Title: **Evolutionary rates for multivariate traits: the role of selection and genetic variation.**

Authors: **William Pitchers[1,3], Jason B. Wolf[2], Tom Tregenza[3], John Hunt[3*] and Ian Dworkin[1*]**

Affiliations:

[1]Department of Zoology, Program in Ecology Evolutionary Biology and Behavior, BEACON Center for the study of Evolution in Action, Michigan State University, East Lansing, MI 48824, USA.

[2]Department of Biology & Biochemistry, University of Bath, Claverton Down, Bath, BA2 7AY, UK.

[3]College of Life and Environmental Sciences, Centre for Ecology and Evolution, University of Exeter, Tremough Campus, Penryn, Cornwall, TR10 9EZ, UK

[*]Corresponding Authors: **John Hunt** – J.Hunt@exeter.ac.uk & **Ian Dworkin** idworkin@msu.edu

Keywords: Quantitative genetics, evolution, haldanes, **G** matrix, natural selection, evolutionary rates, constraint, evolvability, scaling.

Supplemental Material: Data & scripts available at DRYAD DOI:xxxxx

Summary

A fundamental question in evolutionary biology is the relative importance of selection and genetic architecture in determining evolutionary rates. Adaptive evolution can be described by the multivariate breeders' equation ($\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta}$), which predicts evolutionary change for a suite of phenotypic traits ($\Delta\bar{z}$) as a product of directional selection acting on them ($\boldsymbol{\beta}$) and the genetic variance-covariance matrix for those traits (**G**). Despite being empirically challenging to estimate, there are enough published estimates of **G** and $\boldsymbol{\beta}$ to allow for synthesis of general patterns across species. We use published estimates to test the hypotheses that there are systematic differences in the rate of evolution among trait types, and that these differences are in part due to genetic architecture. We find evidence that sexually selected traits exhibit faster rates of evolution compared to life-history or morphological traits. This difference does not appear to be related to stronger selection on sexually selected traits. Using numerous proposed approaches to quantifying the shape, size and structure of **G** we examine how these parameters relate to one another, and how they vary among taxonomic and trait groupings. Despite considerable variation, they do not explain the observed differences in evolutionary rates.

Introduction

Predicting the rate and direction of phenotypic evolution remains a fundamental challenge in evolutionary quantitative genetics [1-4]. Empirical studies have demonstrated that most traits are heritable [5-8] and can respond to selection – a prediction borne out by an abundance of short- (e.g. [9-11] and long-term (e.g. [9,12-14] artificial selection experiments targeting single traits. However, in most biological systems, the targets of selection are suites of traits. Furthermore, different traits are tied together by genetic associations (typically quantified as covariances), and consequently selection on one trait can lead to evolutionary changes in other traits [7,8,11,15-21]. Indeed, genetic covariation between traits appears to be ubiquitous and has the potential to shape the evolution of associated traits [7,10,17,18,20,22,23]. Therefore, to improve our understanding of phenotypic evolution it is necessary to invoke a multivariate perspective [5,17-19,24].

The evolutionary response of a suite of traits can be predicted by the multivariate breeder's equation $\Delta\bar{z} = \mathbf{G}\boldsymbol{\beta}$ where $\Delta\bar{z}$ is the vector of responses in phenotypic means for the suite of traits under consideration, **G** is the additive genetic variance-covariance matrix and $\boldsymbol{\beta}$ is the vector of linear (directional) selection gradients [5-8]. The importance of **G** to phenotypic evolution can be illustrated using the concept of "genetic degrees of freedom" [9,11,15]. Whenever there is genetic covariance between them, the number of trait "combinations" in **G** that can respond to selection can be considerably smaller than the actual number of measured traits. This can be true even

when each trait in **G** is heritable and all pairwise genetic correlations between them are less than one [1-3,9,11,25]. This reduced dimensionality constrains the population to evolve in a genetic space with fewer dimensions than the number of traits (and trait combinations) potentially under selection. A matrix whose variance is concentrated in one or a few dimensions can exhibit "lines of least evolutionary resistance"; directions in which the multivariate evolutionary response can proceed more rapidly than in others [15]. The presence of these lines of least evolutionary resistance can have a major influence in biasing the direction of evolutionary trajectories (Figure 1; ref.s [7,11,15-20]), making the **G** matrix more informative about the short term capacity of a population to respond to selection (i.e. its evolvability) than the heritabilities of individual traits [7,10,17,18,20,22,23].

A variety of measures have been proposed as proxies for the evolutionary potential of a population. Most current approaches represent a function of the components of the multivariate breeder's equation: **G**, $\boldsymbol{\beta}$ and $\Delta\bar{z}$ [5,17-19,21,24]. Unfortunately, few studies simultaneously estimate more than one of these components. The few notable exceptions suggest that the structure of **G** plays an important role in directing phenotypic evolution [26-29]. Even fewer studies provide direct estimates of observed rates of evolution [30,31]. However, many individual estimates of selection and evolutionary rates exist in the literature and evolutionary research has benefitted from reviews that synthesize these parameters [30-38]. There is considerable variation in the strength of selection across different trait types and fitness measures [33,34,38], as well

as over time (but see ref.s [36,39,40]. On average, linear selection appears stronger on morphological than life-history traits and both linear and quadratic selection is stronger when acting on mating success and fecundity compared to viability [1-4,33,38]. It should be acknowledged, however, that such studies are subject to some methodological debate [5-8,35] and potentially publication biases [9-11,40]. In particular, there has been considerable disagreement about trait scaling, and how it influences estimates and broader evolutionary conclusions [19,22,41].

Although they have not received the same attention as selection gradients, reviews based on published genetic parameters also show clear differences across trait types. Morphological traits generally have higher heritabilities than life-history traits, with physiological and behavioural traits intermediate between these extremes [9,12-14,32], but see [6-8,11,15-21]. Sexual traits have also been shown to have higher additive genetic variances compared to non-sexually selected traits [7,10,17,18,20,22,23,42], although this finding is based on few studies. As discussed above, trait scaling has been shown to alter the observed patterns [19,22,41].

There have been even fewer attempts at synthesis from a multivariate perspective. Notably, Kirkpatrick [20], Kirkpatrick & Lofsvold [9], Agrawal & Stinchcombe [23], and Schluter [11,15] collected small samples of **G** matrices from the literature and found that much of the available variance was concentrated in the first few dimensions. This suggests that few genetic degrees of freedom may be the norm, but we know of no

systematic review that reveals how general this pattern is or whether it differs across taxa or trait types. Likewise, although reviews on the rate of contemporary microevolution suggest that rapid evolution should be viewed as the norm rather than the exception [15,30,31], a comprehensive review of evolutionary rates across different taxa and trait types does not currently exist.

We compiled a database of reported genetic parameters from the literature to ask whether different types of traits evolve at different rates, and whether such differences correlate with differences in selection, in patterns of genetic (co)variation or both. We performed a quantitative literature review, to examine whether observed rates of evolutionary response differ across trait types (morphological, life-history and sexual) in plants and animals. We relate these observed rates of evolutionary response to estimates of linear and quadratic selection, as well as measures that capture the size, shape and structure of **G** [7,11,15-20], to determine whether there is an association across trait types and taxa. We find evidence that sexual traits evolve faster than other traits in animals but not in plants, where life-history traits evolve fastest. These increased rates of evolution do not appear to be attributable to the same cause however. In plants we find that selection also appears to be strongest on life-history traits, whereas in animals selection on sexually selected traits appears to be stronger than on life-history but indistinguishable from that on morphology. We then examined how the measures used to capture the size, shape and structure of **G** vary among trait types and between taxa, but find that this incompletely explains the observed pattern of

evolutionary rates. In addition, we compare the various measures based upon **G**, and show that for these empirically observed matrices, many strongly co-vary.

Methods

Compilation of Database

We compiled our datasets by searching for publications on the ISI Web of Science database between March 2006 and August 2012. We then refined this preliminary list of references on the basis of their title, abstract and keywords and attempted to obtain the full text for all papers included in the dataset.

Rates of evolution have been measured using a number of different units, most prominently darwins [7,10,17,18,20,22,23,43,44] and haldanes [5,17-19,21,24,43,45]. Measurements in darwins have proved most appropriate for researchers studying evolution on macro-evolutionary scales (e.g. paleontologists), since they express the rate of evolution per million years (although there are known methodological issues with making comparisons [44,46]). However, for our purposes rates expressed in haldanes are the appropriate unit as they measure change per generation and are used to measure evolution on a micro-evolutionary scale – the scale over which **G** may be important. We therefore compiled a database of evolutionary rate measured in haldanes *only*. We performed searches for the terms '*rate of evolution'*, '*rate of adaptation'*, '*haldanes*', '*response to selection*' and '*experimental evolution*'. This process was aided considerably by making use of the measurements from the studies

144 previously compiled by Hendry *et al* [26-29,47]. Where studies reported the results of
145 experimental evolution without explicitly reporting a rate of response, we contacted the
146 authors to ask for the data needed (e.g. generation time) to calculate a rate in haldanes,
147 standardizing traits as necessary. Previous work has shown that even with log
148 transformation of ratio scale data (where means and variances might co-vary), this had
149 little influence on overall estimates for haldanes [31].

150 For the database of selection gradients, we began with the database compiled by
151 Kingsolver *et al* [30,31,33,37], and supplemented this with additional measures from
152 work published after 2001 by searching for the terms '*natural selection'*, '*sexual*
153 *selection*', '*selection gradient*' or '*selection differential*'. Unlike Kingsolver *et al* [30-38]
154 we included both field and laboratory studies. While there has been discussion about
155 the effects of trait scaling (mean vs. standard deviation) on estimates of selection
156 [19,35], we have only included estimates standardized using the approach as advocated
157 by Lande and Arnold [21], which has been broadly used.

158 For the **G** matrix dataset we searched the Web of Science database using the terms '*G*
159 *matrix*' (or '*G-matrix*'), '*covariance matrix*' (or '*co-variance matrix*' or '*(co)variance*
160 *matrix*') or '*quantitative genetics*'. We recorded **G** matrices expressed both as genetic
161 (co)variances (provided we were able to mean-standardize them, following [19]) and as
162 genetic correlations and narrow sense heritabilities. Where possible (i.e. where
163 estimates of phenotypic variance had been presented alongside genetic correlations and
164 heritabilities) we back-calculated the genetic variances and covariances as: $V_A = h^2 V_P$ and

165 $Cov_{(x,y)} = r_G\sqrt{V_{A(x)}V_{A(y)}}$ where V_A and V_P are the additive genetic and phenotypic variances,
166 h^2 is the narrow sense heritability and r_G is the genetic correlation between traits *x* and
167 *y*. In cases where matrices were incomplete we contacted the author(s) to request the
168 missing estimates. We thus have two **G** datasets; correlation matrices and covariance
169 matrices. Since we found correlations to be reported more often than covariances, the
170 correlation dataset is a superset of matrices that includes those in the covariance
171 dataset. Trait scaling for the co-variance matrices is discussed below. In a number of
172 cases matrices had component traits that had been measured in difficult-to-compare
173 units (e.g. both a length and a volume), or where traits were expressed as residuals (e.g.
174 from regression against size). In these cases we excluded these from the reported
175 analysis, but inclusion had little effect on the results. A number of matrices were also
176 found to include cells with correlations >1 and in these cases we rounded the offending
177 correlation down to 1.

