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

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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

101 systematic review that reveals how general this pattern is or whether it differs across
102 taxa or trait types. Likewise, although reviews on the rate of contemporary
103 microevolution suggest that rapid evolution should be viewed as the norm rather than
104 the exception [15,30,31], a comprehensive review of evolutionary rates across different
105 taxa and trait types does not currently exist.
106
107 We compiled a database of reported genetic parameters from the literature to ask
108 whether different types of traits evolve at different rates, and whether such differences
109 correlate with differences in selection, in patterns of genetic (co)variation or both. We
110 performed a quantitative literature review, to examine whether observed rates of
111 evolutionary response differ across trait types (morphological, life-history and sexual) in
112 plants and animals. We relate these observed rates of evolutionary response to
113 estimates of linear and quadratic selection, as well as measures that capture the size,
114 shape and structure of **G** [7,11,15-20], to determine whether there is an association
115 across trait types and taxa. We find evidence that sexual traits evolve faster than other
116 traits in animals but not in plants, where life-history traits evolve fastest. These
117 increased rates of evolution do not appear to be attributable to the same cause
118 however. In plants we find that selection also appears to be strongest on life-history
119 traits, whereas in animals selection on sexually selected traits appears to be stronger
120 than on life-history but indistinguishable from that on morphology. We then examined
121 how the measures used to capture the size, shape and structure of **G** vary among trait
122 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*', '*haldane*s', '*response to selection*' and '*experimental evolution*'. This process was aided considerably by making use of the measurements from the studies

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

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

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

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

Defining Trait Categories and Measures

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

187 [36,39,40,48]. Thus, for both plants and animals, our sexually selected and morphology
188 categories are not mutually exclusive. In an attempt to reduce error in our study, traits
189 that did not fit clearly into one of our three categories were excluded from our dataset.
190 For **G** matrices whose component traits did not all fit the same category, we split the
191 matrix to produce sub-matrices relating to traits only within a single category. Where
192 matrices contained a single trait whose category differed from all others in the matrix
193 we removed that trait from the matrix.

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

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

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

Statistical Analyses

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

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

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

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

Results

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

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

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

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

The structure of ***G***

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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480

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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' ($Var_{rel}(\lambda)$)
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' ($Var_{rel}(\lambda)$) and (c) 'eigenvalue

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

738

738 **Table 1. G**-matrix metrics used in this study. Eigenvalue variance, relative eigenvalue
739 variance and eigenvalue evenness are calculated from correlation matrices, whereas the
740 other four metrics are calculated from covariance matrices. In all formulae λ are
741 eigenvalues and n is the number of traits in the matrix (rank).* n_D does not measure
742 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)	$\bar{e} = \sum_i \lambda_i / n$
eigenvalue variance (Var(λ))	cor	[49]	n/a (pg 158)	$Var(\lambda) = \sum_{i=1}^{n} (\lambda_i - 1)^2 / n$
Relative eigenvalue variance ($Var_{rel}(\lambda)$)	cor	[49]	n/a (pg 159)	$Var_{rel}(\lambda) = Var(\lambda) / n-1$
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 $\tilde{\lambda}_i = \lvert\lambda_i\rvert / \sum_{j=1}^{n} \lvert\lambda_j\rvert$

