, 60],

256   but it remains unclear what forces drive these changes, and how rapidly they can take place.

257   The various hypotheses listed here suggest that, in many cases, selection on the allometric

258   slope is rather weak and indirect. If combined with a low evolvability, this may result in slow

259   evolutionary change in allometry.

260

261   *Evolvability and evolution in static allometry*

262   Because changes in ontogenetic allometry are expected to provoke changes in static allometry

263   (Eq. 1), we first consider here evidence for the evolution of ontogenetic allometry. Such

264   evidence is provided by several studies comparing ontogenetic allometries among species

265   [e.g. 61, 62, 63, 64]. However, few studies have tested the relationship between ontogenetic

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266 and static allometry [34, 65, 66, 67, 68], and fewer have analyzed how variation in the

267 parameters of ontogenetic allometry affected static allometry. The only study, to our

268 knowledge, that compared the relationship between ontogenetic and static allometry among

269 populations [47], showed that static allometry between caudal fin length and body length in

270 female Guppies (*Poecilia reticulata*) was stepper than the ontogenetic allometry, but was

271 similar among three populations with different adult female length. This was achieved, among

272 other things, by differences in the average ontogenetic allometric slope among populations.

273 The relevance of these results regarding the rate at which ontogenetic allometry evolve is

274 unclear, however, because guppy populations from different drainages may have been

275 separated for hundred thousands of generations [69]. Furthermore, although individual

276 variation in ontogenetic allometry has been observed [47], the genetic basis of this variation

277 remains unknown, and overall we found only one study that reported heritability of

278 ontogenetic slopes of chest circumference ($h^2 = 0.25 \pm 0.07$) and tail length ($h^2 = 0.39 \pm 0.08$)

279 on body weight within six laboratory strains of rats selected for larger or smaller weight [70].

280   Microevolutionary changes in phenotypic covariances among traits are suggested by

281 studies reporting rapid changes in the **G-** or **P-** matrices within populations [71, 72, 73]. These

282 observations are difficult to interpret in terms of evolution of allometry, however, because

283 traits are not always strongly correlated in the first place and **G**-matrices are rarely analyzed

284 on log scale. Furthermore, studies analyzing changes in the **P**-matrix cannot distinguish

285 between environmental and genetic changes in the patterns of covariation among traits.

286   Estimates of genetic variance in static allometric slopes are scarce, and we found only

287 one study reporting heritabilities of allometric slopes measured on log scale [74]. In this

288 study, heritabilities of the static allometric slope between the length of several bones and the

289 cubic root of body weight, and between the weight of internal organs and body weight were

290 all statistically significant but relatively small (all $h^2 < 0.13$) despite being measured in the lab.

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291   Alternatively, artificial selection can be used to uncover genetic variation and

292   covariation in quantitative traits [75]. During the last two decades, several authors have

293   claimed to have altered patterns of static allometry by artificial selection. In addition, a few

294   artificial selection studies on size have shown changes in the covariance patterns between the

295   size of some traits and body size. Unfortunately, most of these studies have adopted the

296   broad-sense definition of allometry, seriously hampering our ability to interpret their results in

297   terms of the evolution of allometry [23]. For example, in a study on a stalk-eyed fly

298   (*Cyrtodiopsis dalmanni*), selection exerted on the ratio between eye span and body length

299   significantly affected the covariance between the two traits when measured on arithmetic

300   scale [76]. Reanalysis of the regression line on the log scale shows that changes in the

301   allometric slope are still present but much weaker than those reported in the original study

302   (Table 1). A similar selection procedure was used in two experiments on the butterfly

303   *Bicyclus anynana* [77, 78]. In both experiments, the intercepts of the relationships on

304   arithmetic scale were strongly affected by selection, but the slopes were apparently not,

305   although no formal tests of change in slope were reported. What were the consequences of the

306   selection on the allometric slope remains unknown.

307   The only artificial selection experiment on narrow-sense allometry conducted so far

308   combined stabilizing and disruptive selection on body area and caudal fin area to select for a

309   change in static allometric slope (procedure similar as the one described in Fig. 2B; [79].

310   Selection to increase and decrease the intercept was also applied on two separate lines.

311   Results suggested that the allometric slopes had very little capacity to vary compared to the

312   allometric intercepts. This conclusion, however, was weakened by the small number of

313   generations of selection.

314   Two studies investigating the effects of artificial selection on body size on correlated

315   traits provide some evidence for rapid change in static allometric slope. In a selection

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316   experiment to increase or decrease body mass in the moth *Manduca sexta*, static allometry

317   between wing mass and body mass became steeper in the line selected for smaller body mass

318   and shallower in the line selected for larger body mass after 10 generations of selection ([80];

319   and see [23] for reanalysis using standard regression). Similarly, estimation of the static

320   allometric slopes in the different lines of a selection experiment to increase body size in

321   *Drosophila melanogaster* [81] reveals that allometries between wing length and thorax length

322   or between wing length and tibia length increased in the line selected for smaller thorax

323   length, and decreased in the line selected for larger thorax length (Table 1). Additionally,

324   Cayetano et al. (2011) [82] while relaxing sexual selection for ca. 21 generations in the seed

325   beetle *Callosobruchus maculatus* observed a change in the allometry between two traits of the

326   genital apparatus in males and elytron length. The reanalysis of the data from this last

327   experiment showed, however, a very poor fit of the traits with the allometric model and casted

328   doubt on the validity of the interpretation of the results [23].

