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One of the best supported patterns in life history evolution is that organisms cope with environmental fluctuations by buffering their most important vital rates against them. This demographic buffering hypothesis is evidenced by a tendency for temporal variation in rates of survival and reproduction to correlate negatively with their contribution to fitness. Here, we show that widespread evidence for demographic buffering can be artefactual, resulting from natural relationships between the mean and variance of vital rates. Following statistical scaling, we find no significant tendency for plant life histories to be buffered demographically. Instead, some species are buffered, while others have labile life histories with higher temporal variation in their more important vital rates. We find phylogenetic signal in the strength and direction of variance-importance correlations, suggesting that clades of plants are prone to being either buffered or labile. Species with simple life histories are more likely to be demographically labile. Our results suggest important evolutionary nuances in how species deal with environmental fluctuations.

All organisms face the challenges of environmental variation through time. One important adaptation to reduce the impacts of environmental changes on fitness is to buffer important life history traits against them[1]. This Demographic Buffering Hypothesis (DBH) is well-established in classical theory[2] and has three interlinked premises. First, the vital rates (age- or stage-specific survival, growth and reproduction) of any life history will vary in their contribution to population growth. Second, variation in vital rates reduces long term geometric mean fitness and increases extinction risk[1,3]. Third, life history constraints prevent organisms from buffering all vital rates. Consequently, natural selection should favour stronger buffering against temporal variability in the demographic rates to which population growth is most sensitive, also termed environmental canalization[4]. Support for the DBH comes from observations of negative correlations between the importance and variability of demographic or vital rates across a wide range of taxa, including birds[5,6], plants[7], large herbivorous mammals[8,9] and reptiles[7,10]. Despite this evidence, demographic buffering has been criticised for two main reasons. First, few studies consider alternative demographic strategies[11]. Second, standard comparative analyses often fail to account for important natural constraints[4,12-14] on the mean-variance relationship for each vital rate.

An alternative, but less explored, life history strategy for dealing with environmental variability is demographic lability, whereby life histories are selected to track environmental fluctuations[15], but are constrained to do this only among their most important vital rates[11]. Demographic lability implies a positive correlation between the importance and variability of a demographic rate. These demographic strategies emerge as a consequence of phenotypic adaptations in response to a changing environment. Whereas buffering of demographic rates is mediated through selection on underlying phenotypes against variability (canalization), lability occurs with the phenotype exhibiting a degree of plasticity in response to changing environmental conditions. Theoretically, temporal variation in life history parameters can

enhance fitness under certain scenarios[11,16]. Jensen's inequality[17,18] reveals that an accelerating response of fitness to environmental parameters, mediated by vital rates, can yield higher geometric mean fitness for life histories that track fluctuations, rather than buffer against them[11].

A further consideration is that evidence for the DBH might arise not because life histories have been favoured by natural selection to buffer their most important vital rates, but because demographic parameters with steepest selection gradients are inevitably those constrained to have low variance. Survival and growth probabilities, which are bounded to lie between zero and one, are constrained to have smallest variance at either limit[4] (Supplementary Fig. 2). Rates of sexual and clonal reproduction are able to take any positive value with variances that tend to increase with an increasing mean[12] (Supplementary Fig. 2). Therefore, survival probabilities with mean magnitudes close to one might be strongly favoured by natural selection but have negligible variance. The coefficient of variation, an alternative measure of variation[19], also suffers from strong statistical constraints (see supplementary material and Supplementary Fig. 3). Bias due to variance constraints manifests itself not only in measures of variance but also as inconsistencies in the sensitivity of population growth to demographic rates[14]. These statistical constraints are well established in the literature[4], yet are often overlooked in analyses.

Although theories of demographic strategies in variable environments have been widely tested among plants and animals[4,7,15], to reveal the biological underpinnings of demographic patterns, we must first consider the influence of statistical constraints on both variance and importance. In doing so we are able to provide the first comparative assessment of the distribution of buffering and labile strategies across plant taxa.

Results

To demonstrate the statistical artefact, we simulated 12000 random life histories as stage-structured population projection matrices (PPMs[20]; Supplementary Fig. 1). We created five temporal replicates of each life history to simulate annual variation. For each simulated time series of structured vital rates, we correlated importance (sensitivity) and variability (standard deviation) of demographic rates. This test for the DBH on simulated life histories revealed consistently negative correlations (96%; Supplementary Table 1), even in the complete absence of natural selection. Therefore, without statistical correction, any naïve analysis of demographic strategies in wild populations will tend to find evidence for the DBH.