743

744

745

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

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

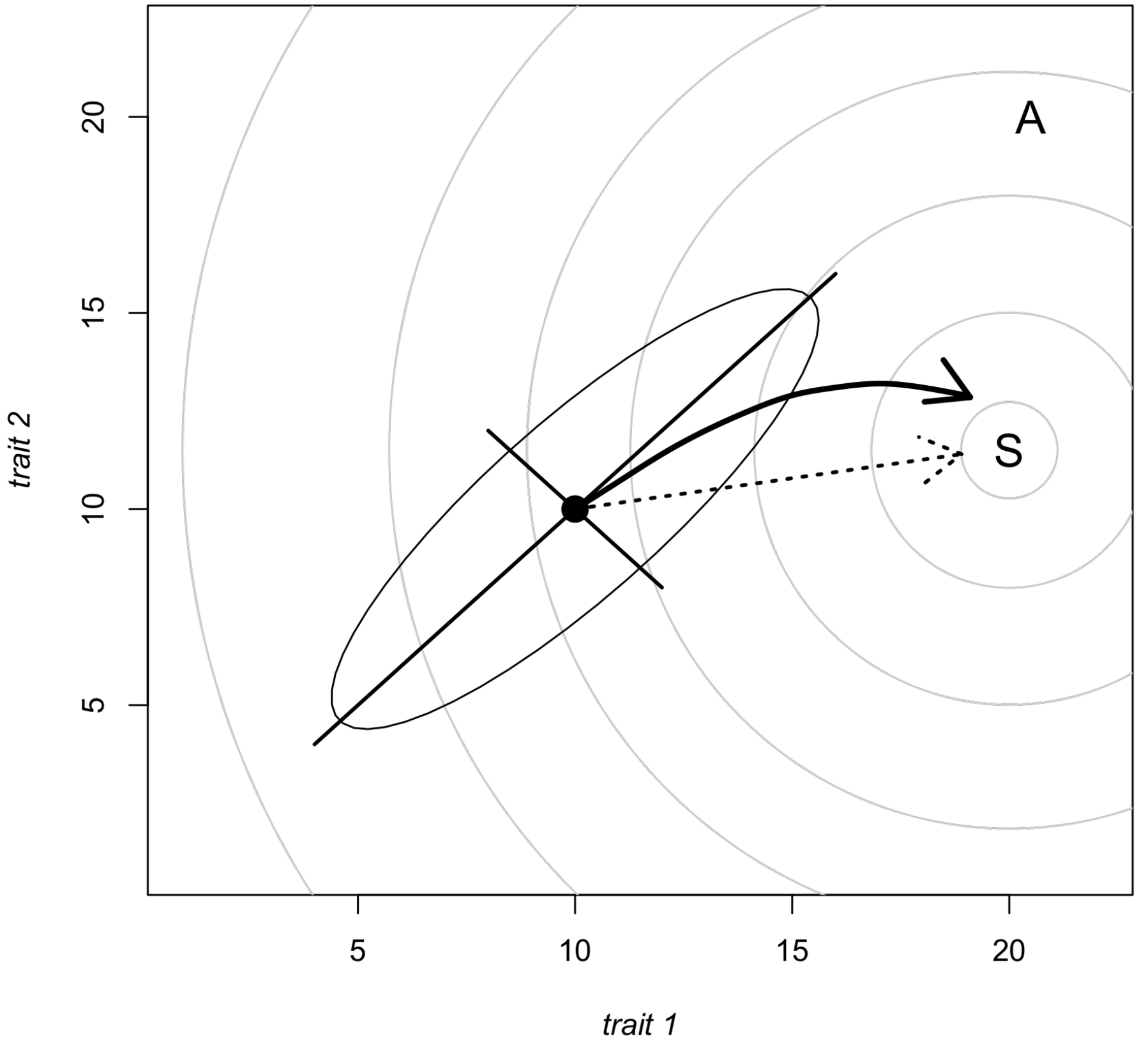
measure	animals			overall	plants	
	LH	**M**	**SS**	all traits	**LH**	**M**
Rate (haldanes)	0.12	0.13	0.18	0.13	0.3	0.15
	0.122	0.12	0.193	0.101	0.332	0.181
	(0.02,0.22)	(0.09,0.17)	(0.10,0.26)	(0.08,0.17)	(0.18,0.42)	(0.05,0.25)
	781	*7*	*1667*	*2571*	*26*	*90*
$\lvert\beta\rvert$	0.09	0.22	0.19	0.21	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**) $Var_{rel}(\lambda)$	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