329   One factor that has not been considered in these experiments, however, is the

330   possibility of plasticity in the allometric slope. Plasticity in allometric relationships has been

331   little studied, but one study clearly shows that static allometry varies in response to different

332   environmental treatments [83]. Similarly, a selection experiment on *Drosophila* wings in

333   which selection was performed on the relative position of some veins [55, 84, 85] shows

334   erratic but sometimes statistically significant variation in static allometry (Fig. 3). The

335   differences in slope apparent in Figure 3, could, if observed in isolation, be misinterpreted as

336   change in allometry due to selection. To avoid such problem we strongly recommend

337   following the changes in allometry from generation to generation, and experiments that fail to

338   do so should be interpreted with caution.

339   The dissection of the insulin/IGF signaling pathway that controls trait size in animals

340   provides a nice illustration of how the growth of specific traits responds to changes in the

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341   growth environment, that is, changes in body size [86, 87]. Interestingly, recent experiments

342   have uncovered mutations at specific loci that could affect the organ sensitivity to variation in

343   the growth environment and therefore affect the slope of the static allometry [74, 88].

344   Although these studies provide clear evidence for genetic variation in allometric slope, they

345   also suggest that this variation results from complex genetic architecture [74] that may not

346   easily respond to selection.

347   Neither inter-population variation nor quantitative genetics experiments provide

348   conclusive evidence for genetic variation in the allometric slope. For the intercept,

349   quantitative genetic studies provide clear evidence for high evolvability.

350

351   Does static allometry constrain phenotypic evolution?

352

353   *Theoretical considerations*

354   Micro-evolutionary studies reviewed in the last section suggest that the evolvability of the

355   allometric slope is low relative to the evolvability of the intercept. At the macro-evolutionary

356   level, reviews on allometry of secondary sexual characters clearly show that allometry of

357   homologous traits can vary among sexes from the same species or among species [89, 90].

358   Such information is by itself, not very informative about the constraint hypothesis because we

359   do not know anything about the strength of selection on the allometric relationships, and the

360   time scale for divergence can be very long. Therefore, it remains unclear whether there are

361   meaningful evolutionary constraints due to allometry.

362   In the absence of empirical knowledge regarding selection on allometry, we are left

363   with the option of generating predictions based on scenarios where static allometry constrains

364   phenotypic evolution under various hypothetical selection regimes. In this context, a general

365   prediction is that, if static allometric parameters represent evolutionary constraints they

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366 should strongly shape patterns of populations and species divergence. This was initially

367 suggested by Gould [6, 7] and placed in a quantitative genetic framework by Lande [32, 33]

368 who showed that, under constant patterns of covariance between traits (constant **G**-matrix),

369 selection acting only on the body size (x), will generate a correlated response on the trait size

370 (z). In this case, the evolutionary allometric slope (b_e) along which populations and species

371 evolve, will correspond to the ratio of the correlated response in z divided by the direct

372 response in x, that is, the slope of the genetic regression between the two traits: $b_s = \sigma_A(x,z)$

373 $/\sigma_A^2(x)$, where $\sigma_A^2(x)$ and $\sigma_A(x,z)$ are the additive genetic variance in x and the covariance

374 between x and z, respectively (Fig. 4 scenario A).

375 Because static allometry is defined at the phenotypic level, the static allometric slope

376 (b_s) combines both additive genetic and residual variances and covariances: $b_s =$

377 $[\sigma_A(x,z) + \sigma_R(x,z)] / [\sigma_A^2(x) + \sigma_R^2(x)]$, where R denotes all other residual components of the

378 variance, including environmental and non-additive genetic variance. Static and evolutionary

379 regression coefficients, b_s and b_e, will be similar when the relative contributions of the

380 residual variance and covariance are similar to the relative contributions of their additive

381 genetic counterparts. In this case, the genetic and phenotypic variance-covariance matrices, **G**

382 and **P**, will be proportional for these elements. If this condition is not fulfilled, evolutionary

383 allometry will not follow the trajectory defined by the static allometry, contrary to previous

384 claims by Gould [91] and others (Fig. 4 scenarios B and C; [33]). Furthermore, if the additive

385 genetic and residual contributions to static allometry are different but remain constant, the

386 static allometric slope should remain constant across populations and species while the

387 intercept will change with changing mean size (Fig. 4 scenario B and C).

388 It is important to realize that when Lande's model [33] is generalized to allow

389 selection on the trait and both size, and there is at least some additive genetic variation in

390 both, the means obtained in the long term depend only on the selective optima for size and the

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391   trait, and not at all on the patterns of covariance among them [35]. If this is the case, and if

392   selective optima are spread more or less randomly in the bivariate morphospace, we would

393   expect no relationship between evolutionary and static allometry (Fig. 4 Scenario C and D).

394   Scenario C represents a situation where the slope is an absolute constraint but the trait and

395   body size means can evolve more or less freely in the morphospace (Fig. 4 Scenario C). This

396   provides the other major explanation for evolutionary allometry: it is not the pattern of genetic

397   variation, but the pattern of natural and sexual selection that dictates allometry.

398   These considerations underline the problem we have of testing the allometry as a

399   constraint hypothesis without knowing the selection patterns acting on allometric

400   relationships, and in most cases, only speculative interpretation of the macro-evolutionary

401   patterns can be achieved. Although specific predictions have been suggested regarding the

402   effect of selection on allometric slope for genitals and secondary sexual characters, these

403   predictions only concerned the type of allometry expected (positive or negative allometry),

404   but not the strength of selection. Furthermore, in the case of secondary sexual characters, it has

405   been shown that positive allometry was only expected under specific selection pressures [16],

406   and a later review [89] confirmed that static allometric slopes in this type of character was

407   not necessarily larger than one.