Resolving the relative prevalence of demographic buffering and lability requires a fair quantitative treatment. We applied a link-scaling correction that removes the functional relationship between mean and variance across rates[14] to create variance-standardised values for measures of both variability and importance (see Supplementary Results). This framework successfully stabilised the structural relationship between the mean and variance both within and across demographic categories (Supplementary Results; Supplementary Figs 2-5). Link scaling removed the spurious bias towards negative correlations in simulated life histories where evidence for demographic buffering should not exist (the prevalence of negative correlations dropped from 96% to 51%; Supplementary Table 1). Link-scaling therefore provides a method to deal with statistical constraints in demographic analyses, allow analyses to work with both demographic probabilities and rates, and better assesses evidence for different demographic strategies across wild populations.

Using data from the COMPADRE Plant Matrix Database[21], we analyse correctly the demographic strategies of 141 different plant populations that are representative of 73 species drawn from a diverse range of plant evolutionary lineages, growth forms and habitats.

Among wild plant populations the prevalence of negative correlations between the importance and variability of uncorrected demographic parameters was 87.2%. This dropped to 67.4% following link-scaling (Fig. 1), with correlations reversed in several individual cases (Supplementary Fig. 6). A mixture of negative, null and positive patterns highlights the existence of divergent demographic strategies (Fig. 1): selection on life histories has yielded species with sets of vital rates that are buffered against environmental change (negative correlations), and others that are labile (positive correlations).

Using Bayesian mixed effects models (MCMCglmm[22]) to account for shared evolutionary history revealed phylogenetic signal accounted for an important amount of heterogeneity in the evidence for demographic buffering (Table 1), resulting in a global mean correlation (at average life-stage complexity) not credibly different from zero across variance-standardised life histories (Fig. 2). As a consequence, evidence for demographic buffering in plants is reduced dramatically. The overall reduction in evidence for buffering, the phylogenetic signal and the reversal of strategies at an individual population level, reveal two things. First, there is a need to account for statistical constraints when assessing demographic strategies. Second, alternative demographic strategies exist across populations and species. Different plant groups distribute unevenly in the global spectrum of demographic strategies (Fig. 3). Note there was no evidence of phylogenetic signal of uncorrected correlations (H^2=0.003 (95% CRI 0.001-0.658)).

To investigate potential characteristics that influence demographic strategy, we tested whether proxies for environmental variability (latitude and ecoregion), demographic variability (mean variance standardised standard deviation across demographic parameters for each population), life history (life expectancy and number of lifestage classes) and ecology (invasive status) affected the degree to which populations were buffered or labile. We consolidated our analysis to four main predictors. First, lability might be more frequent in

more variable environments where plasticity is favoured[23,24], or less frequent due to extinction risks associated with environmental stochasticity[1]. Second, species experiencing more demographic variation might have less labile responses due to extinction risks associated with demographic stochasticity[25]. Third, short-lived species with simple life histories might have more labile responses, because those species are more likely to show convex reaction norms between fitness, vital rates and environmental conditions[11]. Fourth, we considered the possibility that invasive species in their invaded range might be less adapted to their novel environments, might be unusually buffered or labile, and might be over- or under-represented in the COMPADRE database. Phylogenetically-informed MCMCglmm analysis found that buffering increased in strength with increasing number of lifestage classes, while proxies for environmental variation, demographic variation and invasive status had no credible influence (Supplementary Fig. 7).

The observation of stronger demographic buffering among species with more lifestages might be due to impacts on fitness of nonlinear averaging across concave reaction norms. It might reflect the ability of those species to spread risk among stage-specific vital rates. It might also be driven by a correlation between life history complexity and longevity, such that risks are spread among lifestages, across years. However, there are two alternative, statistical explanations. First, stronger evidence for demographic buffering might arise from a tendency of "simplified" models of life histories, with fewer stages, to under-predict the population's degree of demographic buffering by averaging over peaks and troughs in the variation and importance of stage-specific rates of survival and fecundity[26]. Second, the inclusion of multiple demographic rates might simply increase the statistical power to detect any negative correlation between importance and variance.

