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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

40

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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1
2
3 67 is usually the case at the ontogenetic and evolutionary levels. Furthermore, ontogenetic and
4
5 68 static allometric slopes usually vary little among closely related species. These observations
6
7 69 have led several authors to suggest that allometric slopes most likely reflect strong physical,
8
9 70 physiological or biological mechanisms that somehow constrain the rate and direction of
10
11 71 evolution [5,6,7]. For example, the scaling of metabolism with body size, referred to above,
12
13 72 may be explained by the limits of diffusion through the limited surface area per volume of the
14
15 73 larger human than the smaller mouse [8]. Accordingly, allometric relationships have been
16
17 74 taken as prime evidence against the dominance of natural selection as an evolutionary force
18
19 75 [9]. This constraint hypothesis has been widely accepted for physiological and life history
20
21 76 traits [10,11], but has become more controversial for morphological traits.
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23
24

25 77 The alternative to the constraint hypothesis of allometry is that natural selection
26
27 78 persistently favors the particular power relationships between traits and size that are observed.
28
29 79 This hypothesis is at least implicitly widely accepted in the traditional studies of functional
30
31 80 allometry [2]. For example, the relationship between the cross-sectional area of the skeleton
32
33 81 with body mass may be explained in terms of optimal allocation, balancing the chances of
34
35 82 breakage – favoring a robust skeleton – with the costs of locomotion – favoring a lighter
36
37 83 skeleton. Accordingly, several authors have suggested that allometric slope could evolve
38
39 84 under selection [12,13,14,15]. In this context, the evolution of the static allometry of sexually
40
41 85 selected traits has been a particularly popular topic. Secondary sexual displays have been
42
43 86 predicted to evolve particularly steep slopes (i.e. positive allometry: $b > 1$) under handicap
44
45 87 models [12,13,16,17,18], while genitalia are expected to show negative allometry ($b < 1$) due
46
47 88 to stabilizing selection on trait size [14, 19, 20].
48
49
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51 89 Optimally, it should be possible to distinguish between the constraint and selective
52
53 90 explanations for allometry by quantifying both the selection forces and the evolvability of
54
55 91 allometry (i.e. its capacity to evolve) and compare the predicted and observed patterns of
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3 92 evolution in allometry. The general prediction is that a constrained slope will either be
4
5 93 incapable of evolving (an absolute constraint, [21]), or that fitness will decrease so rapidly
6
7 94 when moved away from the optimal value that the possible advantages of the altered slope
8
9 95 would not outweigh the fitness costs. Unfortunately, despite renewed interest in allometry in
10
11 96 the last two decades, progress in understanding the evolution of morphological allometry has
12
13 97 been slow. A key reason for this is the rise of a ‘broad sense’ definition of allometry as any
14
15 98 monotonic relationship between trait size and body size [22, 23] (Box 1). This divorces the
16
17 99 study of scaling from the prevalence of power relationships (Box 2), and in particular from
18
19 100 the centrality of the slope as the essence of allometry [24]. The result is a body of literature
20
21 101 that has measured quantities that cannot be interpreted as parameters of a power relationship.
22
23

24
25 102 Our aim in the current contribution is therefore to define clear predictions concerning
26
27 103 the constraint and selection hypotheses on morphological allometries and review the recent
28
29 104 literature in the light of these predictions.
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31

32 105

33 34 106 Evolutionary constraint and allometry

35
36 107 Evolutionary constraints are defined as any processes that preclude a trait from reaching a
37
38 108 phenotypic optimum, or slow down its evolution towards this optimum [25]. Depending on
39
40 109 the perspective and processes involved, many types of constraint have been defined [25,26].
41
42 110 Initially, allometry has been classified as developmental constraint, that is, constraint imposed
43
44 111 by the developmental architecture in the production of variant phenotypes [27]. Although
45
46 112 developmental constraints may themselves result from selection [28,29], they may still limit
47
48 113 the direction of phenotypic evolution. Such perspective of allometry as developmental
49
50 114 constraint corresponds to the view defended by early students of allometry and heterochrony
51
52 115 [5, 6, 7, 30, 31], who explained patterns of species divergence by changes in timing or rate of
53
54 116 development along constant ontogenetic processes.
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3 117 The introduction of the quantitative genetics framework in the study of allometry [32,
4
5 118 33, 34, 35] has shifted the hypothesis of allometry as a constraint from a developmental to a
6
7 119 genetic perspective. Genetic constraints occur when the amount or pattern of genetic variation
8
9 120 limits or channels the response to selection. Although these two perspectives are intimately
10
11 121 linked because genetic constraints often result from developmental constraints, this change in
12
13 122 perspective may have weakened the constraint hypothesis, given the ubiquity of genetic
14
15 123 variation generally found [36]. But more recently, the hypothesis of constraint due to low
16
17 124 genetic variation has been refueled by the realization that genetic correlations among traits
18
19 125 due to pleiotropy could seriously influence the direction of phenotypic evolution [21, 37, 38,
20
21 126 39, 40, 41, 42, 43], allometry being a perfect example of such a constraint.
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25 127 Importantly, the quantitative genetics approach of allometry underlines the fact that
26
27 128 understanding the evolution of allometry, and testing whether allometry represents an
28
29 129 evolutionary constraint requires quantifying the evolvability of allometry and comparing the
30
31 130 observed evolutionary patterns with those patterns expected under specific selection
32
33 131 pressures. If we are to test the “allometry as a constraint” hypothesis, we should therefore
34
35 132 answer the following questions; 1) Is allometry evolvable? 2) Does allometry constrains
36
37 133 patterns of phenotypic evolution? Static allometry represents the pivotal level at which these
38
39 134 questions should be asked. Indeed, it is the level at which developmental constraints will be
40
41 135 expressed, and patterns of static allometry will allow us to make predictions about phenotypic
42
43 136 evolution.
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46

137

138 **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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3 142 and selection acting on static allometry, we review evidence for both the evolution of static
4
5 143 allometry at the microevolutionary scale and its evolvability.
6