408

409   *Empirical patterns*

410   Although many studies have compared relationships between trait size and body size among

411   populations and species, Voje et al. [23] identified only 10 studies that allowed estimation of

412   the variation in static allometric slope and intercept (studies on log scale with sufficient

413   information about the allometric parameters). Excluding genital traits, their analysis revealed

414   inter-specific variation in static allometric slope within genera (median standard deviation

415   corrected for sampling error: SD = 0.27). Within species, the static allometric slope varies

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416   among populations but this variation is more limited (median SD = 0.07). For the allometric

417   intercept, patterns of variation were similar with higher variation among species (median SD

418   = 0.15) than among populations (median SD = 0.02).

419   Because the slope and intercept are on different scales, their level of variation is not

420   directly comparable. Using the concept of conditional variance [39, 41], Voje et al. [23]

421   estimated the influence of changes in size or in allometric slope and intercept in the evolution

422   of trait size. This method allowed them to compare variation in slope and intercept on a

423   common scale (variance in trait size). At the interspecific level, 74% of the variation in trait

424   size was associated with changes in species mean size. The contribution of the changes in

425   static allometric slope or intercept were more limited (13% and 29% of the log trait variance

426   explained, respectively, e.g. Fig. 5A). The contributions of these three parameters to trait

427   diversification at the among-population level were similar, with size variation explaining

428   71%, slope explaining 36%, and intercept variation explaining 40%. However, as previously

429   mentioned, much less variation in static allometry was observed among populations, and the

430   evolutionary allometry was often very similar to the pattern of static allometry (Fig. 5B).

431   Finally, Voje et al. [23] showed that within species, the average static allometry across

432   populations was a good predictor of the evolutionary allometry, while across species within

433   genera the average static allometry was poorly correlated with the evolutionary allometry.

434   These results are compatible with the "allometry as a constraint" hypothesis if

435   selective optima were spread more or less randomly in the bivariate morphospace. Indeed,

436   morphological evolution more constrained along static allometric trajectories at the within-

437   species level than at the among-species level could be interpreted as signature of evolutionary

438   constraint.

439   In an attempt to estimate the rate of morphological evolution towards a predicted

440   optimum, Voje and Hansen [92] reanalyzed data on the evolution of the static allometry

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441   between eye-span and body length in various species of stalk-eyed fly (Diopsidae). Using

442   sexual size dimorphism as a measure of the strength of sexual selection in order to estimate

443   optima, they showed that the static allometric slope in male trait was tracking these optima,

444   but this took millions of years to accomplish.

445

446   *The "one size fits all" hypothesis*

447   The various studies analyzing static allometry of genital traits in arthropods and vertebrates

448   showed consistently shallow static allometric slopes ($\beta<1$) for these traits, as expected from

449   the "one size fits all" hypothesis [14, 19]. Eberhardt [19] reported few exceptions to this

450   pattern. However, all these exceptions came from studies where static allometry was

451   estimated using major axis regression, a method that will over-estimate the slope for

452   relationships with low r^2. Accordingly, for all exceptions reported, the relationship between

453   the genitalia and the measure of body size was poor (range r^2: 0.0 – 0.58). In all cases where

454   data were reanalyzed using standard regression methods, genital traits showed negative ($b<1$)

455   static allometry [23, 93].

456   The "one size fits all" hypothesis has also been extended for reproductive organs in

457   flowering plants with insect pollination, where the fit between pollen donor and pollen

458   receiver organs and pollinators of relatively constant size and behavior is expected to produce

459   stabilizing selection [94]. Several studies have provided clear evidence for the relative

460   invariance of floral traits compared to vegetative traits [95, 96] and the two studies that have

461   tested the effect of pollination accuracy on the allometry of the pollen transport organs both

462   reported shallow allometry for these traits [97, 98].

463   If results from studies on the "one size fits all" hypothesis provide clear evidence of a

464   possible effect of selection on static allometry, they do not provide evidence for high

465   evolvability of the allometric slope. Indeed, intraspecific comparison of static allometry in

-19-

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466 insect genitalia show that variation in the allometric slope explains only a small proportion of

467 the variation in genitalia size, 92% of the variance of log-size genitalia being independent of

468 the variation in allometric slope [23]. This is particularly clear when observing the allometric

469 slope between genitalia size and body size in various populations of the beetle species *Dorcus*

470 *titanus* (Fig 5C).

471

472 ## Conclusions

473

474 Despite the huge interest morphological allometry has focused among evolutionary biologists

475 for nearly a century, we are left with a limited understanding of its evolution. Key

476 observations such as genetic variation in ontogenetic allometry or in the static allometric

477 slope are surprisingly scarce. Although micro- and macroevolutionary patterns seem to point

478 at a constraining effect of morphological allometry on phenotypic evolution, the complete

479 lack of data on the nature of direct or indirect selection on allometry, and the near absence of

480 data on genetic variation in allometric parameters precludes the interpretation of these

481 patterns as evidence for or against the constraint and adaptation hypotheses. Until such data

482 are obtained the evolution of allometry will remain a mystery.

483

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487

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762   Table 1: Changes in arithmetic slope and allometric slope (log scale) in two artificial selection experiments. In the experiment on the stalk-eyed

763   fly (*Cyrtodiopsis dalmanni*) [76] selection was exerted for 13 generations to change the ratio between eye-span and body length. We estimated

764   the slope on the arithmetic scale from Fig. 3 in the original paper by estimating the values of the extreme points of the regression lines. These

765   data were subsequently log-transformed to obtain the allometric slopes. In the experiment on *Drosophila* [81], selection to increase or decrease

766   thorax length was conducted for 23 generations. Estimates of the allometric slopes were obtained from the variance and covariance parameters

767   scaled by the trait mean (male and female combined). Standard errors of the estimates are not available.