178 *Defining Trait Categories and Measures*

179 Since we wished to make comparisons across different 'trait types' (*sensu* [33,34,38]), it
180 was necessary to assign our measurements from the literature into categories. We
181 chose three trait categories: life-history, morphological and sexually selected traits. It is
182 relatively straightforward to separate life-history from morphological traits and the
183 majority of measurements in the literature fall into these two categories. In animals, we
184 defined sexual traits as those where we were able to find at least one study
185 demonstrating the trait was subject to female preference or used in male-male
186 competition. For plants, we defined floral morphology as sexually selected

[36,39,40,48]. Thus, for both plants and animals, our sexually selected and morphology categories are not mutually exclusive. In an attempt to reduce error in our study, traits that did not fit clearly into one of our three categories were excluded from our dataset. For **G** matrices whose component traits did not all fit the same category, we split the matrix to produce sub-matrices relating to traits only within a single category. Where matrices contained a single trait whose category differed from all others in the matrix we removed that trait from the matrix.

When making comparisons across our trait categories, we acknowledge that our classifications may not be directly equivalent in plants and animals. We therefore included a 'taxon' category in our statistical models. The list of individual measures of evolutionary rate was treated as a single response variable, as were the standardized selection gradients.

In our analysis of the **G** data, we wished to capture those attributes of **G** that might be expected to influence the rate of evolutionary change. Matrices vary principally in terms of size and structure. While numerous studies suggest that the alignment of axes of **G** with $\boldsymbol{\beta}$ is likely to be important, the nature of the data we were able to compile does not allow us to quantify alignment. Instead (as outlined below) we utilized a number of scalar measures derived from **G**, meant to capture aspects of the size and structure as a means to express evolutionary potential, All of the measures we used are summarized in Table 1. One general concern is that not all of the measured we used explicitly accounted for the number of traits included in the matrix (i.e. n_D). While, in general the

number of traits seemed to have a small influence on these measures (Figures 4 & 5), we also took several steps to account for these effects, such as including number of traits as a co-variate in the models (below) and also by examining the effects of scaling n_D by either trait number or its square ("effective subspace", as suggested by one of the manuscript referees). In none of these cases did it substantially alter the results. While we use the name "effective dimensionality" for n_D, as proposed by Kirkpatrick [20], this measure actually captures aspects of matrix eccentricity, not dimensionality.

For the dataset of **G** as mean-standardized covariance matrices we used the three **G**-structure measures suggested by Kirkpatrick [20]: 'total genetic variance' (*tgv*), 'maximum evolvability' ($e_{\max}$) & 'effective number of dimensions' (n_D), and also Hansen and Houle's [19] 'average evolvability' ($\bar{e}$). For the dataset of correlation matrices, we calculated Pavlicev *et al.*'s [49] eigenvalue variance (Var(λ)) and relative eigenvalue variance ($\mathrm{Var}_{\mathrm{rel}}(\lambda)$) and also Agrawal & Stinchcombe's [23] eigenvalue evenness (E_λ). Both sets of **G** matrix measures are defined in Table 1.

While we present results from analyses of both the (co)variance and correlation matrix datasets, it is important to note that results are not directly comparable between them, since it is well known that different methods of scaling (i.e. mean-standardizing (co)variance matrices vs. effectively variance-standardized correlation matrices) produce fundamentally different results for genetic attributes [6,19,35]. Furthermore, though the correlation matrix dataset is larger, we note that the covariance – not

228 correlation – matrix is part of the fundamental formulation for response to selection
229 [21].

230 *Statistical Analyses*

231 Analyses were performed using **R** (version 2.13.0; ref. [50]); we fit generalized linear
232 mixed-effect models using the MCMCglmm package (version 2.15; ref. [51]). A large
233 proportion of studies reporting selection gradients also reported standard errors or
234 confidence intervals (from which standard errors can be calculated). As noted by
235 Kingsolver *et al* [38], this allows for the application of formal meta-analyses, and we
236 followed their lead in modelling selection data with a meta-analysis including random-
237 effects to account for study- and species-level autocorrelation. We analysed estimates
238 of standardised selection gradients ($\boldsymbol{\beta}$) expressed as absolute values.

239 We found that standard errors or confidence intervals were reported much less
240 frequently among studies of **G** or rates of evolution, and so we were unable to account
241 for measurement error variance in these analyses as we had for selection, though the
242 model structure we used was otherwise similar. We fit a set of models, and then
243 evaluated model fit by comparing Deviance Information Criterion values (DIC) [52], and
244 confirmed our selections by refitting the model set using reduced maximum likelihood
245 (lme4 package [53]) and comparing fits using Bayesian Information Criterion scores (BIC)
246 and likelihood ratio tests (Supplemental Methods) using a parametric bootstrap. The
247 selected models for each dataset are described in Table 2, and full model sets are
248 available with the data and scripts on Dryad. Since we modelled the magnitude

249 (absolute value) of our response variables, the appropriate distribution is the folded
250 normal [38]. We therefore extracted the posterior distributions of solutions, took the
251 mean and standard deviation from these distributions and applied these to the folded
252 normal distribution. We then report the mean and credible intervals from these
253 corrected distributions [38].

254 Our data contained 2571 estimates of the rate of evolutionary response (measured in
255 haldanes); there were comparatively few estimates for plants, with no estimates
256 available on the observed rate of evolution for sexually selected (floral) traits. This
257 imbalance caused our estimates to be unstable so we modelled plant and animal rates
258 separately. We had 776 estimates of $\boldsymbol{\beta}$**,** but **G** is reported less frequently in the literature
259 (Table 3) and our sample size of **G** measures was 81 (co)variance matrices and 221
260 correlation matrices.

261

262 **Results**

263 *Observed rates of evolution differ among trait types and between plants and animals*

264 The overall posterior mean for evolutionary rate was 0.13 haldanes, with a 95% credible
265 interval from 0.08 – 0.17. Credible intervals for estimates in plants are quite wide
266 (Figure 2), most likely due to the comparatively low number of studies in these
267 categories. However there is a clear trend for faster rates in life-history traits, with the
268 life-history estimate being 2.02 times as large (95% credible interval 1.00 – 3.03) as that
269 for morphology (Table 3). In animals, life-history and morphology have similar

estimates, but the posterior mean estimate for sexually selected traits is higher – 1.48 times that for morphology (95% CI 0.78 – 2.11), and 1.51 times that for life-history (95% CI 0.50 – 2.54). These results are consistent with similar rates of evolution for morphology in both plants and animals, with higher rates for life-history traits in plants and for sexually selected traits in animals.

Standardised selection gradients show different patterns between plants and animals

The overall posterior mean for absolute linear selection gradients was 0.21 (95% CI = 0.17 – 0.26), which was somewhat higher than the estimate reported by Kingsolver et al. [38] (0.14, 95% CI = 0.13 – 0.16), most likely due to our inclusion of lab studies. The credible intervals from our full model are again wider for plants, likely reflecting smaller sample size (Table 3). For both plants and animals there is little difference between the estimates for morphological and sexually selected traits. In plants, the model suggests that selection is stronger on life-history traits, whose estimate is 40% larger than that for morphology and approximately twice that for sexually selected traits. By contrast, in animals selection appears to be weaker for life-history; the estimate for selection on life-history traits is 0.43 times (95% CI 0.11 – 0.97) that for morphology, and 0.49 times (95% CI 0.17 – 0.80) that for sexually selected traits (Figure 3).

The marginal utility of multiple measures

The magnitude, shape and alignment of the **G** matrix all have the potential to influence the rate of evolution, but with the data available we are able to use measures intended to quantify only the first two of these properties. Of the measures we report *tgv*, e_{max}

291 and $\bar{e}$ can be thought of as measures of magnitude, whereas n_D, Var(λ), $\mathrm{Var}_{\mathrm{rel}}(\lambda)$ and E_λ
292 are intended to quantify the departure of the matrix from symmetricality (how
293 dissimilar variances are along the multiple axes of **G**). It is immediately obvious that the
294 magnitude measures are doing a good job of quantifying the same property of each
295 matrix (Table 1, Figures 4 & 5), since *tgv*, $e_{\max}$ and $\bar{e}$ are all very strongly inter-correlated
296 ($r > 0.96$ in all cases). Given that these measures of magnitude are also strongly
297 correlated ($r > 0.93$ in all cases) with the magnitude of $\boldsymbol{g}_{max}$ (i.e. the principal eigenvalue
298 of **G**), it is perhaps unsurprising that they are only poorly predicted by the number of
299 traits measured, with which they are correlated only at $r = 0.15 – 0.19$.

300 With respect to the measures of matrix eccentricity, the first thing we note is that Var(λ)
301 and $\mathrm{Var}_{\mathrm{rel}}(\lambda)$ are strongly correlated with each other ($r = 0.87$), and negatively correlated
302 with E_λ ($r = -0.32$ & -0.55 respectively). Though E_λ was defined as a measure of
303 correlation matrices [23], when we applied the evenness formula to our dataset of
304 covariance matrices we find that the resulting measure is strongly correlated with
305 Kirkpatrick's [20] n_D ($r = 0.82$).

306 *The structure of **G***

307 We performed separate analyses and model selection procedures for each of our
308 measures describing the structure of **G**. Our models comparing covariance matrices
309 revealed very similar patterns of estimates for $e_{\max}$, *tgv* and $\bar{e}$. Furthermore the pattern
310 of estimates among trait types was consistent between plants and animals (Figure 6). In
311 all cases the estimates for life-history and sexually selected traits were similar and those

312 for morphology were higher, but with much overlap in credible intervals our confidence
313 in these differences is low. Our results for n_D also show consistent patterns of estimates
314 between plants and animals, with the estimates showing a shallow increasing trend
315 from life-history to morphology to sexually selected traits (Figure 6(d)), but once again
316 there is wide overlap among credible intervals, indicating low confidence in this trend.