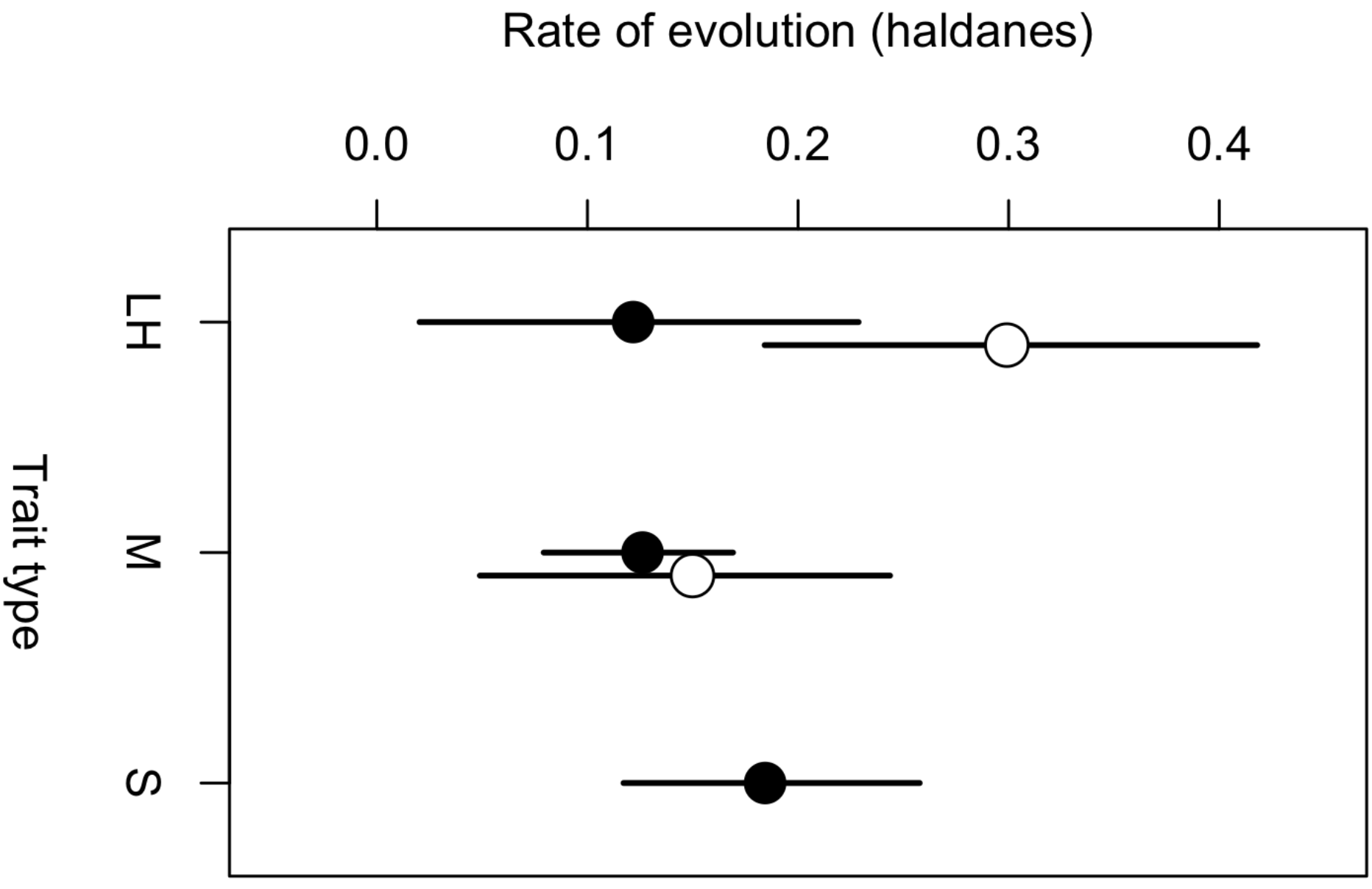
	0.78 (0.67,0.84)	0.77 (0.61,0.77)	0.69 (0.57,0.77)	0.76 (0.70,0.77)	0.80 (0.77,0.94)	0.81 (0.71,0.87)
n (cor)	42	82	27	*221*	14	26