768

Species	Trait	Body size	Sex	Line	Arithmetic slope	Allometric slope
Cyrtodiopsis dalmanni	Eye-span	Body length	♀ rep1	Down	0.71	0.87
				Up	1.00	1.10
			♂ rep 1	Down	1.37	1.19
				Up	1.73	1.38
			♀ rep2	Down	0.56	0.68
				Up	0.66	0.74
			♂ rep 2	Down	1.10	0.98
				Up	1.43	1.10
Drosophila melanogaster	Wing length	Thorax length	♀+♂	large	0.49	0.30
			♀+♂	Small	0.68	0.38
			♀+♂	Control	0.42	0.24
	Tibia length	Thorax length	♀+♂	large	0.39	0.58
			♀+♂	Small	0.65	0.93
			♀+♂	Control	0.40	0.60

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770   Figure 1.   Evolution of static allometry. The scenarios considered here correspond to the

771   expected evolution of static allometry from an ancestral state depending on the constraining

772   parameter (i.e. the parameter that is not evolvable). Vertical and horizontal dash lines

773   represent the mean trait value and body size. Body size is mean centered, so the allometric

774   intercept represent the trait value at the population mean (i.e. elevation of the allometric

775   regression). In the scenario A, both the slope and the intercept are constraining parameters.

776   Any change in body size will generate a change in trait size and vice versa. In the scenario B,

777   only the allometric slope changes while the intercept (elevation) does not change. In the

778   scenario C, the slope is the constraining parameter while the intercept can change. In the

779   scenario D, slope and intercept can evolve. This pattern may be also generated by the effect of

780   a negative covariance between body size and the ontogenetic slope when selection on body

781   size occurs (see Eq. 1).

782

783   Figure 2.   Selection to change allometric slope via correlated selection on the trait and

784   body size. A) Selection is generated by the difference in the direction of the phenotypic

785   regression and the adaptive ridge. Black dots represent individuals and the blue dots represent

786   the selected individuals (with the highest fitness). B) Saddle fitness landscape that generates

787   disruptive selection on one of the two traits. This selection regime is more efficient to change

788   the slope because individuals in the middle of the distribution are not selected.

789

790   Figure 3.   Phenotypic plasticity in static allometry. The figure presents the variation in the

791   slope of the static allometry between wing size (estimated by the centroid size) and the inter-

792   landmark distance 2 - 12 (see diagram for landmarks number) in two populations of *D.*

793   *melanogaster* selected to increase (grey arrows) or decrease (back arrows) a selection index.

794   Selection was performed for 26 generations. Idiosyncratic variation of the slope (estimated on

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795   100 males at each generation) generates statistically significant differences between selection

796   lines at generation 4, 9 and 11. The data presented here correspond to the LHM 1 replicate,

797   but similar results were observed for the other three replicates, LHM 2 and IV 1 and 2 (see

798   [55] for more detail).

799

800   Figure 4.   Static allometry as an evolutionary constraint. The various scenarios represent

801   the effect of constraining parameters of the static allometry on the evolutionary allometry,

802   assuming that selective optima are spread more or less randomly in the bivariate

803   morphospace. In scenario A, neither the slope nor the intercept vary. The divergence of

804   population means follow the genetic allometric regression (see text). If the slopes of the

805   genetic and phenotypic allometry are similar, evolutionary allometry will follow the patterns

806   of static allometry. In scenario B, the intercept is allowed to change but not the slope.

807   Although such a pattern may result from the evolution of the intercept itself, it may also result

808   from the difference between the phenotypic and genetic allometry (see text). Scenario C

809   presents a similar pattern but where selection does not favor any particular direction in the

810   morphospace. In scenario D, both intercept and slope can evolve (no constraint).

811

812   Figure 5.   Example of variation in static allometric and effect on evolutionary allometry

813   A) among population within species B) among species within genus C) among species

814   genitals (Figure from [23] Voje et al. 2014).

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817   **Box 1 – Narrow sense and broad sense allometry: conceptual and methodological issues**

818

819   In the recent years, the term allometry has been used for any type of monotonic relationships

820   between two morphological variables, independently of the scale on which these variables

821   were expressed. This broad definition of allometry is inconsistent with the biological

822   interpretation of morphological allometry originally suggested by Huxley [5, 99]. Huxley [5]

823   showed that if an arbitrary trait Z and body size X, grow at different rate but under the control

824   of a common growth parameter G, such that $dX/dt = \alpha XG$, and $dZ/dt = \beta ZG$, where α and β

825   are specific constants for X and Y, respectively, and t the time during growth, the relationship

826   between Z and X follows a power law $Z = AX^{\beta/\alpha}$, where A is a constant that depends on the

827   initial values of Z and X. On a log scale, this relationship is linear $z = a + bx$, where $z =$

828    $\log(Z)$, $x = \log(X)$, $a = \log(A)$. Savageau [100] generalized this model and showed that

829   whenever two or more variables are connected in a dynamic synergistic system controlled by

830   one variable, their relationship follows an allometric relationship. Therefore, allometry, in its

831   narrow sense is defined by two parameters of a power relation that can be expressed as the

832   intercept a and the slope b of a linear regression on log scale. When the explanatory variable

833   (x) is mean centered, the intercept, a, becomes the elevation of the static allometry, that is, the

834   trait size at the population mean body size [101, 102, 103].

835   Which statistical model should be used to estimate these parameters has been the

836   subject of long debates. First, it has been suggested that the best estimation of these

837   parameters should be done from a power relationship fitted on arithmetic scale [104, 105].