317 The results of our analyses of **G** matrices expressed as correlations were more diverse.
318 The pattern of estimates for Var(λ) showed a trend for values to increase from life-
319 history to morphology to sexually selected traits in both plants and animals, though the
320 estimates for animals were larger than those for plants (Figure 7(a)). A similar trend was
321 present in estimates for $\mathrm{Var}_{\mathrm{rel}}(\lambda)$ for animals, thought the direction of the trend is
322 reversed in plants (Figure 7(b)). The wide overlap of credible intervals indicates low
323 confidence in both these trends however. Finally, our estimates for E_λ show a decreasing
324 trend from life-history to morphology to sexually selected traits in both plants and
325 animals, with higher estimates for plants than for animals (Figure 7(c)).

326 **Discussion**

327 Predicting the rate and direction of phenotypic evolution remains a fundamental
328 challenge in evolutionary genetics [1-4,54], with the multivariate breeders' equation
329 playing a central role. Researchers have published estimates of selection and of **G** from
330 many systems (though not commonly both in the same system). Here we have
331 integrated these data to ask if some traits generally evolve more rapidly than others,
332 and whether any differences correspond to differences in selection, **G** or both. Reviews

333 such as this are unavoidably limited by the availability of published genetic parameters,
334 and the resulting imbalances in the data. Nevertheless, we find that in animals, but not
335 plants, sexual traits evolve ~50% faster than morphological and life-history traits. We
336 find no evidence that the increased rate of evolution observed for sexual traits was due
337 to stronger selection operating on these traits relative to morphological and life-history
338 traits. We found weak evidence for differences in the evolutionary potential of **G** among
339 trait types, though this fails to provide a satisfactory explanation for the increased rates
340 of evolution associated with sexually selected traits. In addition, we confronted our
341 compiled data sets with a number of the scalar measures used to examine the size,
342 shape and structure of **G** (Table 1). We observed that many of these measures have
343 considerable shared information (Figures 4 & 5), though in general this pattern of
344 relationships would recommend the use of at least two measures; one to express the
345 magnitude of **G** and a second relating to evenness/variance of the eigenvalues. While
346 there may be particular instances where these measures result in widely divergent
347 estimates, at least with respect to the empirical estimates we have collated, the
348 marginal benefits of using all of them are an illustration of diminishing returns. We
349 speculate that one potential use (which would require considerable additional research)
350 would be in a fashion analogous to the molecular population geneticists' use of the
351 parameter Tajima's D, which is simply a scaled measure of two different estimates of
352 the population mutation rate, $4N_e\mu$. It is possible that subtle differences among scalar **G**
353 measures may ultimately provide important insights into the structure of **G**. One
354 surprising observation that emerges from our results, is that the number of traits used

355 to estimate **G** is not well correlated with any of the scalar measures we used. One
356 explanation for this becomes clear when considering that the magnitudes of the
357 principal eigenvalue of **G** is so highly correlated with total genetic variation (the trace of
358 **G**). This suggests that an overwhelming proportion of all of the variation is found along
359 this principal vector (which would differ for each **G**). However, it is well known that
360 estimating G can be difficult and insufficient sampling at the level of families can inflate
361 the magnitude of the principal eigenvalue [55,56].

362 Reviews based on published estimates of evolutionary rates [30,31] have provided a
363 number of important insights into the evolutionary process. Hendry & Kinnison [30]
364 provided the theoretical foundations for measuring evolutionary rates and used a small
365 sample of published estimates to propose that rapid evolution should be viewed as the
366 norm rather than the exception. In a much larger study, however, Kinnison & Hendry
367 [31] showed that the frequency distribution of evolutionary rates measured in haldanes
368 is log-normal (i.e. many slow rates and few fast rates, median haldanes = 5.8×10^{-3}) and
369 that life-history and morphological traits appear to evolve equally as fast when
370 measured in haldanes. In agreement with these reviews, we found that the frequency
371 distribution of evolutionary rates in our study was also log-normal and that the median
372 rate across trait types and taxa was similar (median haldanes = 7.6×10^{-3}) to that
373 reported in Kinninson & Hendry [31]. Moreover, we found little evidence to suggest that
374 the evolutionary rates of life-history and morphological traits differed in either plants or
375 animals. A novel outcome of our analysis, however, is the finding that sexual traits
376 evolve faster than life-history and morphological traits in animals. Our findings provide

evidence for a general pattern of faster evolution in sexual traits in animals to add to the highly cited individual examples of very rapid evolution of sexual traits [57,58] and their role in speciation [59,60]. More work is needed to determine whether this pattern also exists in plants.

Reviews synthesizing estimates of selection gradients are far more extensive in the literature [33-39]. In their seminal review, Kingsolver *et al*. [33] found that the frequency distributions of absolute linear and quadratic selection gradients were exponential and generally symmetrical around zero, suggesting that stabilizing and disruptive selection occur equally frequently and with similar strength in nature. Kingsolver *et al.* [33] also found that linear selection was stronger on morphological than life-history traits. The most recent review [38] containing an updated data set and using formal Bayesian meta-analysis to control for potential biases [34,35,37] confirmed many of the main findings of Kingsolver *et al*. [33], with the notable exception that linear selection appears stronger in plants than animals.

In agreement with this most recent review [38], we found that the distribution of absolute linear and quadratic selection gradients were exponential (see Supplement). However, our estimates for absolute linear selection gradients were higher than reported by Kingsolver *et al.* [38] (0.24 (0.17, 0.26) versus 0.14 (0.13, 0.16)). This raises the obvious question of why this difference occurs. There has been much discussion on the general limitations of using selection gradients in synthetic reviews (e.g. [33,35,37,38] and these arguments undoubtedly also apply to our study. However, as

398 most of these limitations are inherent to both studies, it is unlikely that they explain the
399 observed differences. Furthermore, given that we used the same Bayesian framework as
400 Kingsolver et al. [38] it is also unlikely that our analytical approach has generated the
401 observed differences. The most likely reason for the observed differences is the way
402 that traits and taxa were categorized across these studies. Kingsolver et al. [38] used
403 four different trait categories (size, morphological (not including size), phenology and
404 life-history (not including phenology)) and categorized taxa as invertebrates, vertebrates
405 or plants in their analysis. In contrast, we only distinguished between animals and plants
406 and used three different trait categories (morphological, life-history and sexual) in our
407 analysis, the latter of which includes a mixture of morphological and behavioural traits.
408 Thus, there are likely to be some differences in how selection gradients are distributed
409 amongst categories in our analyses compared to those in Kingsolver et al. [38] and this
410 may account for the observed differences between studies. Irrespective of the
411 underlying reasons for these differences, our main finding that there is little difference
412 in selection gradients across trait types and taxa suggests that selection alone is unlikely
413 to explain the higher rate of evolutionary response we observe for sexual traits in
414 animals.

415 After decades of quantitative genetic research it is now widely accepted that the
416 additive genetic variance-covariance matrix (**G**) plays a major role in
417 facilitating/constraining phenotypic evolution [16,19,20]. The way in which **G** shapes
418 phenotypic evolution can be envisaged using the concept of genetic degrees of freedom
419 (Figure 1; [9,15]). Whenever there is genetic covariation between the individual traits

420 contained in **G**, there is the potential for fewer axes of genetic variation than observed
421 traits [9,15,61,62] (but see [63]), which can influence evolutionary rates [64]. Where the
422 majority of the genetic variance is concentrated in a few direction – known as "lines of
423 least evolutionary resistance" [15] – these have been shown to play an important role in
424 directing the short-term evolutionary trajectory of a population [15,65-69]. Quantifying
425 these properties of **G** is an essential step if we are to explore these ideas empirically.
426 Our comparison of a number of the measures that have been proposed to fit this role
427 indicates that, however informative it may or may not prove to be, we are able to
428 reliably quantify the magnitude of **G**, since we find broad agreement among magnitude
429 measures. Perhaps unsurprisingly, it seems that the magnitude of a matrix is somewhat
430 more straightforward to describe with a scalar measure than the eigenvalue
431 evenness/eccentricity/dimensionality. The measures available for quantification of the
432 shape of **G** in multiple dimensions are much less tightly inter-correlated than those
433 dealing with matrix magnitude when compared using empirical data. What this
434 ultimately means for our understanding of evolvability is unclear, but it is important to
435 acknowledge the gaps in out current understanding if we are to progress.

436 The finding that genetic variance for sexual traits may be spread less evenly across
437 dimensions in animals runs counter to our hypothesis, and suggests that the potential
438 for genetic constraints does not explain the higher rate of evolution we observe for
439 these traits. We found at best, only weak evidence for differences in the measures to
440 capture the size and shape of **G** with respect to our trait groupings. There has been
441 debate over the importance of sexual selection in plants [70], but there is theoretical

442 [48] and empirical [71] evidence suggesting that floral morphology is indeed subject to
443 sexual selection. Unfortunately though, there are currently no data on evolutionary
444 rates for sexual traits in plants, making it difficult to understand the implications of this
445 increased dimensionality. Our findings indicate that the subject warrants greater
446 attention. Additionally, when considering these issues, researchers also need to keep in
447 mind that their decisions about measurement scaling issues are likely to be important
448 when measuring selection [35] and genetic variability [6]. This is especially important
449 when addressing the question of evolvability, where both these measures must be
450 brought together [19].

451 Collectively, our results suggest that the higher rate of evolution observed for sexual
452 traits in animals is only weakly associated with these scalar measures summarizing **G** for
453 these traits rather than stronger selection. However, as our data set is based on derived
454 estimates of evolutionary rates, standardized selection gradients and **G**, there are a
455 number of inevitable limitations that apply to our findings. First, there are limitations
456 with using the matrix structure measures (n_D, $E\lambda$, $Var(\lambda)$ or $Var_{rel}(\lambda)$) to capture the
457 dimensionality of **G** [20]. Although these measure are calculable from published
458 estimates of **G**, they do not explicitly test how many of the dimensions of **G** actually
459 exist (i.e. have statistical support). A number of approaches [63,72] have been taken to
460 directly estimate the dimensionality of **G** [72,73] though such studies have found both
461 populations that have evolutionary access to all dimensions of **G** [63] and others that
462 are constrained by LLER's [72,74]. Second, our analysis does not consider the alignment
463 between the vectors of selection and **G**. LLER's only constrain the response to selection

when they are poorly aligned with vectors of selection [26,28,75]. These limitations can only be resolved by further analysis of the raw data sets contained in the original studies we review. This is particularly true for better estimation of **G** itself, as well as its actual dimensionality, which can only be performed with the raw data [56,61,63,76-79]. Future studies would therefore greatly benefit from researchers publishing their raw datasets in open repositories [80] and we strongly encourage researchers to do so. Our database can be found at DRYAD DOI:xxxxxxxx.

Acknowledgements

We thank S.F. McDaniel and W.U. Blanckenhorn for donating unpublished matrices and to R. Snook, S. Chenoweth, T. Chapman, R. Firman, and M. Reuter for data on experimental evolution. I. Stott, F. Ingleby and two anonymous reviewers provided comments on an earlier draft of this manuscript. JH, TT and JBW were funded by NERC, JH and JBW by the BBSRC and JH by a University Royal Society Fellowship. WP was supported by a NERC studentship (awarded to JH and TT) and ID & WP were funded by NIH grant no. 1R01GM094424.