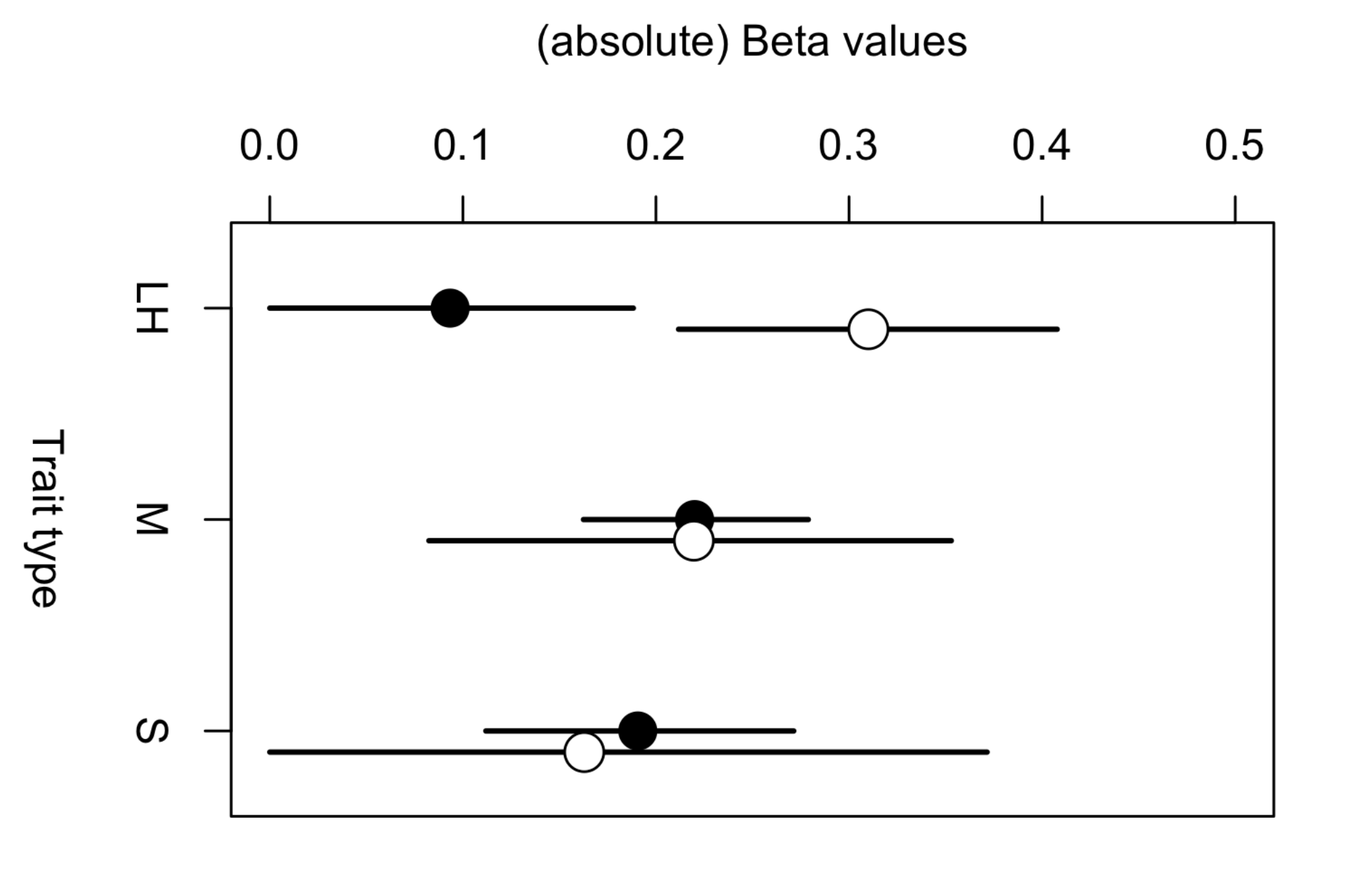
761

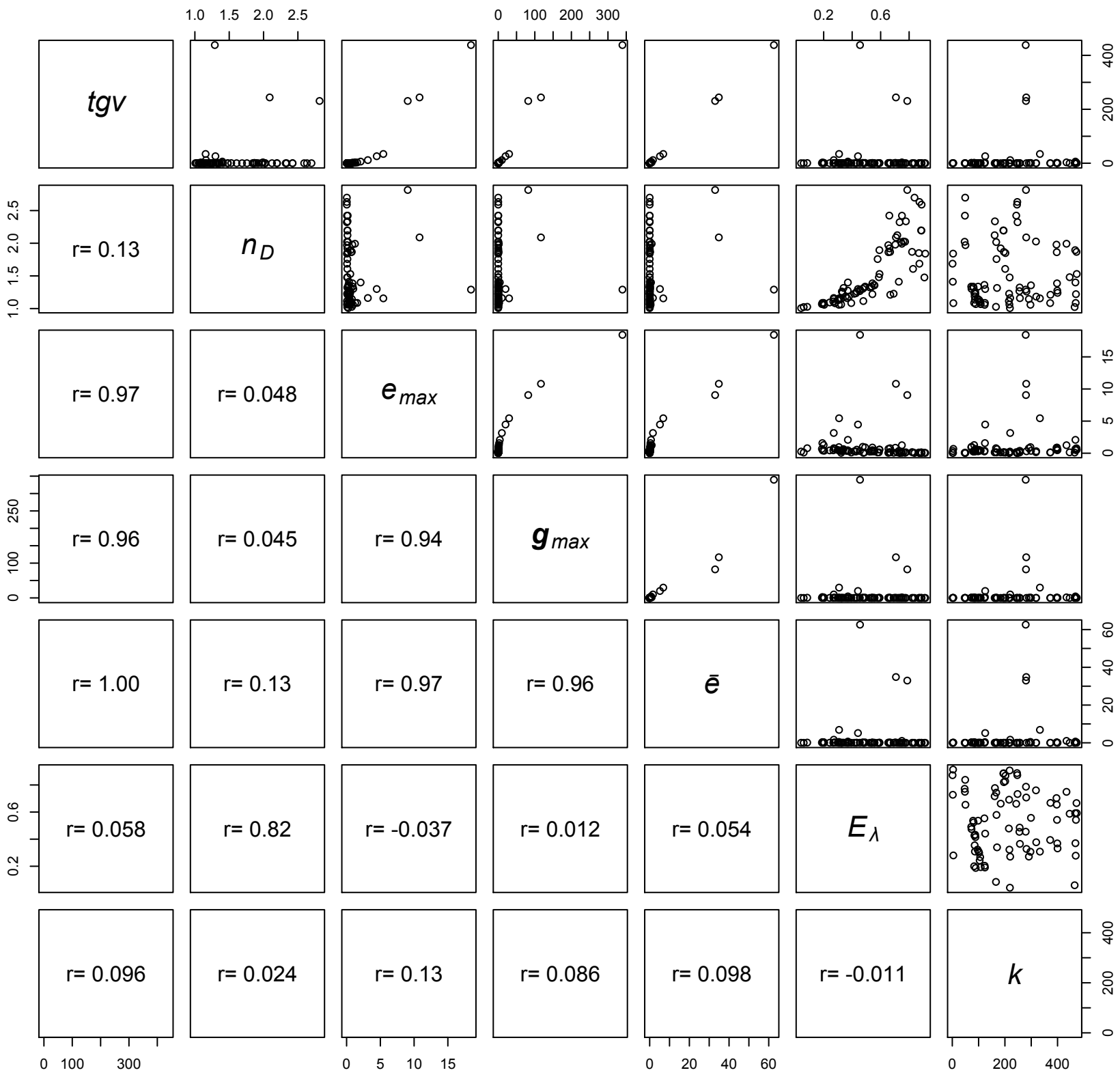
762 Short Title for Page Headings: **Evolutionary rate as a function of selection & the G**