7 144

9 145 *Sources of constraint*

10 146 Evolution of static allometry depends on the evolution of the static allometric slopes and
11
12 147 intercepts. One key challenge is that an individual organism expresses neither a slope nor an
13
14 148 intercept. Therefore, if these parameters represent quantitative traits, estimating their genetic
15
16 149 variation requires clonal organisms where genetically similar organisms of different size can
17
18 150 be measured, measurement of "allometries" across relatives in family groups, or across
19
20 151 modules in modular organisms. Alternatively, because ontogenetic, static and evolutionary
21
22 152 allometries of morphological traits all result from a single process, namely growth, testing the
23
24 153 evolvability of static allometry could be achieved by estimating the evolvability of the growth
25
26 154 processes that generate covariance among traits. Several growth models have been suggested
27
28 155 to explain how static allometry is generated from simple growth patterns [5, 16, 31, 45, 46].
29
30 156 Using these models one can identify possible constraints on the variation of static allometry.
31
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34
35
36 157 From Huxley's (1932) [5] model of relative growth (Box 1), it can be shown that when
37
38 158 two traits present an ontogenetic allometry such as $z = a + bx$, with x and z varying during
39
40 159 growth, the static allometric slope at any specific time t can be expressed as:
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42

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45
46 161
$$b_s = \bar{b} + \frac{Cov(x_t, a) + \bar{x}_t Cov(x_t, b)}{Var(x)}, \quad (1)$$

47

48 162

49
50
51 163 where \bar{b} is the ontogenetic allometric slope averaged across all individuals, (i.e. the mean
52
53 164 ontogenetic allometry of the population), and \bar{x}_t , the mean body size at time t [47]. This
54
55 165 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, \bar{x}_t , in the following way:

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

172
 173 where \bar{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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3 191 growth environment (see [16] for such a model). Variation in the allometric slope could then
4
5 192 have a component due to variation in the trait sensitivity to the growth state of the whole
6
7 193 organism. Lack of genetic variance in trait growth sensitivity to the size of the body or the
8
9 194 sharing of a large proportion of the developmental pathway therefore seem the most likely
10
11 195 sources of constraint on changes in static allometry. Importantly, such constraints would
12
13 196 affect the allometric slope, but not necessarily the intercept.
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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.
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3 216 *Selection on the slope* – Alternatively the static allometric slope can evolve as a result of
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5 217 selection on the slope itself, with no change in \bar{x}_i or \bar{z}_i (Fig. 1, scenario B), which is
6
7
8 218 equivalent to assuming correlated selection on size and the trait. With correlated selection,
9
10 219 there will be an adaptive ridge that links the bivariate distribution of the traits to fitness (Fig.
11
12 220 2A). We can completely separate selection on the allometric slope from selection on trait
13
14 221 means by imagining an adaptive landscape that selects on trait (co)variances but not on trait
15
16 222 mean (i.e. no directional selection). We generally expect that trait means will evolve more
17
18 223 rapidly than trait variation, so when a change in selection regime affects both means and
19
20 224 (co)variances, we will rapidly approach the situation where only the (co)variances continue to
21
22 225 be selected. A simple example of such changes would be selection for a decrease in trait
23
24 226 variance combined with either an increase or constant variance in body size, which would
25
26 227 decrease the allometric slope. Selection for increasing variance in trait size combined with a
27
28 228 decreasing variance in body size should generate an increase in the allometric slope. Figure
29
30 229 2B shows a case of disruptive selection favoring extreme combinations of trait and body size
31
32 230 over those near the means. This type of selection maximizes selection on variances and
33
34 231 covariances, and therefore should lead to the maximum rate of response in the allometric
35
36 232 slope. Strong disruptive selection balanced precisely to lead to no directional selection is
37
38 233 probably an extremely rare event in nature, however. In theory, the presence of a selective
39
40 234 ridge should be sufficient to favor a particular slope in the absence of disruptive selection, but
41
42 235 the strength of selection on the slope will be quite weak, because many individuals the center
43
44 236 of the distribution (i.e. with non-informative genotype) will be selected (Compare Fig. 2A and
45
46 237 B).

47
48 238 Verbal models of selection on allometric slope have been proposed to explain the
49
50 239 positive allometry often observed in sexually selected traits [12,13, 17, 18, 51]. In these
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52 240 models, positive allometry evolves either because large males, presumably in better condition,
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3 241 are able to invest more in costly traits, or because the benefits of large traits increased with
4
5 242 body size. By applying various selection regimes on an allocation model of growth,
6
7 243 Bonduriansky and Day (2003) [16] showed that the conditions under which positive allometry
8
9 244 evolved were more restrictive than previously thought, but that an increase in the relative
10
11 245 fitness gain for larger traits with an increase in body size should select for positive allometry.
12
13 246 Canalizing selection on trait size, on the other hand, has also been suggested to affect static
14
15 247 allometry by generating negative allometries as for example for male copulatory organs in
16
17 248 insects [14, 19].

20
21 249 The variational properties that generate variance and covariance among traits are
22
23 250 pivotal to the evolution of static allometry. Although selection experiments have suggested
24
25 251 that variation may respond to selection [52] it remains unclear how efficiently selection can
26
27 252 mold genetic and environmental variation [53, 54, 55, 56]. The evolution of covariance
28
29 253 between trait size and body size directly links the evolution of the static allometric slope with
30
31 254 the evolution of the phenotypic and genetic covariance matrices (**P** and **G** on log scale). Much
32
33 255 theoretical and empirical work shows that genetic covariances do evolve [54, 57, 58, 59, 60],
34
35 256 but it remains unclear what forces drive these changes, and how rapidly they can take place.
36
37 257 The various hypotheses listed here suggest that, in many cases, selection on the allometric
38
39 258 slope is rather weak and indirect. If combined with a low evolvability, this may result in slow
40
41 259 evolutionary change in allometry.
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261 *Evolvability and evolution in static allometry*

48
49 262 Because changes in ontogenetic allometry are expected to provoke changes in static allometry
50
51 263 (Eq. 1), we first consider here evidence for the evolution of ontogenetic allometry. Such
52
53 264 evidence is provided by several studies comparing ontogenetic allometries among species
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55 265 [e.g. 61, 62, 63, 64]. However, few studies have tested the relationship between ontogenetic
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3 266 and static allometry [34, 65, 66, 67, 68], and fewer have analyzed how variation in the
4
5 267 parameters of ontogenetic allometry affected static allometry. The only study, to our
6
7 268 knowledge, that compared the relationship between ontogenetic and static allometry among
8
9 269 populations [47], showed that static allometry between caudal fin length and body length in
10
11 270 female Guppies (*Poecilia reticulata*) was steeper than the ontogenetic allometry, but was
12
13 271 similar among three populations with different adult female length. This was achieved, among
14
15 272 other things, by differences in the average ontogenetic allometric slope among populations.
16
17 273 The relevance of these results regarding the rate at which ontogenetic allometry evolve is
18
19 274 unclear, however, because guppy populations from different drainages may have been
20
21 275 separated for hundred thousands of generations [69]. Furthermore, although individual
22
23 276 variation in ontogenetic allometry has been observed [47], the genetic basis of this variation
24
25 277 remains unknown, and overall we found only one study that reported heritability of
26
27 278 ontogenetic slopes of chest circumference ($h^2 = 0.25 \pm 0.07$) and tail length ($h^2 = 0.39 \pm 0.08$)
28
29 279 on body weight within six laboratory strains of rats selected for larger or smaller weight [70].
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34 280 Microevolutionary changes in phenotypic covariances among traits are suggested by
35
36 281 studies reporting rapid changes in the **G**- or **P**- matrices within populations [71, 72, 73]. These
37
38 282 observations are difficult to interpret in terms of evolution of allometry, however, because
39
40 283 traits are not always strongly correlated in the first place and **G**-matrices are rarely analyzed
41
42 284 on log scale. Furthermore, studies analyzing changes in the **P**-matrix cannot distinguish
43
44 285 between environmental and genetic changes in the patterns of covariation among traits.
45
46