References

1. Arnold, S., Pfrender, M. & Jones, A. 2001 The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* **112**, 9–32.

2. Merilä, J., Kruuk, L. & Sheldon, B. 2001 Natural selection on the genetical

component of variance in body condition in a wild bird population. *Journal of Evolutionary Biology* **14**, 918–929.

3. Bégin, M. & Roff, D. A. 2003 The constancy of the G matrix through species divergence and the effects of quantitative genetic constraints on phenotypic evolution: A case study in crickets. *Evolution* **57**, 1107–1120.

4. Walsh, B. & Blows, M. W. 2009 Abundant genetic variation+ strong selection= multivariate genetic constraints: a geometric view of adaptation. *Annual Review of Ecology*

5. Lande, R. 1979 Quantitative Genetic-Analysis of Multivariate Evolution, Applied to Brain - Body Size Allometry. *Evolution* **33**, 402–416.

6. Houle, D. 1992 Comparing evolvability and variability of quantitative traits. *Genetics* **130**, 195–204.

7. Roff, D. A. 1997 Evolutionary quantitative genetics.

8. Roff, D. A. & Mousseau, T. A. 1987 Quantitative genetics and fitness: lessons from Drosophila. *Heredity* **58 (Pt 1)**, 103–118.

9. Kirkpatrick, M. & Lofsvold, D. 1992 Measuring selection and constraint in the evolution of growth. *Evolution* **46**, 954–971.

10. Bell, G. 1997 *Selection: the mechanism of evolution*. Springer.

11. Schluter, D. 2000 *The Ecology of Adaptive Radiation (Oxford Series in Ecology & Evolution)*. 1st edn. Oxford University Press, USA.

12. Schluter, D. 2001 Ecology and the origin of species. *Trends Ecol Evol* **16**, 372–380.

13. Moose, S. P., Dudley, J. W. & Rocheford, T. R. 2004 Maize selection passes the century mark: a unique resource for 21st century genomics. *Trends in Plant Science* **9**, 358–364. (doi:10.1016/j.tplants.2004.05.005)

14. Powell, R. L. & Norman, H. D. 2006 Major Advances in Genetic Evaluation Techniques. *J Dairy Sci* **89**, 1337–1348. (doi:10.3168/jds.S0022-0302(06)72201-9)

15. Schluter, D. 1996 Adaptive radiation along genetic lines of least resistance. *Evolution* **50**, 1766–1774.

16. Blows, M. & Hoffmann, A. 2005 A reassessment of genetic limits to evolutionary change. *Ecology* **86**, 1371–1384.

17. Blows, M. W. 2007 A tale of two matrices: multivariate approaches in evolutionary biology. *Journal of Evolutionary Biology* **20**, 1–8. (doi:10.1111/j.1420-9101.2006.01164.x)

18. Blows, M. & Walsh, B. 2009 Spherical cows grazing in flatland: constraints to selection and adaptation. *Adaptation and Fitness in Animal Populations*, 83–101.

19. Hansen, T. F. & Houle, D. 2008 Measuring and comparing evolvability and constraint in multivariate characters. *Journal of Evolutionary Biology* **21**, 1201–1219. (doi:10.1111/j.1420-9101.2008.01573.x)

20. Kirkpatrick, M. 2008 Patterns of quantitative genetic variation in multiple dimensions. *Genetica* **136**, 271–284. (doi:10.1007/s10709-008-9302-6)

21. Lande, R. & Arnold, S. 1983 The Measurement of Selection on Correlated Characters. *Evolution* **37**, 1210–1226.

22. Hansen, T. F., Pélabon, C. & Houle, D. 2011 Heritability is not Evolvability. *Evol Biol* **38**, 258–277. (doi:10.1007/s11692-011-9127-6)

23. Agrawal, A. F. & Stinchcombe, J. R. 2008 How much do genetic covariances alter the rate of adaptation? *P R Soc B* **276**, 1183–1191. (doi:10.1098/rspb.2008.1671)

24. Hunt, J., Wolf, J. & Moore, A. 2007 The biology of multivariate evolution. *Journal of Evolutionary Biology* **20**, 24–27.

25. Dickerson, G. E. 1955 Genetic Slippage in Response to Selection for Multiple Objectives. *Cold Spring Harbor Symposia on Quantitative Biology* **20**, 213–224. (doi:10.1101/SQB.1955.020.01.020)

26. Blows, M. W., Chenoweth, S. F. & Hine, E. 2004 Orientation of the Genetic Variance-Covariance Matrix and the Fitness Surface for Multiple Male Sexually Selected Traits. *Am Nat* **163**, 329–340. (doi:10.1086/381941)

27. Hine, E., Chenoweth, S. F. & Blows, M. W. 2004 Multivariate quantitative genetics and the lek paradox: Genetic variance in male sexually selected traits of Drosophila serrata under field conditions. *Evolution* **58**, 2754–2762.

28. van Homrigh, A., Higgie, M., McGuigan, K. & Blows, M. W. 2007 The depletion of genetic variance by sexual selection. *Curr Biol* **17**, 528–532. (doi:10.1016/j.cub.2007.01.055)

29. Simonsen, A. K. & Stinchcombe, J. R. 2010 Quantifying Evolutionary Genetic Constraints in the Ivyleaf Morning Glory, Ipomoea hederacea. *Int J Plant Sci*

171, 972–986. (doi:10.1086/656512)

30. Hendry, A. & Kinnison, M. 1999 Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653.

31. Kinnison, M. & Hendry, A. 2001 The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112**, 145–164.

32. Mousseau, T. & Roff, D. 1987 Natural-selection and the heritability of fitness components. *Heredity* **59**, 181–197.

33. Kingsolver, J., Hoekstra, H., Hoekstra, J., Berrigan, D., Vignieri, S., Hill, C., Hoang, A., Gibert, P. & Beerli, P. 2001 The strength of phenotypic selection in natural populations. *Am Nat* **157**, 245–261.

34. Hoekstra, H., Hoekstra, J., Berrigan, D., Vignieri, S., Hoang, A., Hill, C., Beerli, P. & Kingsolver, J. 2001 Strength and tempo of directional selection in the wild. *P Natl Acad Sci Usa* **98**, 9157–9160.

35. Hereford, J., Hansen, T. F. & Houle, D. 2004 Comparing strengths of directional selection: how strong is strong? *Evolution* **58**, 2133–2143.

36. Siepielski, A. M., DiBattista, J. D. & Carlson, S. M. 2009 It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol Lett* **12**, 1261–1276. (doi:10.1111/j.1461-0248.2009.01381.x)

37. Kingsolver, J. G. & Diamond, S. E. 2011 Phenotypic Selection in Natural Populations: What Limits Directional Selection? *Am Nat* **177**, 346–357. (doi:10.1086/658341)

38. Kingsolver, J. G., Diamond, S. E., Siepielski, A. M. & Carlson, S. M. 2012 Synthetic analyses of phenotypic selection in natural populations: lessons, limitations and future directions. *Evol Ecol* **26**, 1101–1118. (doi:10.1007/s10682-012-9563-5)

39. Siepielski, A. M., DiBattista, J. D., Evans, J. A. & Carlson, S. M. 2011 Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *P R Soc B* **278**, 1572–1580. (doi:10.1098/rspb.2010.1973)

40. Morrissey, M. B. & Hadfield, J. D. 2012 Directional selection in temporally replicated studies is remarkably consistent. *Evolution* **66**, 435–442. (doi:10.1111/j.1558-5646.2011.01444.x)

41. Houle, D., Pélabon, C., Wagner, G. P. & Hansen, T. F. 2011 Measurement

and meaning in biology. *Q Rev Biol* **86**, 3–34.

42. Pomiankowski, A. & Moller, A. 1995 A resolution of the lek paradox. *P Roy Soc Lond B Bio* **260**, 21–29.

43. Haldane, J. B. S. 1949 Suggestions as to quantitative measurement of rates of evolution. *Evolution* **3**, 51–56.

44. Gingerich, P. D. 1983 Rates of evolution: effects of time and temporal scaling. *Science* **222**, 159–161. (doi:10.1126/science.222.4620.159)

45. Gingerich, P. 1993 Quantification and comparison of evolutionary rates. *American Journal of Science* **293-A**, 453–478.

46. Uyeda, J. C., Hansen, T. F., Arnold, S. J. & Pienaar, J. 2011 The million-year wait for macroevolutionary bursts. *Proceedings of the National Academy of Sciences* **108**, 15908–15913. (doi:10.1073/pnas.1014503108)

47. Hendry, A. P., Farrugia, T. J. & Kinnison, M. T. 2008 Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* **17**, 20–29. (doi:10.1111/j.1365-294X.2007.03428.x)

48. Moore, J. C. & Pannell, J. R. 2011 Sexual selection in plants. *Curr Biol* **21**, R176–82. (doi:10.1016/j.cub.2010.12.035)

49. Pavlicev, M., Cheverud, J. M. & Wagner, G. P. 2009 Measuring Morphological Integration Using Eigenvalue Variance. *Evol Biol* **36**, 157–170. (doi:10.1007/s11692-008-9042-7)

50. Team, R. C. D. In press. R: A language and environment for statistical computing.

51. Hadfield, J. D. 2010 MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software* **33**, 1–22.

52. Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & Van Der Linde, A. 2002 Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **64**, 583–639.

53. Bates, D., Maechler, M. & Bolker, B. In press. lme4: Linear mixed-effects models using S4 classes.

54. Hill, W. G. & Zhang, X. S. 2012 On the Pleiotropic Structure of the Genotype-Phenotype Map and the Evolvability of Complex Organisms. *Genetics* **190**, 1131–1137. (doi:10.1534/genetics.111.135681)

618 55. Hill, W. G. & Thompson, R. 1978 Probabilities of Non-Positive Definite
619 Between-Group or Genetic Covariance Matrices. *Biometrics* **34**, 429–439.