Discussion

Despite suggestions that a range of demographic strategies can be selected for in variable environments, the weight of empirical evidence has, to date, favoured demographic buffering. However, issues of statistical scaling with measures of both sensitivity and variability, which are inherent in comparative analysis of demographic rates, despite being previously identified[4,12,14], are commonly neglected. We have accounted for mean-variance relationships across demographic rates, and revealed a continuum of demographic strategies across the plant kingdom, from demographic buffering to demographic lability. An important challenge is now to understand the environmental, phylogenetic and demographic properties that favour buffering or lability

Our observation, that buffering is more likely among species with many lifestages, supports the contention that lability is more likely among short-lived species, because they exploit nonlinear averaging across convex reaction norms[11]. This was also supported by evidence for lability within a group of herbaceous perennials in the subfamily Asteroideae, of the family Asteraceae, whose average life expectancies were all less than 18 months. However, we also find lability to be present among some long-lived trees (e.g. firs, genus *Abies*), even when controlling for number of lifestages. This runs counter to the argument that only short-lived species should be labile. We consider three explanations for lability among some trees. First, long-lived plants might spread their reproductive output across several years, and can therefore hedge their bets against environmental fluctuations[27]. Second, greater storage of resources in large adult lifestages might allow them to exploit good reproductive and/or growth conditions in a stochastic environment[16,28], but suffer little loss in bad years. Third, trees might persist only in predictable environments where buffering is not required and the cost of lability is reduced.

Better understanding of links between life history and environmental fluctuations should inform management strategies for endangered or invasive species, particularly in the face of

present and future environmental change. However we currently lack the environmental data to capture such effects using the COMPADRE database. This suggests a rich future research programme to discover the ecological, evolutionary and environmental predictors of demographic strategy.

Methods

Empirical data

Demographic data was obtained from an open source, online repository of plant PPMs (COMPADRE[21]). These matrices summarize the life cycle transitions for over 500 plant species, such as rates of stasis, progression and recruitment for stage-based matrices. Only replicated studies of the same population, using a yearly time period, were included. Therefore we excluded mean PPMs (where demographic traits have been averaged across time), studies of populations undergoing experimental treatment and PPMs quantifying seasonal transitions (< 1 year). Reducible and non-ergodic matrices were also removed to prevent potential problems associated with these model structures[29]. To prevent conflicting demographic rates and probabilities we used matrices in COMPADRE where the matrix population model had been divided into the process based submatrices, enabling us to identify and distinguish between survival based transitions and reproduction (both sexual and clonal).

Matrices were classified by species, matrix dimension, as well as replicate population, to ensure calculations of variability were of temporal and not spatial origin. Only demographic data that spanned a minimum of three annual transitions were included, with the number of temporal replicates ranging from three to 12 matrices per population.

A total of 839 PPMs describing 141 different populations representing 73 unique species satisfied our demographic requirements and were included in the analysis.

Simulated data

We generated a series of 12000 random populations. For every population, five replicate matrices were generated (five years was the mean number of replicates in the plant demographic data). The dimensions of the simulated PPMs were set to lie between four and 15 classes, with 1000 populations randomly generated for each matrix dimension.

The Lefkovitch matrix structure[30], composed of stage classes, was chosen to represent our simulated life histories. We simulated stage-specific survival and growth probabilities (σ and γ, respectively) and stage-specific rates of reproduction (φ). Surviving individuals either remained in stage i (stasis = σ_i (1- γ_i)) or moved to the next stage class i+1 (progression = σ_i γ_i). For simplicity we did not incorporate negative growth or retrogression. We assumed a pre-breeding census so that the reproduction elements in the first row did not include survival of adults. We also assumed survival occurred before transition, that is transition from stage class i required survival of individuals in stage i.

Demographic parameters were randomly generated for every non-zero matrix entry. Parameters bounded between zero and one (survival σ and growth γ) were initially simulated from a uniform distribution between these two values. To generate temporal variability in these vital rates, replicate values were drawn from a normal distribution specifying the logit-transformed vital rate as the mean and a standard deviation of one, thus variation was equivalent across all vital rates. The inverse-logit transformation then scaled the parameters to lie between zero and one. The subsequent value for each matrix coefficient was calculated from these vital rates using the equations in Supplementary Fig. 1. The bounded probability

nature of the vital rates (σ and γ) guarantees that stasis and progression rates from each stage class cannot sum to more than one.