47 286 Estimates of genetic variance in static allometric slopes are scarce, and we found only
48
49 287 one study reporting heritabilities of allometric slopes measured on log scale [74]. In this
50
51 288 study, heritabilities of the static allometric slope between the length of several bones and the
52
53 289 cubic root of body weight, and between the weight of internal organs and body weight were
54
55 290 all statistically significant but relatively small (all $h^2 < 0.13$) despite being measured in the lab.
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3 291 Alternatively, artificial selection can be used to uncover genetic variation and
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5 292 covariation in quantitative traits [75]. During the last two decades, several authors have
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7 293 claimed to have altered patterns of static allometry by artificial selection. In addition, a few
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9 294 artificial selection studies on size have shown changes in the covariance patterns between the
10
11 295 size of some traits and body size. Unfortunately, most of these studies have adopted the
12
13 296 broad-sense definition of allometry, seriously hampering our ability to interpret their results in
14
15 297 terms of the evolution of allometry [23]. For example, in a study on a stalk-eyed fly
16
17 298 (*Cyrtodiopsis dalmanni*), selection exerted on the ratio between eye span and body length
18
19 299 significantly affected the covariance between the two traits when measured on arithmetic
20
21 300 scale [76]. Reanalysis of the regression line on the log scale shows that changes in the
22
23 301 allometric slope are still present but much weaker than those reported in the original study
24
25 302 (Table 1). A similar selection procedure was used in two experiments on the butterfly
26
27 303 *Bicyclus anynana* [77, 78]. In both experiments, the intercepts of the relationships on
28
29 304 arithmetic scale were strongly affected by selection, but the slopes were apparently not,
30
31 305 although no formal tests of change in slope were reported. What were the consequences of the
32
33 306 selection on the allometric slope remains unknown.

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37
38 307 The only artificial selection experiment on narrow-sense allometry conducted so far
39
40 308 combined stabilizing and disruptive selection on body area and caudal fin area to select for a
41
42 309 change in static allometric slope (procedure similar as the one described in Fig. 2B; [79].
43
44 310 Selection to increase and decrease the intercept was also applied on two separate lines.
45
46 311 Results suggested that the allometric slopes had very little capacity to vary compared to the
47
48 312 allometric intercepts. This conclusion, however, was weakened by the small number of
49
50 313 generations of selection.

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54 314 Two studies investigating the effects of artificial selection on body size on correlated
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56 315 traits provide some evidence for rapid change in static allometric slope. In a selection
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3 316 experiment to increase or decrease body mass in the moth *Manduca sexta*, static allometry
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5 317 between wing mass and body mass became steeper in the line selected for smaller body mass
6
7 318 and shallower in the line selected for larger body mass after 10 generations of selection ([80];
8
9 319 and see [23] for reanalysis using standard regression). Similarly, estimation of the static
10
11 320 allometric slopes in the different lines of a selection experiment to increase body size in
12
13 321 *Drosophila melanogaster* [81] reveals that allometries between wing length and thorax length
14
15 322 or between wing length and tibia length increased in the line selected for smaller thorax
16
17 323 length, and decreased in the line selected for larger thorax length (Table 1). Additionally,
18
19 324 Cayetano et al. (2011) [82] while relaxing sexual selection for ca. 21 generations in the seed
20
21 325 beetle *Callosobruchus maculatus* observed a change in the allometry between two traits of the
22
23 326 genital apparatus in males and elytron length. The reanalysis of the data from this last
24
25 327 experiment showed, however, a very poor fit of the traits with the allometric model and casted
26
27 328 doubt on the validity of the interpretation of the results [23].
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32 329 One factor that has not been considered in these experiments, however, is the
33
34 330 possibility of plasticity in the allometric slope. Plasticity in allometric relationships has been
35
36 331 little studied, but one study clearly shows that static allometry varies in response to different
37
38 332 environmental treatments [83]. Similarly, a selection experiment on *Drosophila* wings in
39
40 333 which selection was performed on the relative position of some veins [55, 84, 85] shows
41
42 334 erratic but sometimes statistically significant variation in static allometry (Fig. 3). The
43
44 335 differences in slope apparent in Figure 3, could, if observed in isolation, be misinterpreted as
45
46 336 change in allometry due to selection. To avoid such problem we strongly recommend
47
48 337 following the changes in allometry from generation to generation, and experiments that fail to
49
50 338 do so should be interpreted with caution.
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53
54 339 The dissection of the insulin/IGF signaling pathway that controls trait size in animals
55
56 340 provides a nice illustration of how the growth of specific traits responds to changes in the
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3 341 growth environment, that is, changes in body size [86, 87]. Interestingly, recent experiments
4
5 342 have uncovered mutations at specific loci that could affect the organ sensitivity to variation in
6
7 343 the growth environment and therefore affect the slope of the static allometry [74, 88].
8
9 344 Although these studies provide clear evidence for genetic variation in allometric slope, they
10
11 345 also suggest that this variation results from complex genetic architecture [74] that may not
12
13 346 easily respond to selection.