620 56. Meyer, K. & Kirkpatrick, M. 2010 Better Estimates of Genetic Covariance
621 Matrices by 'Bending' Using Penalized Maximum Likelihood. *Genetics* **185**,
622 1097–1110. (doi:10.1534/genetics.109.113381)

623 57. Mendelson, T. C. & Shaw, K. L. 2005 Sexual behaviour: rapid speciation in an
624 arthropod. *Nature* **433**, 375–376. (doi:10.1038/433375a)

625 58. Zuk, M., Rotenberry, J. T. & Tinghitella, R. M. 2006 Silent night: adaptive
626 disappearance of a sexual signal in a parasitized population of field crickets.
627 *Biol Lett-Uk* **2**, 521–524. (doi:10.1098/rsbl.2006.0539)

628 59. Panhuis, T. M., Butlin, R., Zuk, M. & Tregenza, T. 2001 Sexual selection and
629 speciation. *Trends Ecol Evol* **16**, 364–371. (doi:10.1016/S0169-
630 5347(01)02160-7)

631 60. Ritchie, M. G. 2007 Sexual Selection and Speciation. *Annu Rev Ecol Evol S* **38**,
632 79–102. (doi:10.1146/annurev.ecolsys.38.091206.095733)

633 61. Hine, E. & Blows, M. W. 2006 Determining the effective dimensionality of
634 the genetic variance-covariance matrix. *Genetics* **173**, 1135–1144.
635 (doi:10.1534/genetics.105.054627)

636 62. McGuigan, K. & Blows, M. W. 2007 The phenotypic and genetic covariance
637 structure of drosphilid wings. *Evolution* **61**, 902–911. (doi:10.1111/j.1558-
638 5646.2007.00078.x)

639 63. Mezey, J. & Houle, D. 2005 The dimensionality of genetic variation for wing
640 shape in Drosophila melanogaster. *Evolution* **59**, 1027–1038.

641 64. McGuigan, K. 2006 Studying phenotypic evolution using multivariate
642 quantitative genetics. *Molecular Ecology* **15**, 883–896. (doi:10.1111/j.1365-
643 294X.2006.02809.x)

644 65. Badyaev, A. V. & Foresman, K. R. 2000 Extreme environmental change and
645 evolution: stress-induced morphological variation is strongly concordant
646 with patterns of evolutionary divergence in shrew mandibles. *Proc. Biol. Sci.*
647 **267**, 371–377. (doi:10.1098/rspb.2000.1011)

648 66. McGuigan, K., Chenoweth, S. F. & Blows, M. W. 2005 Phenotypic divergence
649 along lines of genetic variance. *Am Nat* **165**, 32–43.

650 67. Renaud, S., Auffray, J.-C. & Michaux, J. 2006 Conserved phenotypic variation
651 patterns, evolution along lines of least resistance, and departure due to

652 selection in fossil rodents. *Evolution* **60**, 1701–1717.

653 68. Chenoweth, S. F. & McGuigan, K. 2010 The Genetic Basis of Sexually
654 Selected Variation - Annual Review of Ecology, Evolution, and Systematics,
655 41(1):81. *Annual Review of Ecology*

656 69. Boell, L. 2013 Lines of least resistance and genetic architecture of house
657 mouse (Mus musculus) mandible shape. *Evol Dev* **15**, 197–204.
658 (doi:10.1111/ede.12033)

659 70. Skogsmyr, I. & Lankinen, S. 2002 Sexual selection: an evolutionary force in
660 plants? *Biol Rev* **77**, 537–562. (doi:10.1017/S1464793102005973)

661 71. Carlson, J. E. 2008 Hummingbird responses to gender-biased nectar
662 production: are nectar biases maintained by natural or sexual selection? *P R*
663 *Soc B* **275**, 1717–1726. (doi:10.1098/rspb.2008.0017)

664 72. Hine, E. & Blows, M. 2006 Determining the effective dimensionality of the
665 genetic variance-covariance matrix. *Genetics* **173**, 1135–1144.
666 (doi:10.1534/genetics.105.054627)

667 73. Mezey, J. G. 2005 Naturally Segregating Quantitative Trait Loci Affecting
668 Wing Shape of Drosophila melanogaster. *Genetics* **169**, 2101–2113.
669 (doi:10.1534/genetics.104.036988)

670 74. Hunt, J., Blows, M. W., Zajitschek, F., Jennions, M. D. & Brooks, R. 2007
671 Reconciling strong stabilizing selection with the maintenance of genetic
672 variation in a natural population of black field crickets (*Teleogryllus*
673 *commodus*). *Genetics* **177**, 875–880. (doi:10.1534/genetics.107.077057)

674 75. McGuigan, K. 2006 Studying phenotypic evolution using multivariate
675 quantitative genetics. *Molecular Ecology* **15**, 883–896. (doi:10.1111/j.1365-
676 294X.2006.02809.x)

677 76. Meyer, K. 2007 WOMBAT—A tool for mixed model analyses in quantitative
678 genetics by restricted maximum likelihood (REML). *J. Zhejiang Univ. - Sci. B*
679 **8**, 815–821. (doi:10.1631/jzus.2007.B0815)

680 77. Kirkpatrick, M. 2004 Direct Estimation of Genetic Principal Components:
681 Simplified Analysis of Complex Phenotypes. *Genetics* **168**, 2295–2306.
682 (doi:10.1534/genetics.104.029181)

683 78. de los Campos, G. & Gianola, D. 2007 Factor analysis models for structuring
684 covariance matrices of additive genetic effects: a Bayesian implementation.
685 *Genet Sel Evol* **39**, 481–494. (doi:10.1186/1297-9686-39-5-481)

686 79. Runcie, D. E. & Mukherjee, S. 2013 Dissecting High-Dimensional Phenotypes
687 with Bayesian Sparse Factor Analysis of Genetic Covariance Matrices.
688 *Genetics* **194**, 753–767. (doi:10.1534/genetics.113.151217)

689 80. Whitlock, M. C., McPeek, M. A., Rausher, M. D., Rieseberg, L. & Moore, A. J.
690 2010 Data Archiving. *Am Nat* **175**, 145–146. (doi:10.1086/650340)

691

692

692 **Figure Legends**

693 **Figure 1.** The effect of $\mathbf{g}_{max}$ on the response to selection where traits genetically covary.
694 The axes represent the breeding values for 2 hypothetical traits. The population mean is
695 at the solid point and the surrounding ellipse is the 95% confidence region for the
696 distribution of trait values about the mean. That these traits covary is evident as the
697 ellipse is at an angle relative to the trait axes. The axes of the ellipse represent the 2
698 orthogonal directions (eigenvectors) of variance present – there is more standing
699 genetic variance along the major axis ($\mathbf{g}_{max}$) than the minor axis. They grey lines are
700 'contours' on a fitness landscape, with an adaptive peak at 'S'. Rather than evolving
701 directly toward the peak (dashed arrow), the influence of $\mathbf{g}_{max}$ may cause the population
702 to evolve along an indirect course (bold arrow). In some cases this may even, result in
703 the population evolving toward an alternate fitness peak (e.g. at 'A', modified contours
704 not shown) in line with $\mathbf{g}_{max}$, even though it is more distant from the current mean.

705

706 **Figure 2.** Posterior means and 95% credible intervals for estimates of absolute rate of
707 evolution (haldanes). Open points are for plants and filled points for animals. Trait types
708 are life-history (LH), morphology (M) and sexually selected (S) and filled points are for
709 animals and open points for plants (no data available for sexual traits in plants).

710

711 **Figure 3.** Posterior means and 95% credible intervals for estimates of standardized
712 selection gradients ($\boldsymbol{\beta}$) by trait type. Trait labels and taxon symbols are as in Figure 2.

713

714 **Figure 4.** Pairs plot to illustrate the relationships between measures used to describe
715 the structure of G expressed as covariance matrices. Measures are 'total genetic
716 variance' (*tgv*), 'maximum evolvability' ($e_{\max}$) & 'effective number of dimensions' (n_D)
717 [20], the first eigenvalue of **G** ($\mathbf{g}_{\max}$), 'average evolvability' ($\bar{e}$) [19], 'eigenvalue evenness'
718 (E_λ – originally intended for use with correlation matrices [23]) and the number of traits
719 included in the matrix (k). Figures in the lower off-diagonal are pairwise correlations
720 between the measures.

721

722 **Figure 5.** Pairs plot to illustrate the relationships between measures used to describe
723 the structure of G expressed as correlation matrices. Measures are 'eigenvalue variance'
724 (Var(λ)) [49], 'eigenvalue evenness' (E_λ) [23], 'relative eigenvalue variance' ($\mathrm{Var}_{\mathrm{rel}}(\lambda)$)
725 [49], the first eigenvalue of **G** ($\mathbf{g}_{\max}$) and the number of traits included in the matrix (k).
726 Figures in the lower off-diagonal are pairwise correlations between the measures.

727

728 **Figure 6.** Posterior means and 95% credible intervals for the four measures used to
729 characterise **G** matrices expressed as covariances (see methods section); (a) 'maximum
730 evolvability' ($e_{\max}$), (b) 'total genetic variance' (*tgv*), (c) 'average evolvability' ($\bar{e}$) and (d)

731 ‘effective dimensionality’ (n_D). Trait types are life-history (LH), morphology (M) and

732 sexually selected (S) and filled points are for animals and open points for plants.

733

734 **Figure 7.** Posterior means and 95% credible intervals for the four measures used to

735 characterise **G** matrices expressed as correlations (see methods section); (a) ‘eigenvalue

736 variance’ (Var(λ)), (b) relative eigenvalue variance’ ($\mathrm{Var}_{\mathrm{rel}}(\lambda)$) and (c) ‘eigenvalue

737 evenness’ (E_λ). Trait labels and taxon symbols are as in Figure 6.

738

Table 1. G-matrix metrics used in this study. Eigenvalue variance, relative eigenvalue variance and eigenvalue evenness are calculated from correlation matrices, whereas the other four metrics are calculated from covariance matrices. In all formulae λ are eigenvalues and n is the number of traits in the matrix (rank).* n_D does not measure dimensionality per se, but eccentricity.

Measure	Cov/cor	Reference	Equation #	Formula
effective number of dimensions* (n_D)	cov	[20]	#2 (pg 273)	$n_D = \sum_{i=1}^{n} \lambda_i / \lambda_1$
maximum evolvability (e_{max})	cov	[20]	#3 (pg 274)	$e_{\max} = \sqrt{\lambda_1}$
total genetic variance (v_T)	cov	[20]	#4 (pg 274)	$v_T = \sum_{i=1}^{n} \lambda_i$
average evolvability ($\bar{e}$)	cov	[19]	#4 (pg 1206)	$\bar{e} = \sum_i \lambda_i \big/ n$
eigenvalue variance (Var(λ))	cor	[49]	n/a (pg 158)	$Var(\lambda) = \sum_{i=1}^{n} (\lambda_i - 1)^2 \big/ n$
Relative eigenvalue variance ($Var_{rel}(\lambda)$)	cor	[49]	n/a (pg 159)	$Var_{rel}(\lambda) = Var(\lambda) \big/ n-1$
eigenvalue evenness (E_λ)	cor	[23]	#3.2 (pg 1187)	$E_\lambda = -\sum_{i=1}^{n} \frac{\tilde{\lambda}_i \ln(\tilde{\lambda}_i)}{\ln(n)}$ where $\tilde{\lambda}_i = \lvert\lambda_i\rvert / \sum_{j=1}^{n} \lvert\lambda_j\rvert$

745 **Table 2.** The main effects included in the final models for each analysis. (Effects of 'trait
746 type' refer to life-history, morphology or sexual and 'taxa' to plant or animal. 'Study
747 type' refers to field observation or experimental evolution. Random effects of 'study'
748 and 'species' refer to models where an intercept was fitted to each species and study,
749 and the random effect of 'trait type:species' indicates where both a species-level
750 intercept and a species-level trait type effect were fitted.) Full sets of models can be
751 found in the scripts and data on Dryad.