838   This approach would be justified if the processes producing the error would act in an additive

839   manner. Although this may be the case for measurement error, it is most likely that the

840   biological error will be generated by multiplicative processes similar to those responsible for

841   the growth of the trait [106]. Because most of the error on the response variable is likely to be

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842   of biological origin, estimates produced by linear regression on log scale should be better than

843   those produced by a power model fitted on arithmetic scale. Both approaches are valid,

844   however, and should ideally be conducted with proper modeling of both biological and

845   measurement error.

846   It has been repeatedly suggested that major-axis or reduced major-axis regression

847   should be used in place of ordinary least-squares regression to estimate allometric parameters

848   in order to account for the effect of observational error in the predictor variables. However,

849   neither of these models provides sensible estimates of allometric regression slopes when there

850   is biological 'error' (i.e. biological deviations from the allometric line) in the model [107,

851   108]. These models provide estimates of slopes, but these slopes are not proper estimates of

852   the exponent b in the narrow-sense allometric relation. A dramatic consequence of the

853   reduced major-axis regression is that, even in absence of covariance between the two traits, an

854   "allometric" slope can be estimated and its statistical significance tested [e.g. 82].

855   Finally, we notice that ignoring the consequences of trait dimension on the allometric

856   slope has led to some erroneous statements in the recent study of allometry. For example, a

857   positive allometry between testes size and body length has been reported in Hottentot golden

858   mole (*Amblysomus hottentotus*) as an exception to the "one size fits all" hypothesis [109].

859   However, this positive allometry is most likely generated by the difference in dimension

860   between the traits (body length – length vs. testes mass - volume).

861

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863   **Box 2: From bivariate to multivariate allometry: drifting away from the Huxley's model**

864

865   Jolicoeur [110] suggested analyzing multivariate relative growth using the first principal

866   component (or eigenvector) of the variance-covariance matrix of log-scaled trait values

867   (herein PC1). He showed the relation between this approach and the Huxley model [5]

868   arguing that the trait's loadings on PC1 are equivalent to their allometric exponents. This

869   approach formalized multivariate isometric variation as a PC1 vector with all elements or

870   loadings equal to $1/\sqrt{k}$, where k is the number of traits measured. Variation along such a

871    $\{1/\sqrt{k}, \ldots, 1/\sqrt{k}\}$ vector is associated to variation in organism size while its proportions

872   remain constant. Group difference in multivariate allometry is commonly estimated as the

873   angle between two within-group PC1 in the multivariate space [67]. This approach has been

874   used to describe the plasticity of static multivariate allometry of *Drosophila* exposed to

875   different environmental conditions [83], or to investigate the evolutionary diversity among

876   species [111, 112].

877   However, the biological meaning of the PC1 loadings in this approach is not

878   equivalent to the one of the standard regression estimates (i.e. Huxley's allometric exponent).

879   Instead, these estimates are the slopes of the standard regressions of trait variables on size, as

880   defined by PC1. Importantly, the ratios of the loadings do not correspond to the "variables'

881   bivariate allometric coefficient" [67], at least not if they are properly estimated with a

882   standard regression (Box 1), but these correspond to the ratio of their respective covariances

883   with PC1. This can be interpreted as the relative change in the two traits for a given change

884   along PC1. However, the orientation of the PC1 vector in the morphospace can vary with an

885   increase in trait(s) variance even if covariances are kept constant.