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15
16 347 Neither inter-population variation nor quantitative genetics experiments provide
17
18 348 conclusive evidence for genetic variation in the allometric slope. For the intercept,
19
20 349 quantitative genetic studies provide clear evidence for high evolvability.
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22

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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2
3 366 should strongly shape patterns of populations and species divergence. This was initially
4
5 367 suggested by Gould [6, 7] and placed in a quantitative genetic framework by Lande [32, 33]
6
7 368 who showed that, under constant patterns of covariance between traits (constant **G**-matrix),
8
9 369 selection acting only on the body size (x), will generate a correlated response on the trait size
10
11 370 (z). In this case, the evolutionary allometric slope (b_e) along which populations and species
12
13 371 evolve, will correspond to the ratio of the correlated response in z divided by the direct
14
15 372 response in x , that is, the slope of the genetic regression between the two traits: $b_s = \sigma_A(x,z)$
16
17 373 $/\sigma_A^2(x)$, where $\sigma_A^2(x)$ and $\sigma_A(x,z)$ are the additive genetic variance in x and the covariance
18
19 374 between x and z , respectively (Fig. 4 scenario A).
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21
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23 375 Because static allometry is defined at the phenotypic level, the static allometric slope
24
25 376 (b_s) combines both additive genetic and residual variances and covariances: $b_s =$
26
27 377 $[\sigma_A(x,z) + \sigma_R(x,z)] / [\sigma_A^2(x) + \sigma_R^2(x)]$, where R denotes all other residual components of the
28
29 378 variance, including environmental and non-additive genetic variance. Static and evolutionary
30
31 379 regression coefficients, b_s and b_e , will be similar when the relative contributions of the
32
33 380 residual variance and covariance are similar to the relative contributions of their additive
34
35 381 genetic counterparts. In this case, the genetic and phenotypic variance-covariance matrices, **G**
36
37 382 and **P**, will be proportional for these elements. If this condition is not fulfilled, evolutionary
38
39 383 allometry will not follow the trajectory defined by the static allometry, contrary to previous
40
41 384 claims by Gould [91] and others (Fig. 4 scenarios B and C; [33]). Furthermore, if the additive
42
43 385 genetic and residual contributions to static allometry are different but remain constant, the
44
45 386 static allometric slope should remain constant across populations and species while the
46
47 387 intercept will change with changing mean size (Fig. 4 scenario B and C).
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51
52 388 It is important to realize that when Lande's model [33] is generalized to allow
53
54 389 selection on the trait and both size, and there is at least some additive genetic variation in
55
56 390 both, the means obtained in the long term depend only on the selective optima for size and the
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3 391 trait, and not at all on the patterns of covariance among them [35]. If this is the case, and if
4
5 392 selective optima are spread more or less randomly in the bivariate morphospace, we would
6
7 393 expect no relationship between evolutionary and static allometry (Fig. 4 Scenario C and D).
8
9 394 Scenario C represents a situation where the slope is an absolute constraint but the trait and
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11 395 body size means can evolve more or less freely in the morphospace (Fig. 4 Scenario C). This
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13 396 provides the other major explanation for evolutionary allometry: it is not the pattern of genetic
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15 397 variation, but the pattern of natural and sexual selection that dictates allometry.

16
17 398 These considerations underline the problem we have of testing the allometry as a
18
19 399 constraint hypothesis without knowing the selection patterns acting on allometric
20
21 400 relationships, and in most cases, only speculative interpretation of the macro-evolutionary
22
23 401 patterns can be achieved. Although specific predictions have been suggested regarding the
24
25 402 effect of selection on allometric slope for genitals and secondary sexual characters, these
26
27 403 predictions only concerned the type of allometry expected (positive or negative allometry),
28
29 404 but not the strength of selection. Furthermore, in the case of secondary sexual characters, it has
30
31 405 been shown that positive allometry was only expected under specific selection pressures [16],
32
33 406 and a later review [89] confirmed that static allometric slopes in this type of character was
34
35 407 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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2
3 416 among populations but this variation is more limited (median SD = 0.07). For the allometric
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5 417 intercept, patterns of variation were similar with higher variation among species (median SD
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7 418 = 0.15) than among populations (median SD = 0.02).

9
10 419 Because the slope and intercept are on different scales, their level of variation is not
11
12 420 directly comparable. Using the concept of conditional variance [39, 41], Voje et al. [23]
13
14 421 estimated the influence of changes in size or in allometric slope and intercept in the evolution
15
16 422 of trait size. This method allowed them to compare variation in slope and intercept on a
17
18 423 common scale (variance in trait size). At the interspecific level, 74% of the variation in trait
19
20 424 size was associated with changes in species mean size. The contribution of the changes in
21
22 425 static allometric slope or intercept were more limited (13% and 29% of the log trait variance
23
24 426 explained, respectively, e.g. Fig. 5A). The contributions of these three parameters to trait
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26 427 diversification at the among-population level were similar, with size variation explaining
27
28 428 71%, slope explaining 36%, and intercept variation explaining 40%. However, as previously
29
30 429 mentioned, much less variation in static allometry was observed among populations, and the
31
32 430 evolutionary allometry was often very similar to the pattern of static allometry (Fig. 5B).

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36 431 Finally, Voje et al. [23] showed that within species, the average static allometry across
37
38 432 populations was a good predictor of the evolutionary allometry, while across species within
39
40 433 genera the average static allometry was poorly correlated with the evolutionary allometry.

41
42 434 These results are compatible with the “allometry as a constraint” hypothesis if
43
44 435 selective optima were spread more or less randomly in the bivariate morphospace. Indeed,
45
46 436 morphological evolution more constrained along static allometric trajectories at the within-
47
48 437 species level than at the among-species level could be interpreted as signature of evolutionary
49
50 438 constraint.

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53
54 439 In an attempt to estimate the rate of morphological evolution towards a predicted
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56 440 optimum, Voje and Hansen [92] reanalyzed data on the evolution of the static allometry

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2
3 441 between eye-span and body length in various species of stalk-eyed fly (Diopsidae). Using
4
5 442 sexual size dimorphism as a measure of the strength of sexual selection in order to estimate
6
7 443 optima, they showed that the static allometric slope in male trait was tracking these optima,
8
9 444 but this took millions of years to accomplish.
10

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13 446 *The “one size fits all” hypothesis*