752

measure	fixed effects	random effects
Rate (Animals)	trait type + study type	study + trait type:species
Rate (Plants)	trait type	species
|β|	trait type + taxon + trait type x taxon	study + species
(**G**) *n*D	trait type + taxon + trait no.	study
(**G**) e_{max}	trait type + taxon + trait no.	study + trait type:species
(**G**) *tgv*	trait type + taxon + trait no.	study + trait type:species
(**G**) $\bar{e}$	trait type + taxon + trait no.	study + trait type:species
(**G**) Var(λ)	trait type + taxon + trait no.	study
(**G**) $Var_{rel}(\lambda)$	trait type + taxon + trait no.	study
(**G**) E_{λ}	trait type + taxon + trait no.	study

753

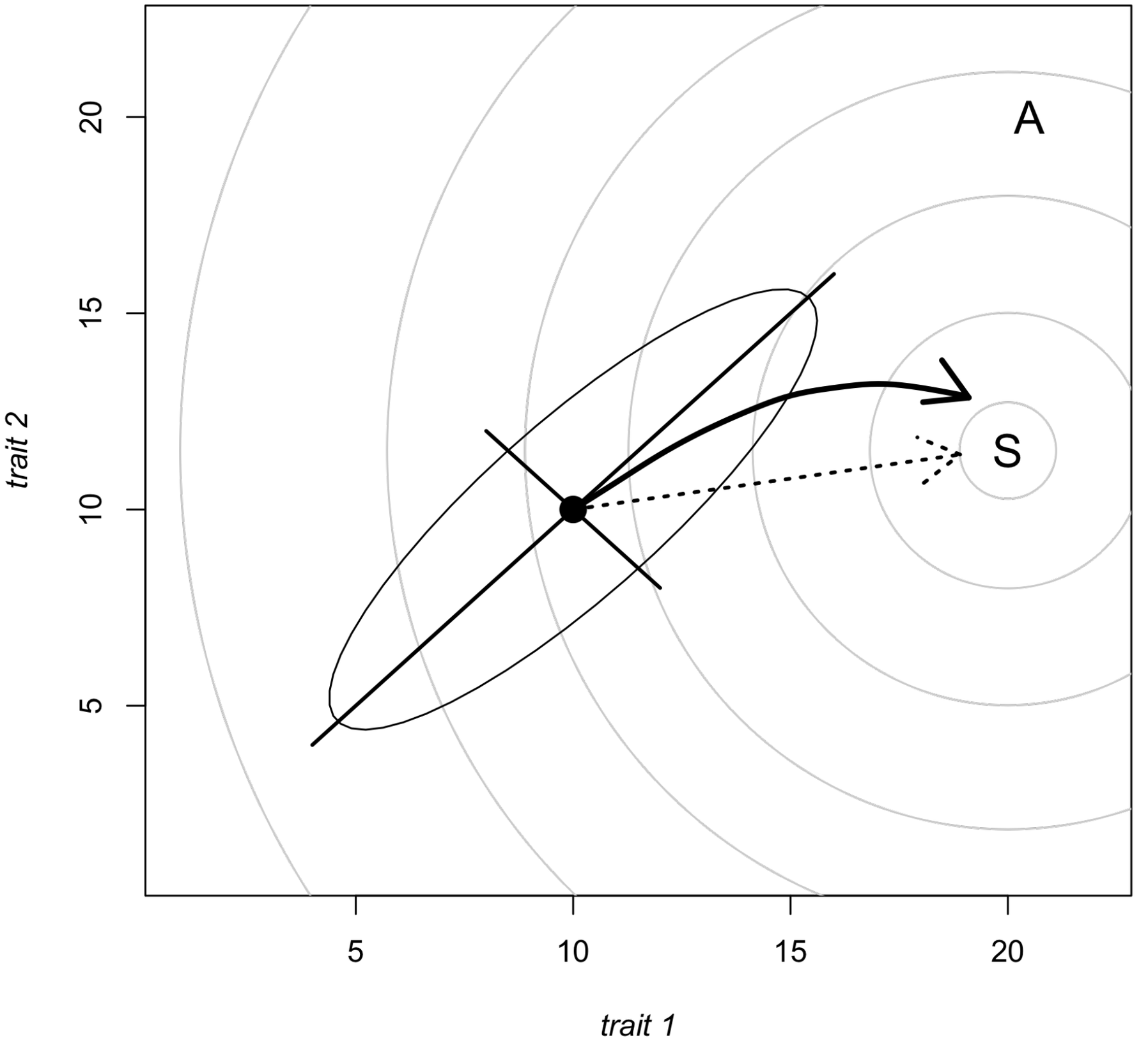
754

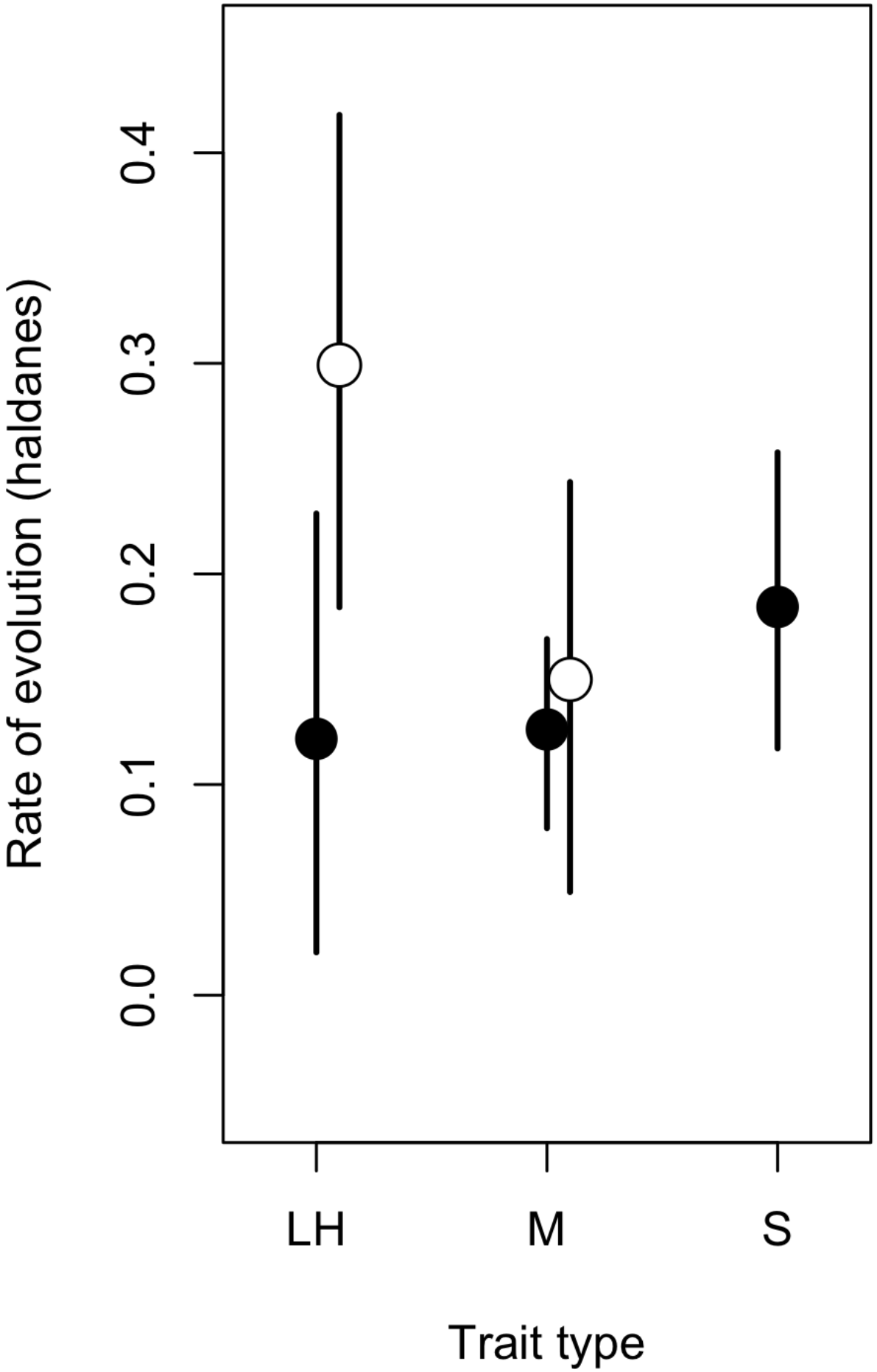
Table 3. Summary statistics for estimates of the rate of evolutionary response, linear and quadratic selection gradients and measure capturing the size, shape and structure of **G**. (Statistics are reported by taxa and trait type, together with overall estimates across trait types and taxa. For each combination of taxa and trait type, the summary statistics for each measure are provided in the following order: posterior mean, posterior mode, lower and upper 95% credible intervals (in parenthesis) and sample size (in italics).)