886   This raises the problem of the use of an adequate definition of size in the study of its

887   relation with shape (see [113] for review). The two most commonly used approaches for
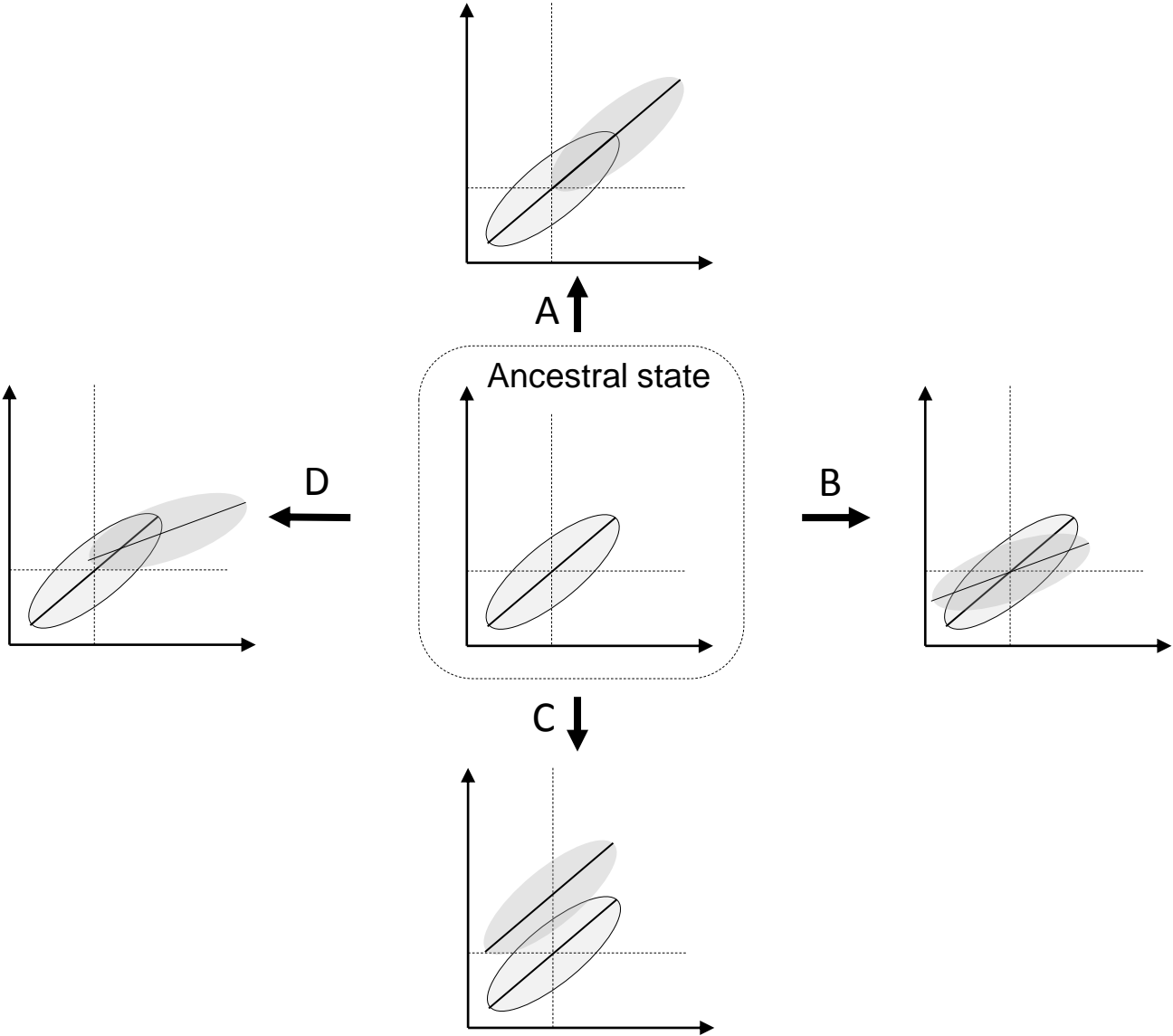
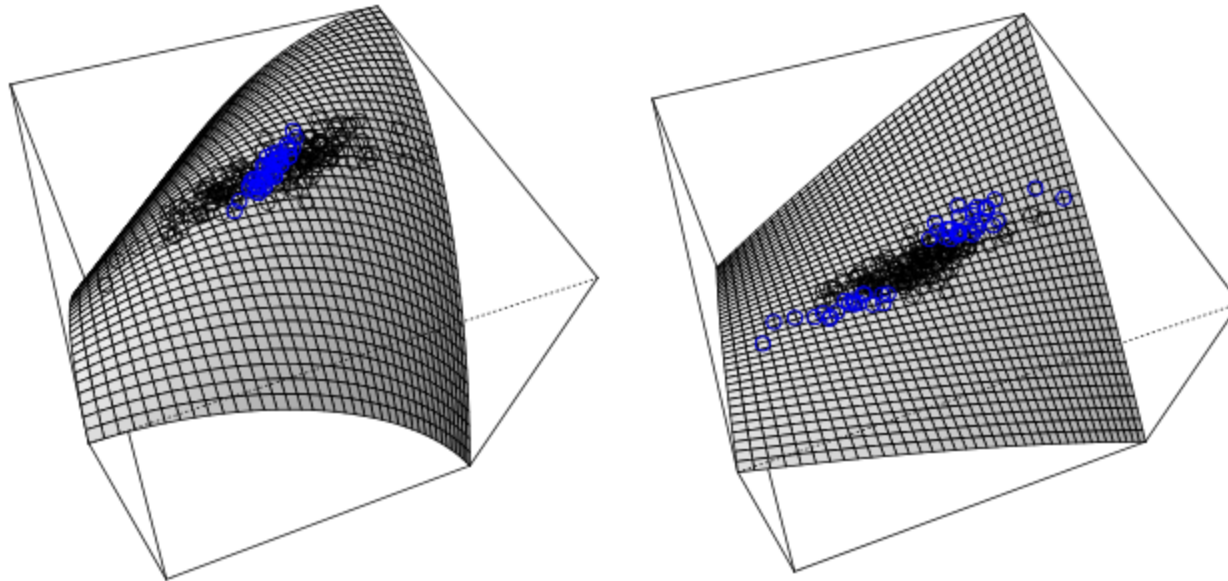Pélabon et al.   The evolvability of allometry

888   estimating size are the PC1-as-size approach described above and Mosimann's [114]

889   definition. Mosimann [114] defined size as any function G of the measurement vector $\mathbf{x}$ that

890   satisfies the property: $G(a\mathbf{x})=aG(\mathbf{x})$, $G(\mathbf{x})$ having the same dimension than any element of $\mathbf{x}$.

891   Indeed, shape being on a ratio scale, multiplication of each element of the ratios by a constant

892   a does not change shape and G is uncorrelated with any ratios under fully isometric

893   multivariate variation. It is worth noticing that Huxley [5] already defined traits' growth rate

894   as affected by a common growth factor ("G") that vanishes when the growth rates of the traits

895   are put in relation in the exponential relationship.

896   Contrary to the PC1 approach, this geometric definition of size is not directly

897   dependent of the variance-covariance properties of the studied samples. As a measure of size,

898   geometric morphometrics conventionally use centroid size (CS), the square root of the sum of

899   squared distances of a set of landmarks from the centroid of the entire landmarks

900   configuration. Although this choice does not generally rely on biological arguments, centroid

901   size corresponds to a size vector according to Mosimann's definition. The Procrustes

902   superimposition algorithm scales landmark coordinates with CS, providing Mosimann's shape

903   vectors. The effect of CS on remaining shape variation therefore corresponds to multivariate

904   allometry. The effect of size variation on shape can be graphically depicted in computing the

905   product $\mathbf{y}\beta'(\beta\ \beta')^{-0.5}$ [115] where $\mathbf{y}$ is the shape variables and β the multivariate regression

906   coefficients, allowing to compare multivariate allometric patterns across different groups

907   [116, 117].