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15
16 447 The various studies analyzing static allometry of genital traits in arthropods and vertebrates
17
18 448 showed consistently shallow static allometric slopes ($\beta < 1$) for these traits, as expected from
19
20 449 the “one size fits all” hypothesis [14, 19]. Eberhardt [19] reported few exceptions to this
21
22 450 pattern. However, all these exceptions came from studies where static allometry was
23
24 451 estimated using major axis regression, a method that will over-estimate the slope for
25
26 452 relationships with low r^2 . Accordingly, for all exceptions reported, the relationship between
27
28 453 the genitalia and the measure of body size was poor (range r^2 : 0.0 – 0.58). In all cases where
29
30 454 data were reanalyzed using standard regression methods, genital traits showed negative ($b < 1$)
31
32 455 static allometry [23, 93].
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36 456 The “one size fits all” hypothesis has also been extended for reproductive organs in
37
38 457 flowering plants with insect pollination, where the fit between pollen donor and pollen
39
40 458 receiver organs and pollinators of relatively constant size and behavior is expected to produce
41
42 459 stabilizing selection [94]. Several studies have provided clear evidence for the relative
43
44 460 invariance of floral traits compared to vegetative traits [95, 96] and the two studies that have
45
46 461 tested the effect of pollination accuracy on the allometry of the pollen transport organs both
47
48 462 reported shallow allometry for these traits [97, 98].
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52 463 If results from studies on the “one size fits all” hypothesis provide clear evidence of a
53
54 464 possible effect of selection on static allometry, they do not provide evidence for high
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56 465 evolvability of the allometric slope. Indeed, intraspecific comparison of static allometry in
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3 466 insect genitalia show that variation in the allometric slope explains only a small proportion of
4
5 467 the variation in genitalia size, 92% of the variance of log-size genitalia being independent of
6
7 468 the variation in allometric slope [23]. This is particularly clear when observing the allometric
8
9 469 slope between genitalia size and body size in various populations of the beetle species *Dorcus*
10
11 470 *titanus* (Fig 5C).
12

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14 471

15 16 472 Conclusions

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19
20 474 Despite the huge interest morphological allometry has focused among evolutionary biologists
21
22 475 for nearly a century, we are left with a limited understanding of its evolution. Key
23
24 476 observations such as genetic variation in ontogenetic allometry or in the static allometric
25
26 477 slope are surprisingly scarce. Although micro- and macroevolutionary patterns seem to point
27
28 478 at a constraining effect of morphological allometry on phenotypic evolution, the complete
29
30 479 lack of data on the nature of direct or indirect selection on allometry, and the near absence of
31
32 480 data on genetic variation in allometric parameters precludes the interpretation of these
33
34 481 patterns as evidence for or against the constraint and adaptation hypotheses. Until such data
35
36 482 are obtained the evolution of allometry will remain a mystery.
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41 483

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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
<i>Cyrtodiopsis dalmanni</i>	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
<i>Drosophila melanogaster</i>	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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3 770 Figure 1. Evolution of static allometry. The scenarios considered here correspond to the
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5 771 expected evolution of static allometry from an ancestral state depending on the constraining
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7 772 parameter (i.e. the parameter that is not evolvable). Vertical and horizontal dash lines
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9 773 represent the mean trait value and body size. Body size is mean centered, so the allometric
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11 774 intercept represent the trait value at the population mean (i.e. elevation of the allometric
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13 775 regression). In the scenario A, both the slope and the intercept are constraining parameters.
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15 776 Any change in body size will generate a change in trait size and vice versa. In the scenario B,
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17 777 only the allometric slope changes while the intercept (elevation) does not change. In the
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19 778 scenario C, the slope is the constraining parameter while the intercept can change. In the
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21 779 scenario D, slope and intercept can evolve. This pattern may be also generated by the effect of
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23 780 a negative covariance between body size and the ontogenetic slope when selection on body
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25 781 size occurs (see Eq. 1).
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32 783 Figure 2. Selection to change allometric slope via correlated selection on the trait and
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34 784 body size. A) Selection is generated by the difference in the direction of the phenotypic
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36 785 regression and the adaptive ridge. Black dots represent individuals and the blue dots represent
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38 786 the selected individuals (with the highest fitness). B) Saddle fitness landscape that generates
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40 787 disruptive selection on one of the two traits. This selection regime is more efficient to change
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42 788 the slope because individuals in the middle of the distribution are not selected.
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47 790 Figure 3. Phenotypic plasticity in static allometry. The figure presents the variation in the
48
49 791 slope of the static allometry between wing size (estimated by the centroid size) and the inter-
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51 792 landmark distance 2 - 12 (see diagram for landmarks number) in two populations of *D.*
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53 793 *melanogaster* selected to increase (grey arrows) or decrease (back arrows) a selection index.
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55 794 Selection was performed for 26 generations. Idiosyncratic variation of the slope (estimated on
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3 795 100 males at each generation) generates statistically significant differences between selection
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5 796 lines at generation 4, 9 and 11. The data presented here correspond to the LHM 1 replicate,
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7 797 but similar results were observed for the other three replicates, LHM 2 and IV 1 and 2 (see
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9 798 [55] for more detail).

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14 800 Figure 4. Static allometry as an evolutionary constraint. The various scenarios represent
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16 801 the effect of constraining parameters of the static allometry on the evolutionary allometry,
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18 802 assuming that selective optima are spread more or less randomly in the bivariate
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20 803 morphospace. In scenario A, neither the slope nor the intercept vary. The divergence of
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22 804 population means follow the genetic allometric regression (see text). If the slopes of the
23
24 805 genetic and phenotypic allometry are similar, evolutionary allometry will follow the patterns
25
26 806 of static allometry. In scenario B, the intercept is allowed to change but not the slope.
27
28 807 Although such a pattern may result from the evolution of the intercept itself, it may also result
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30 808 from the difference between the phenotypic and genetic allometry (see text). Scenario C
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32 809 presents a similar pattern but where selection does not favor any particular direction in the
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34 810 morphospace. In scenario D, both intercept and slope can evolve (no constraint).

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40 812 Figure 5. Example of variation in static allometric and effect on evolutionary allometry
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42 813 A) among population within species B) among species within genus C) among species
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44 814 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

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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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2
3 842 of biological origin, estimates produced by linear regression on log scale should be better than
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5 843 those produced by a power model fitted on arithmetic scale. Both approaches are valid,
6
7 844 however, and should ideally be conducted with proper modeling of both biological and
8
9 845 measurement error.

11 846 It has been repeatedly suggested that major-axis or reduced major-axis regression
12
13 847 should be used in place of ordinary least-squares regression to estimate allometric parameters
14
15 848 in order to account for the effect of observational error in the predictor variables. However,
16
17 849 neither of these models provides sensible estimates of allometric regression slopes when there
18
19 850 is biological ‘error’ (i.e. biological deviations from the allometric line) in the model [107,
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21 851 108]. These models provide estimates of slopes, but these slopes are not proper estimates of
22
23 852 the exponent b in the narrow-sense allometric relation. A dramatic consequence of the
24
25 853 reduced major-axis regression is that, even in absence of covariance between the two traits, an
26
27 854 “allometric” slope can be estimated and its statistical significance tested [e.g. 82].