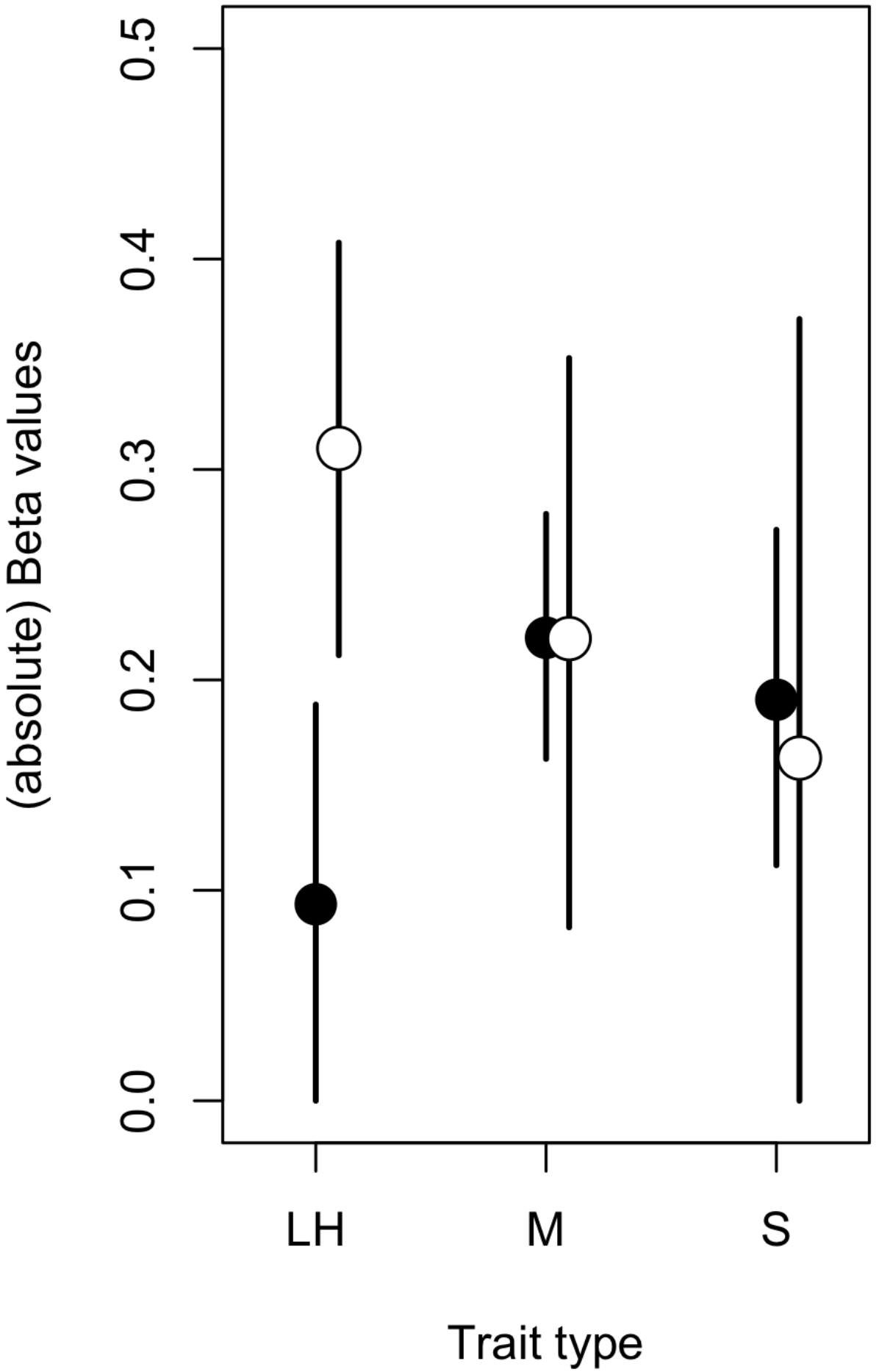
measure	**animals**			**overall**		**plants**
	LH	**M**	**SS**	all traits	**LH**	**M**
Rate (haldanes)	0.12	0.13	0.18	0.13	0.3	0.15
	0.122	0.12	0.193	0.101	0.332	0.181
	(0.02,0.22)	(0.09,0.17)	(0.10,0.26)	(0.08,0.17)	(0.18,0.42)	(0.05,0.25)
	781	*7*	*1667*	*2571*	*26*	*90*
$\lvert\beta\rvert$	0.09	0.22	0.19	0.21	0.31	0.22
	0.157	0.215	0.167	0.242	0.334	0.344
	(0.00,0.19)	(0.16,0.28)	(0.11,0.27)	(0.17,0.26)	(0.22,0.41)	(0.09,0.36)
	65	*342*	*150*	*776*	*156*	*44*
(**G**) *n*D	1.13	1.20	1.31	1.53	1.23	1.29
	1.40	1.19	2.06	1.50	1.28	0.98
	(0.76,1.5)	(0.82,1.54)	(0.85,1.82)	(1.39,1.67)	(0.77,1.65)	(0.86,1.71)
(**G**) e_{max}	0.43	1.25	0.78	0.61	0.59	0.91
	0.26	0.01	0.86	0.47	0.89	0.57
	(0,1.04)	(0,2.83)	(0,1.88)	(0.26,0.97)	(0,1.39)	(0,2.22)
(**G**) *tgv*	8.62	25.41	14.32	3.14	9.38	24.09
	17.16	23.57	21.19	7.67	17.37	39.68
	(0.01,18.11)	(0.3,52.47)	(0,30.89)	(0,7.57)	(0.01,19.64)	(0.01,50.48)
(**G**) $\bar{e}$	1.17	3.69	1.95	0.48	1.29	3.40
	0.55	1.74	1.29	0.25	0.80	0.67
	(0,2.94)	(0.01,8.55)	(0,4.75)	(0,1.15)	(0,3.2)	(0,7.83)
n (cov)	*14*	*38*	*10*	*81*	*1*	*3*
(**G**) Var(λ)	0.43	0.60	0.80	1.40	0.63	0.49
	0.39	0.79	1.19	1.11	0.99	0.25
	(0,1.04)	(0,1.32)	(0,1.68)	(0.92,1.86)	(0,1.41)	(0,1.17)
(**G**) $\mathrm{Var}_{rel}(\lambda)$	0.36	0.43	0.50	0.32	0.16	0.23
	0.45	0.46	0.49	0.35	0.07	0.24
	(0.15,0.56)	(0.22,0.63)	(0.25,0.75)	(0.23,0.41)	(0,0.33)	(0,0.42)
(**G**) E_{λ}	0.76	0.70	0.67	0.73	0.86	0.79

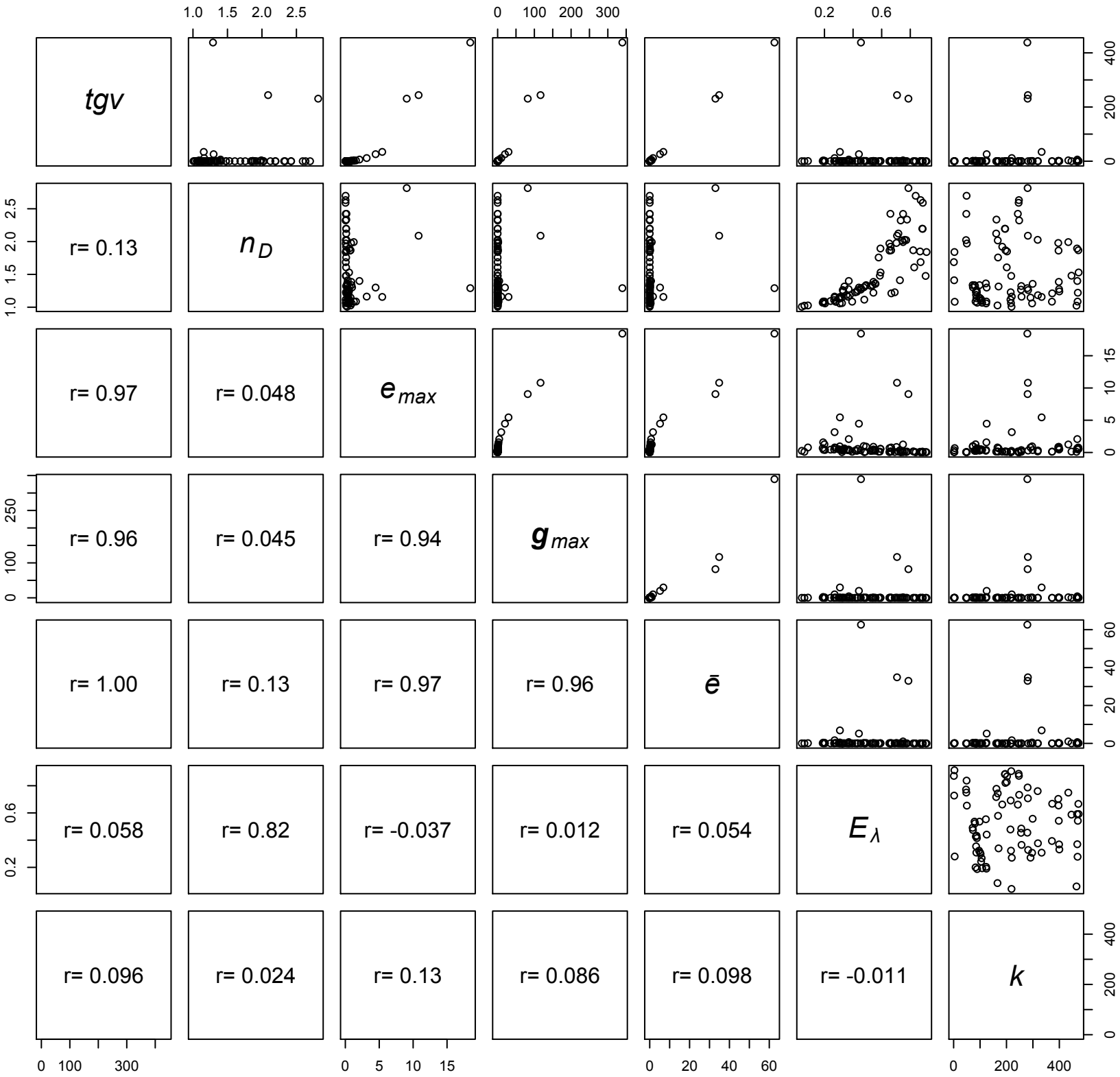
	0.78 (0.67,0.84)	0.77 (0.61,0.77)	0.69 (0.57,0.77)	0.76 (0.70,0.77)	0.80 (0.77,0.94)	0.81 (0.71,0.87)
n (cor)	42	82	27	*221*	14	26