908   Under specific conditions, a multivariate regression of shape on size certainly

909   represents the multivariate approach the most closely related to the original bivariate model

910   from Huxley. On the other hand, the broadly used geometric morphometric approach

911   abandons the notion of trait for a notion of shape analyzed as a whole, and hampers

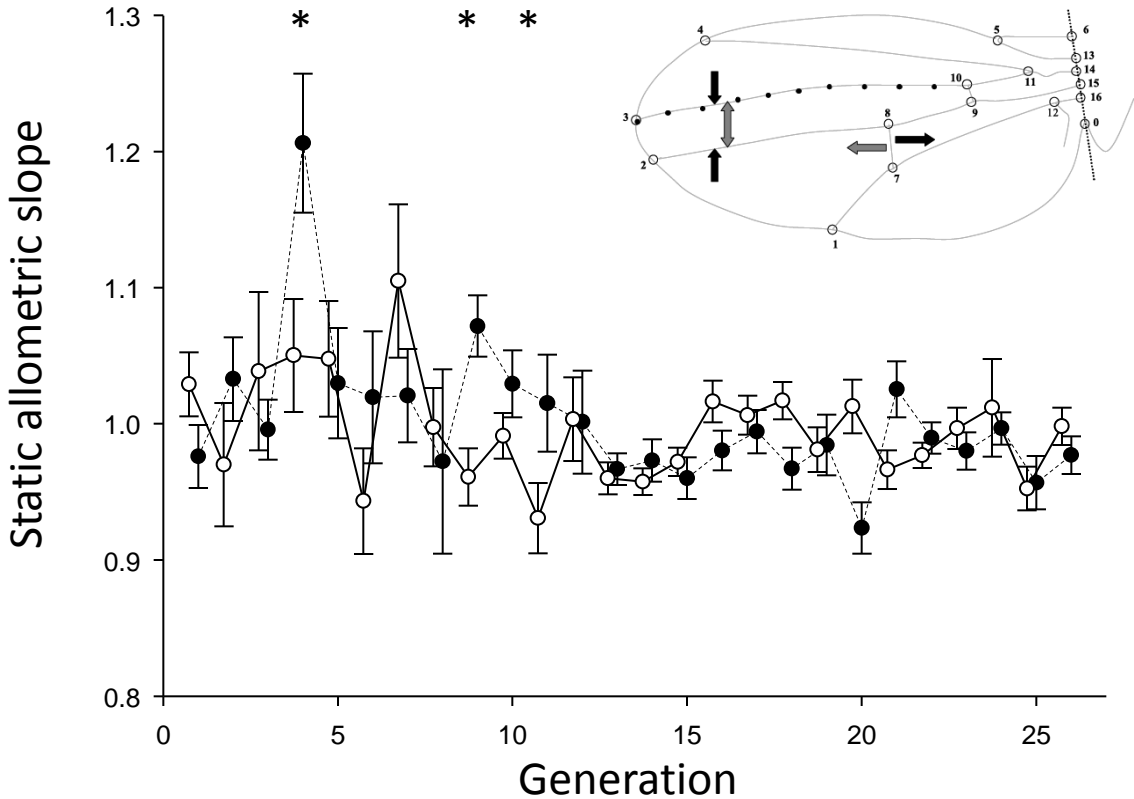912   interpretations of allometry in a context of relative growth.