29 855 Finally, we notice that ignoring the consequences of trait dimension on the allometric
30
31 856 slope has led to some erroneous statements in the recent study of allometry. For example, a
32
33 857 positive allometry between testes size and body length has been reported in Hottentot golden
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35 858 mole (*Amblysomus hottentotus*) as an exception to the “one size fits all” hypothesis [109].
36
37 859 However, this positive allometry is most likely generated by the difference in dimension
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39 860 between the traits (body length – length vs. testes mass - volume).
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Box 2: From bivariate to multivariate allometry: drifting away from the Huxley's model

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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 $\{1/\sqrt{k}, \dots, 1/\sqrt{k}\}$ 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

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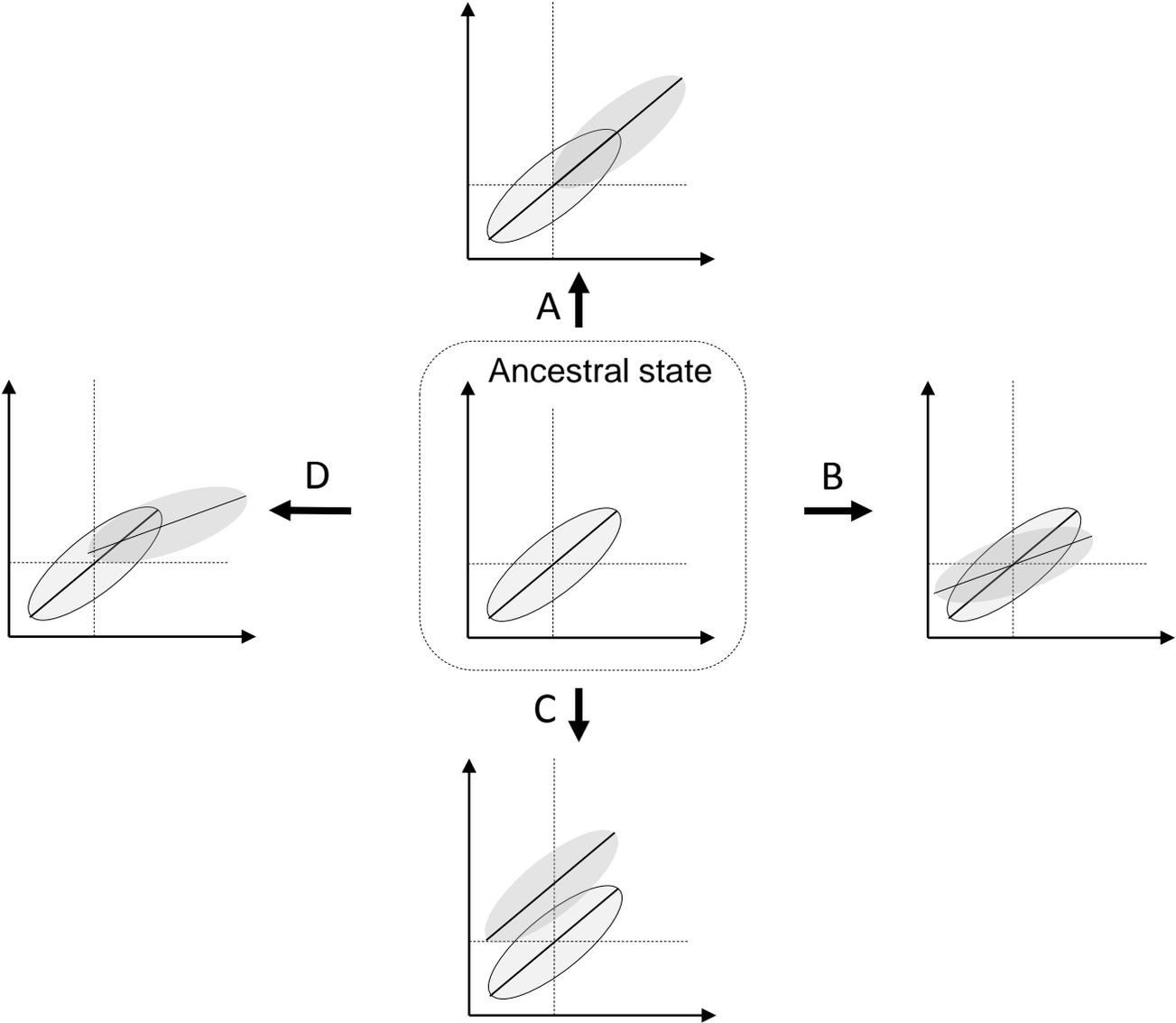
The evolvability of allometry