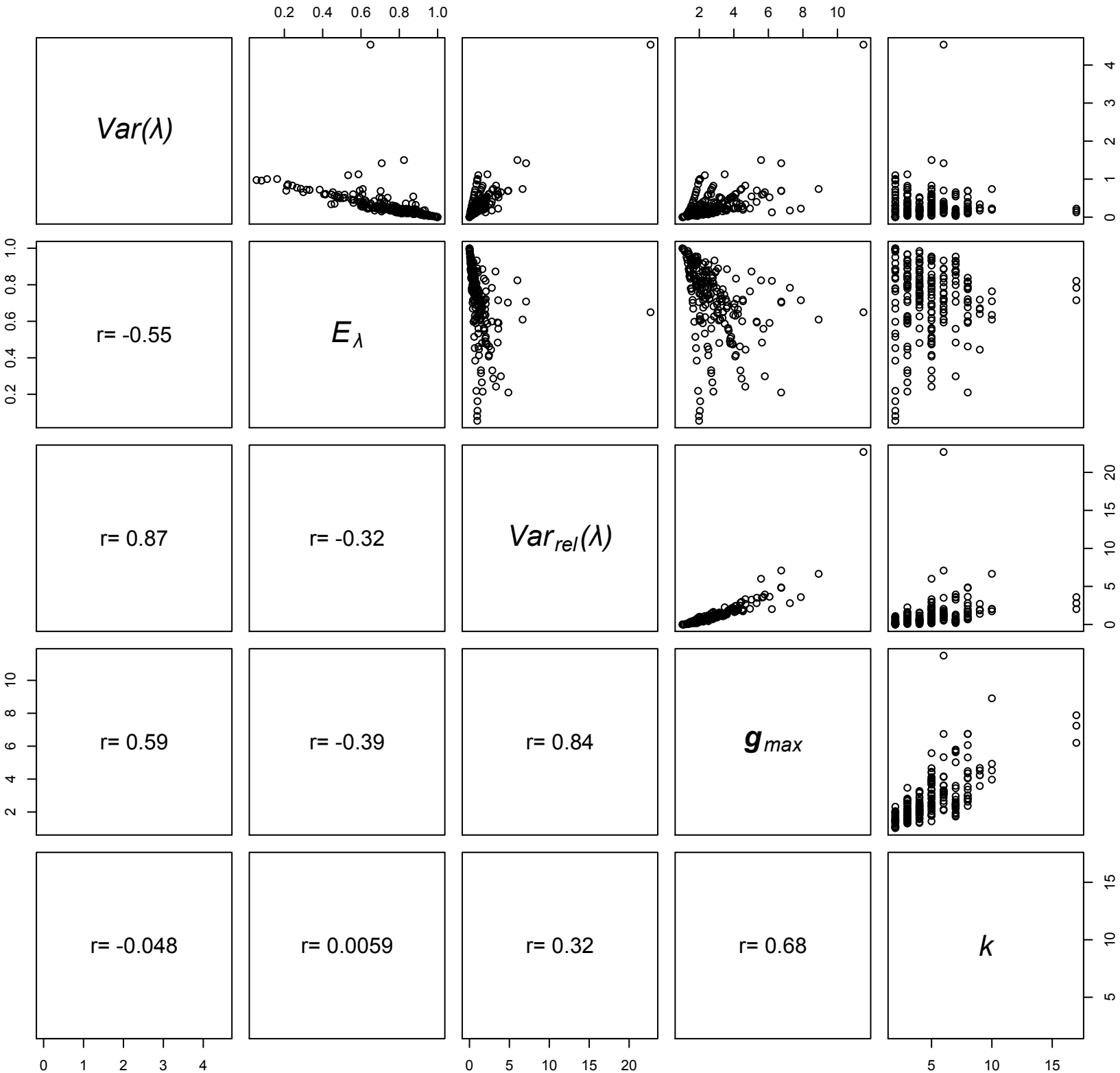
Short Title for Page Headings: **Evolutionary rate as a function of selection & the G matrix**

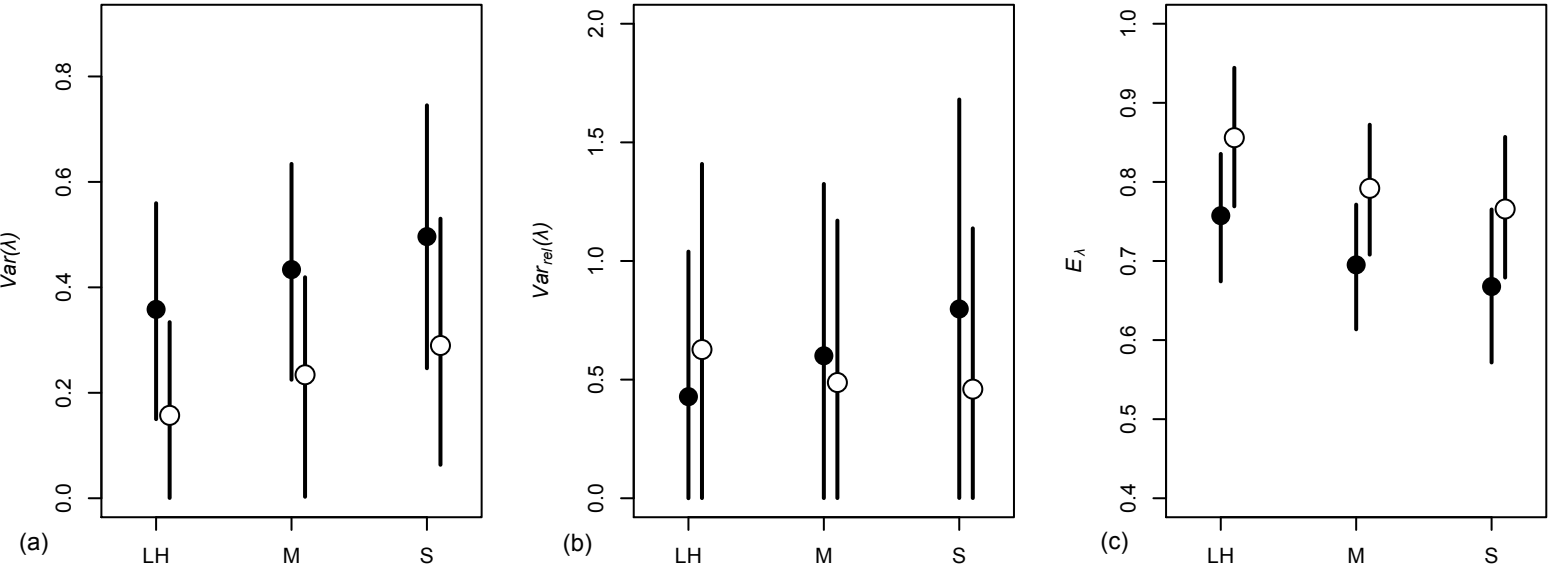

A
S
trait 2
trait 1
5
10
15
20
5
10
15
20

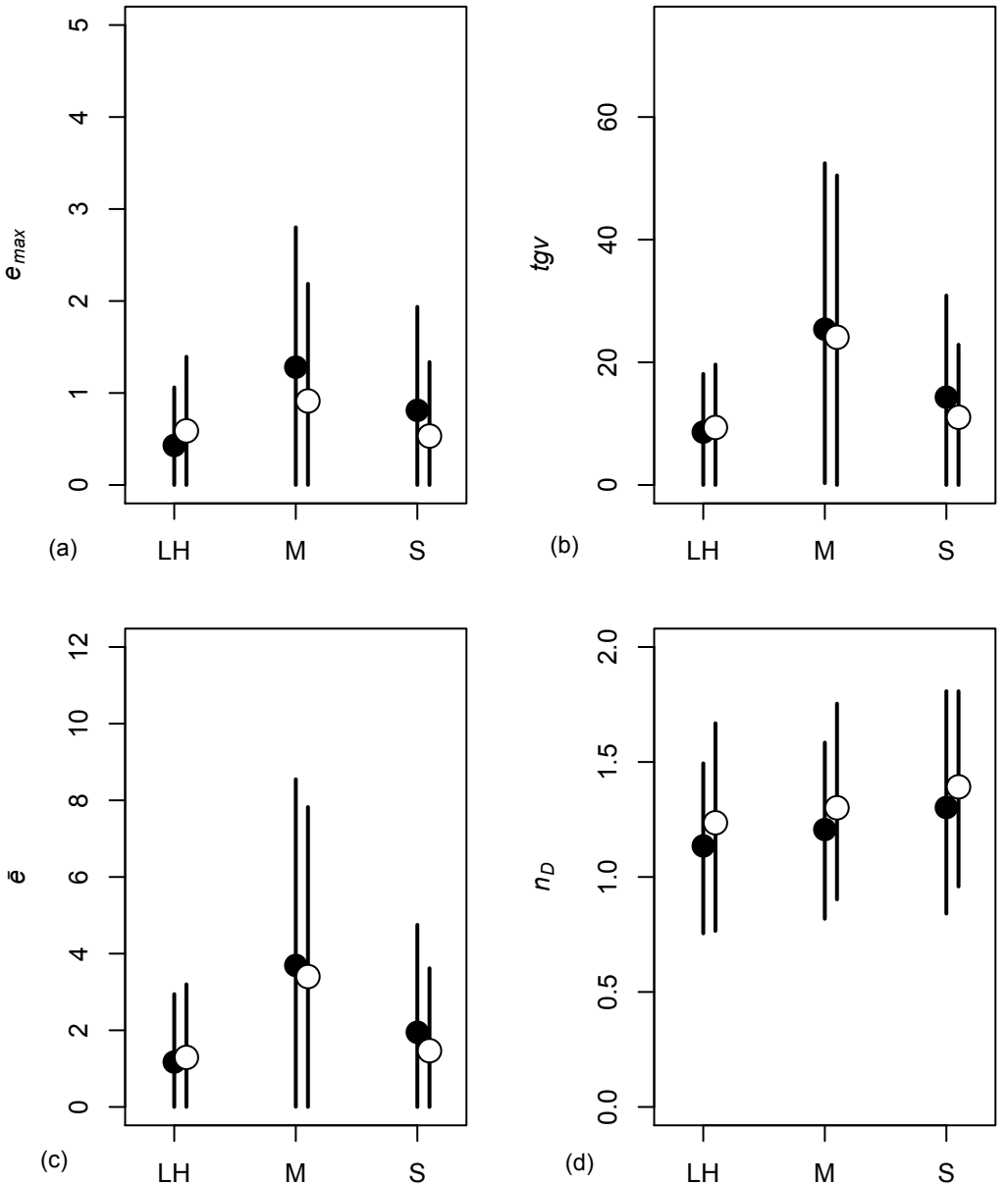

Rate of evolution (haldanes)
0.0
0.1
0.2
0.3
0.4
LH
M
S
Trait type


(absolute) Beta values
0.0
0.1
0.2
0.3
0.4
0.5
LH
M
S
Trait type


tgv
r= 0.13
n_D
r= 0.97
r= 0.048
e_{max}
r= 0.96
r= 0.045
r= 0.94
g_{max}
r= 1.00
r= 0.13
r= 0.97
r= 0.96
$\bar{e}$
r= 0.058
r= 0.82
r= -0.037
r= 0.012
r= 0.054
E_λ
r= 0.096
r= 0.024
r= 0.13
r= 0.086
r= 0.098
r= -0.011
k


Var(λ)
r= -0.55
E λ
r= 0.87
r= -0.32
Var rel(λ)
r= 0.59
r= -0.39
r= 0.84
g max
r= -0.048
r= 0.0059
r= 0.32
r= 0.68
k


Var(λ)
0.0
0.2
0.4
0.6
0.8
(a)
LH
M
S
Var_rel(λ)
0.0
0.5
1.0
1.5
2.0
(b)
LH
M
S
E_λ
0.4
0.5
0.6
0.7
0.8
0.9
1.0
(c)
LH
M
S


e_{max}
0
1
2
3
4
5
(a)
LH
M
S
tgv
0
20
40
60
(b)
LH
M
S
$\bar{e}$
0
2
4
6
8
10
12
(c)
LH
M
S
n_D
0.0
0.5
1.0
1.5
2.0
(d)
LH
M
S