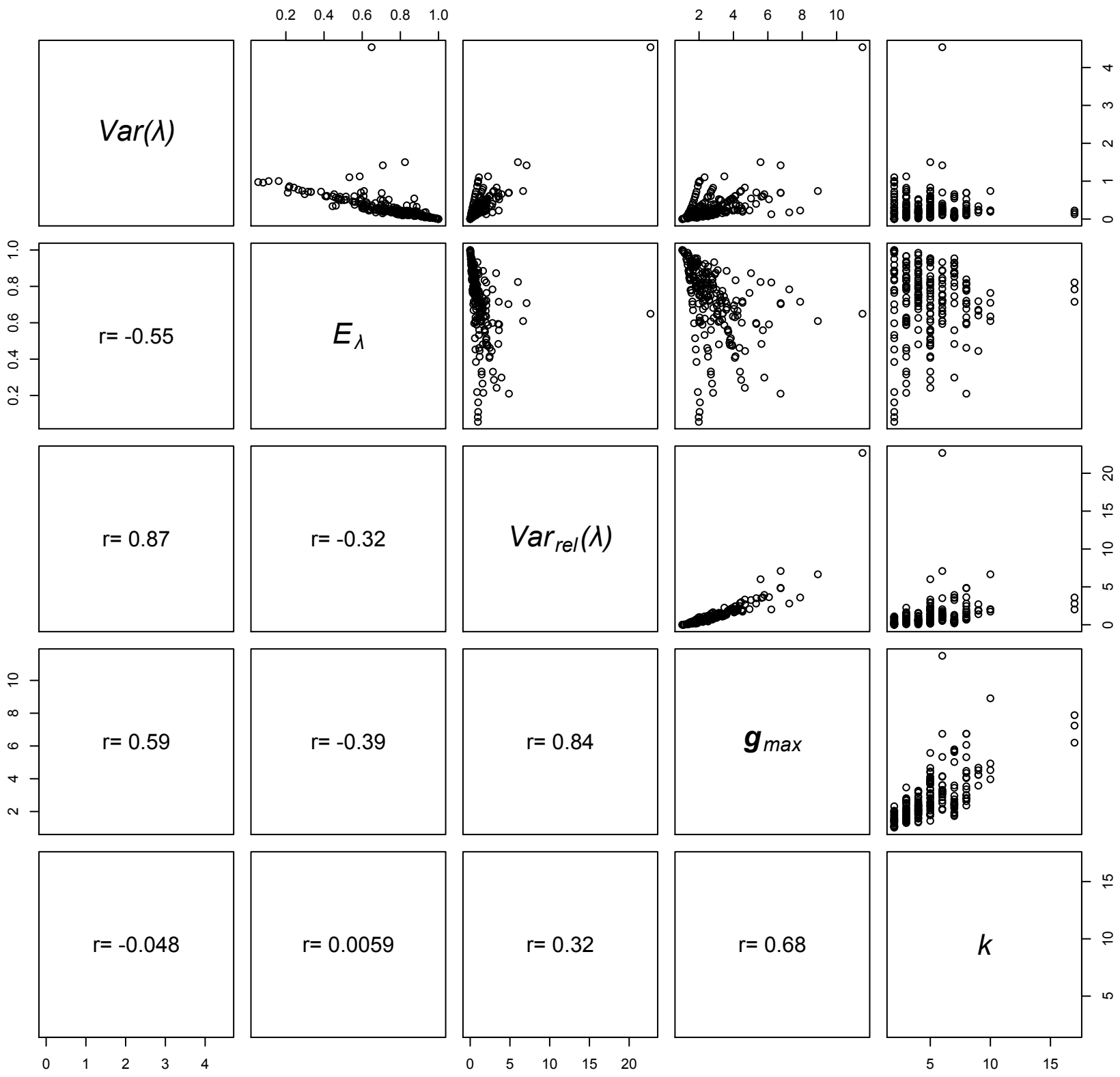
763 **matrix**


A
S
5
10
15
20
trait 1
trait 2


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


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


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
$Var_{rel}(\lambda)$
r= 0.59
r= -0.39
r= 0.84
g_{max}
r= -0.048
r= 0.0059
r= 0.32
r= 0.68
k

(a)
Var(λ)
0.0
0.2
0.4
0.6
0.8
LH
M
S
(b)
$Var_{rel}(\lambda)$
0.0
0.5
1.0
1.5
2.0
LH
M
S
(c)
E_{λ}
0.4
0.5
0.6
0.7
0.8
0.9
1.0
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