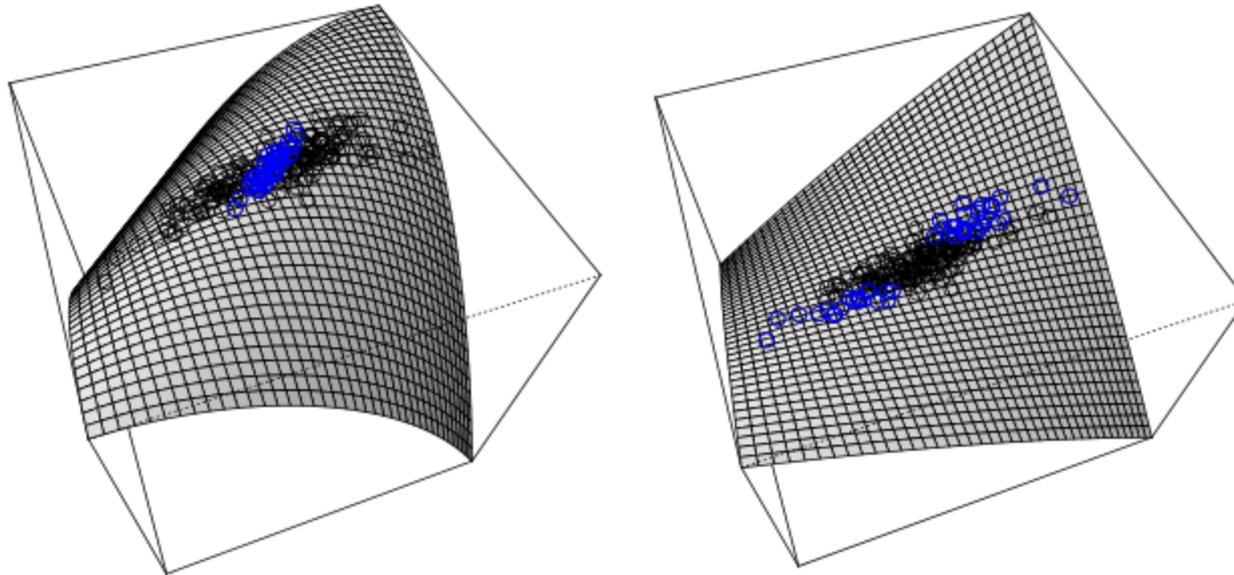
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3 888 estimating size are the PC1-as-size approach described above and Mosimann's [114]
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5 889 definition. Mosimann [114] defined size as any function G of the measurement vector \mathbf{x} that
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7 890 satisfies the property: $G(a\mathbf{x})=aG(\mathbf{x})$, $G(\mathbf{x})$ having the same dimension than any element of \mathbf{x} .
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9 891 Indeed, shape being on a ratio scale, multiplication of each element of the ratios by a constant
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11 892 a does not change shape and G is uncorrelated with any ratios under fully isometric
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13 893 multivariate variation. It is worth noticing that Huxley [5] already defined traits' growth rate
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15 894 as affected by a common growth factor (" G ") that vanishes when the growth rates of the traits
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17 895 are put in relation in the exponential relationship.
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21 896 Contrary to the PC1 approach, this geometric definition of size is not directly
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23 897 dependent of the variance-covariance properties of the studied samples. As a measure of size,
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25 898 geometric morphometrics conventionally use centroid size (CS), the square root of the sum of
26
27 899 squared distances of a set of landmarks from the centroid of the entire landmarks
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29 900 configuration. Although this choice does not generally rely on biological arguments, centroid
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31 901 size corresponds to a size vector according to Mosimann's definition. The Procrustes
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33 902 superimposition algorithm scales landmark coordinates with CS, providing Mosimann's shape
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35 903 vectors. The effect of CS on remaining shape variation therefore corresponds to multivariate
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37 904 allometry. The effect of size variation on shape can be graphically depicted in computing the
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39 905 product $\mathbf{y}\beta'(\beta\beta')^{-0.5}$ [115] where \mathbf{y} is the shape variables and β the multivariate regression
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41 906 coefficients, allowing to compare multivariate allometric patterns across different groups
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43 907 [116, 117].
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47 908 Under specific conditions, a multivariate regression of shape on size certainly
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49 909 represents the multivariate approach the most closely related to the original bivariate model
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51 910 from Huxley. On the other hand, the broadly used geometric morphometric approach
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53 911 abandons the notion of trait for a notion of shape analyzed as a whole, and hampers
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55 912 interpretations of allometry in a context of relative growth.
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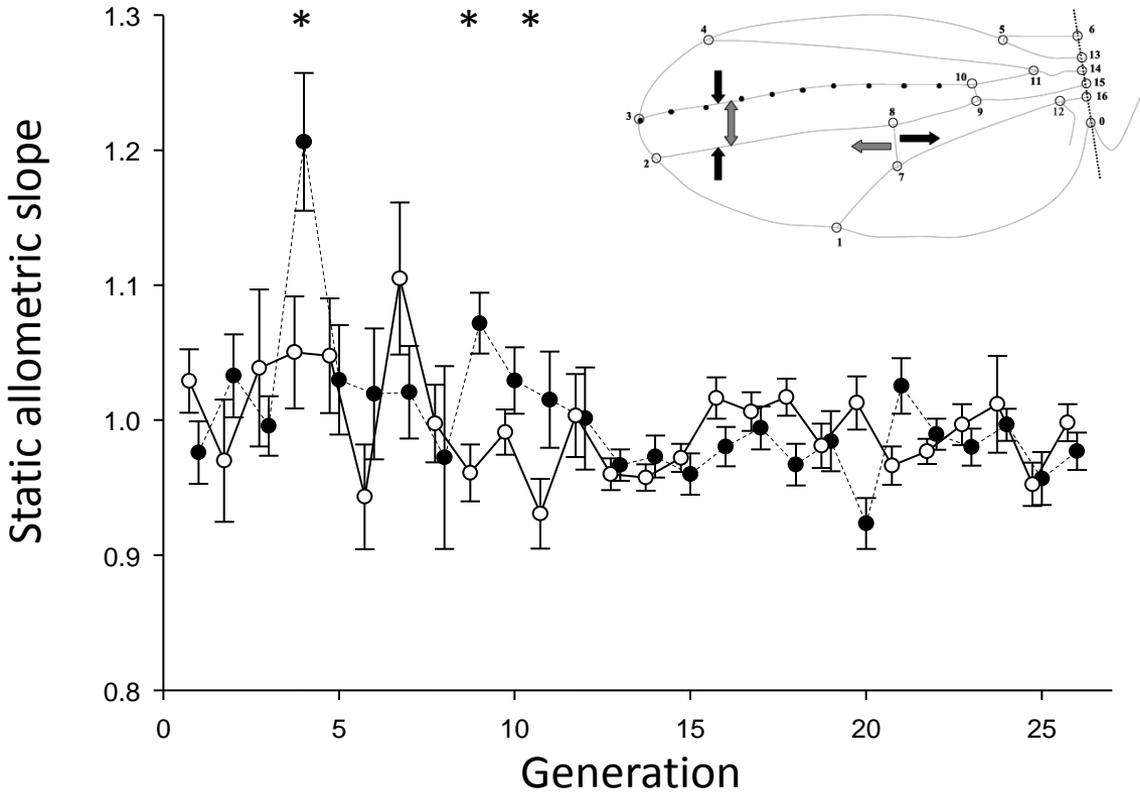
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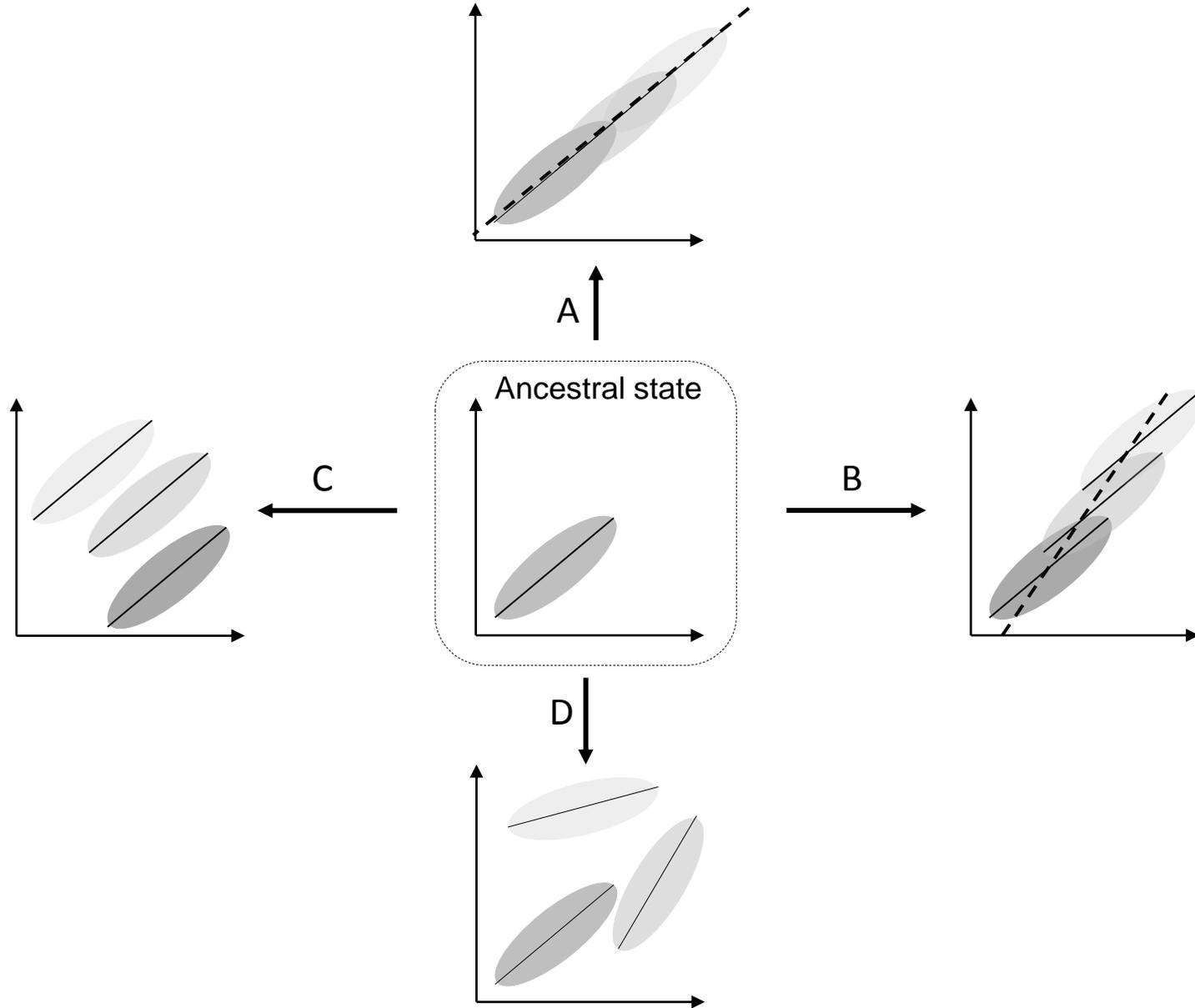