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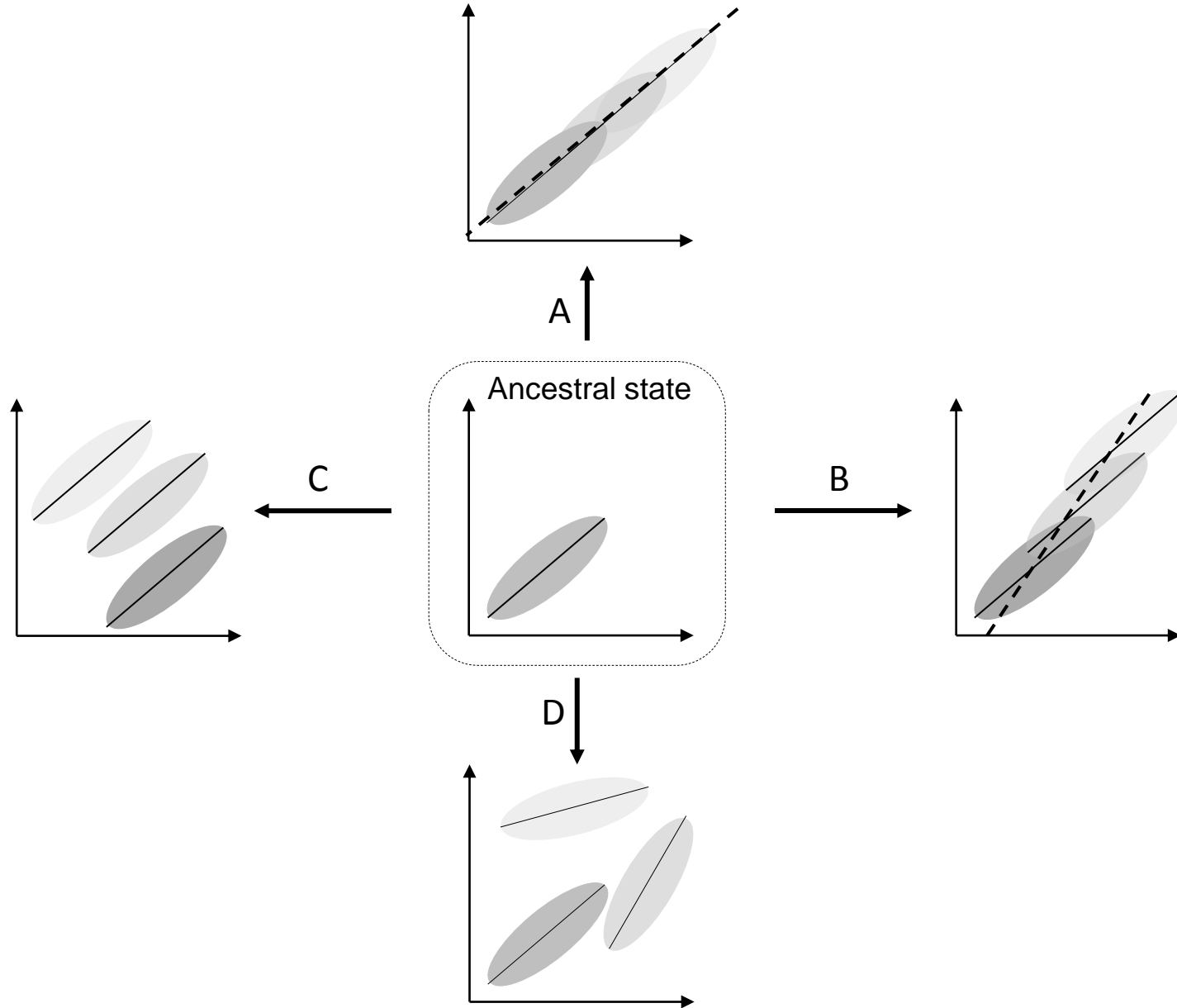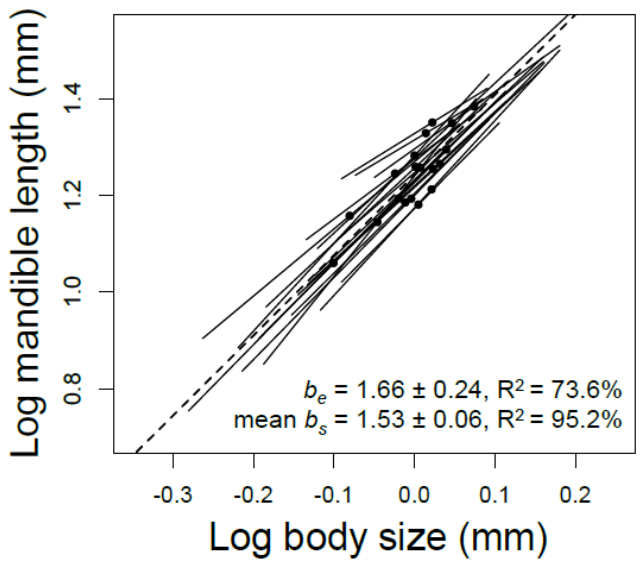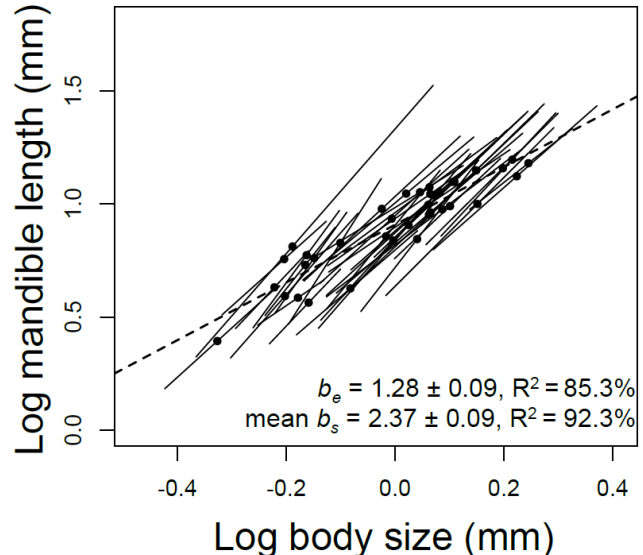
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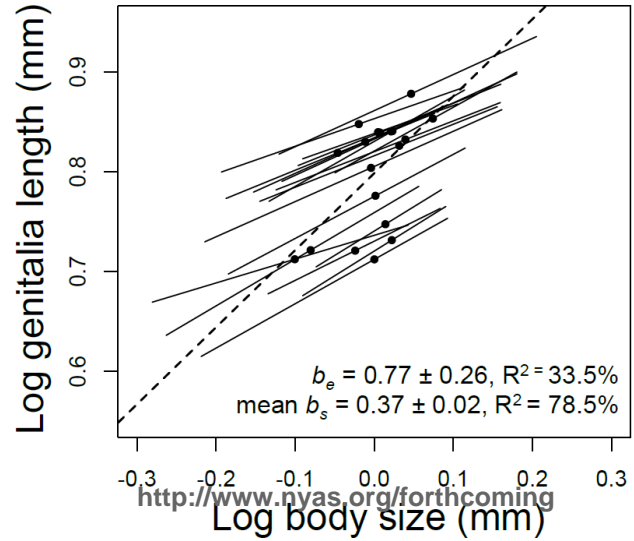
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Dorcus titanus (males) N = 19

b_e = 1.66 ± 0.24, R² = 73.6%
mean b_s = 1.53 ± 0.06, R² = 95.2%

Dorcus (males) N = 37

b_e = 1.28 ± 0.09, R² = 85.3%
mean b_s = 2.37 ± 0.09, R² = 92.3%

Dorcus titanus (males) N = 19

b_e = 0.77 ± 0.26, R² = 33.5%
mean b_s = 0.37 ± 0.02, R² = 78.5%