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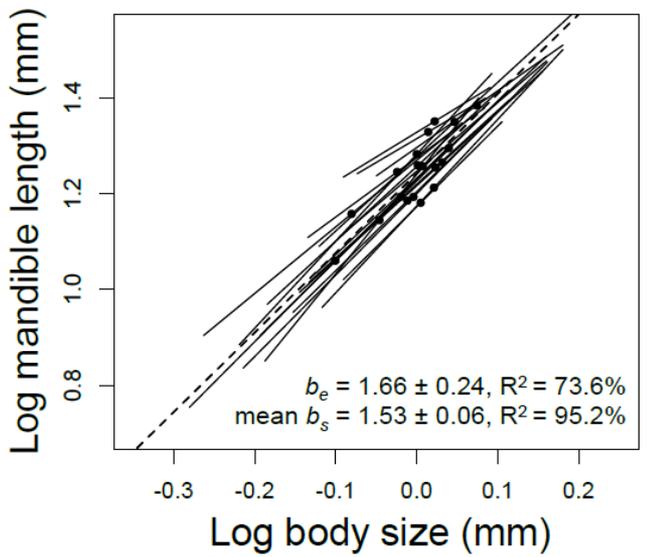
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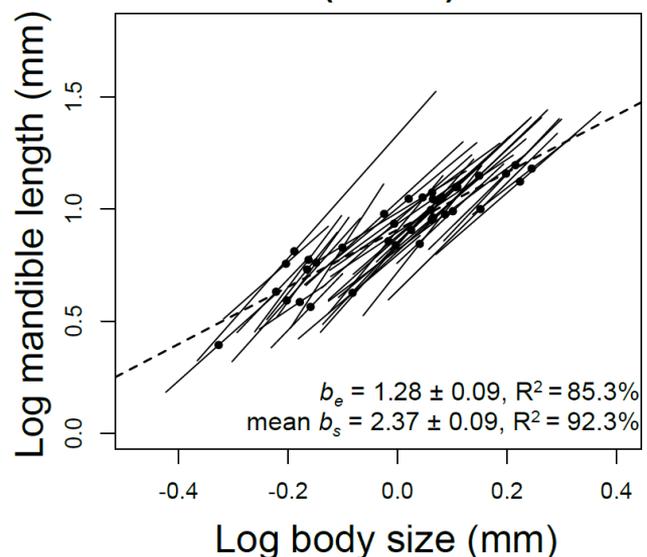


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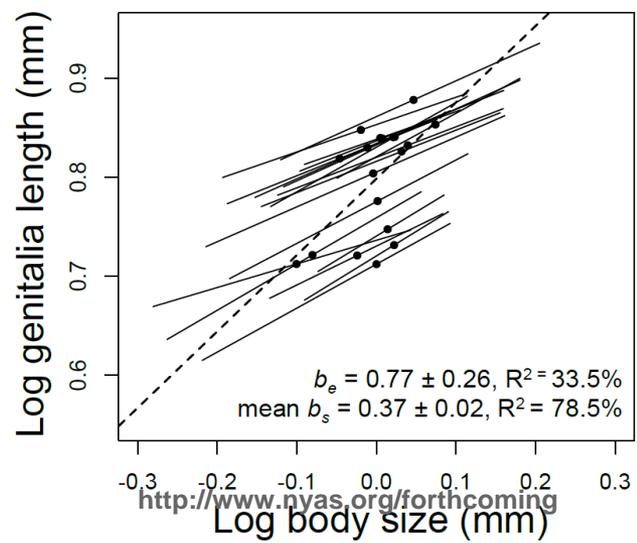
Dorcus titanus
(males) N = 19



***Dorcus* (males) N = 37**



Dorcus titanus
(males) N = 19



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