Initial mean reproduction rates (φ) were randomly sampled from a uniform distribution between 2 and 8. To generate temporal variation in these rates, replicate values were drawn from a normal distribution specifying the log-transformed reproductive rate as the mean and a standard deviation of one. The exponential function then back-transformed the parameters, ensuring values did not fall below zero. The choice of one for standard deviation was representative of plant demographies, and changing this value did not qualitatively change the results.

Observing the mean variance relationship

For every simulated and average matrix from COMPADRE we estimated the variation of each matrix entry in terms of the standard deviation (sd) of the mean and also the coefficient of variation (CV; σ/μ).

Testing the demographic buffering hypothesis

We tested for evidence of demographic buffering by exploring whether the standard deviation of matrix entries correlated with the contribution of a demographic rate to population growth, estimated as its sensitivity, for the simulated dataset and for the COMPADRE populations. Measures of absolute perturbations (sensitivity) were estimated using the popdemo package[31] in R[32]. We looked at the direction (positive/negative) of Spearman rank coefficients to provide insight into the ubiquity of negative associations, and the mean correlation coefficient (and 95% confidence intervals) to indicate the strength of the associations.

Link-scaling

We used a transformation approach to account for dissimilar demographic scales and heterogeneity of sensitivity estimates[14]. To achieve this, matrix entries were corrected by logit- and log- transformation of demographic probabilities (stasis and growth) and demographic rates (reproduction or recruitment) respectively. Specifically, for matrix entries that are probabilities (θ; e.g. survival and growth between classes) the variance is dependent upon the mean (μ). This restriction arises because[14]

$0 \leq \mathrm{Var}(\theta) \leq \mu(1-\mu)$

To avoid this, and ensure survival and mortality have equal rankings, we apply a variance-stabilizing transformation to sensitivity calculations. We use logit variance stabilised sensitivity (VSS), logit (θ) = ln (θ/ (1-θ)) and applied the following formula adapted from Link and Doherty Jr [14], logit VSS = $\frac{\theta(1-\theta)}{\lambda}\frac{\partial\lambda}{\partial\theta}$. For fecundities, which are constrained below by zero but can have any positive value, the logarithm transforms the parameter to a scale on which changes are independent of the mean[14], thus we applied log–scaled sensitivity (elasticity). Additionally, we applied a logit transformation to probabilities and log transformed rates to every replicate matrix to calculate a matrix of link-scaled standard deviations for each population. The simulated and COMPADRE dataset was retested using link-scaling in addition to observing the mean-variance relationship. We also tested that link-scaling removed within species associations between the variance and mean of demographic rates.

We initially applied an intercept only model to test whether the (overall) mean of the correlation coefficients was different from zero. We also tested for the effect of environmental variability, demographic variability and life history. Two covariates were used to explore whether environmental variability informs demographic strategy; *latitude* and

ecoregions. The ecoregions in COMPADRE were collapsed into major habitat classes to increase the statistical power: Alpine & Arctic, Arid, Temperate and Tropical and Subtropical[33]. To test whether demographic variability influenced demographic strategy we used the *mean variance standardised standard deviation* as a predictor value. This was calculated for each population from the variance standardised standard deviations of vital rates. *Life expectancy* was calculated as a life history index, as the mean time to death given that the individual starts in the first year of their lifecycle. This was calculated from the fundamental matrix (N) of a transition matrix that includes transitions that depend only on survival. Methods described in Caswell[20] . The number of *stage classes* was also included as a measure of life history complexity. Additionally, to account for potential bias in species studied we incorporated *invasive status*. Each of the plant species was classified as native or invasive at the location in which they were studied. Plant status was determined by searching the Global Invasive Species Database (GISD)[34], the Invasive Species Compendium[35], the Australian Invasive Weed List[36], the Australian Plant Census[37], the European and Mediterranean Plant Protection Organization database[38], Schedule 9 of the Wildlife and Countryside Act (1981), the United States Department of Agriculture (USDA) Plant Database[39] and by using the following search term in Google '*Latin name* invasive'. Species are considered invasive when designated as 'invasive' (also 'weedy' or 'noxious' in the USDA Plant Database[39]) in one or more of the databases listed above or when designated as invasive by a Government Agency or Academic Institution. Twelve populations comprising two plant species were identified as invasive plants at the study location.

We fitted our model using a Bayesian MCMCglmm package[22] in R v.3.1.1[32] to account for non-independence due to species and phylogeny, by scaling random effects by the inverse variance–covariance distance matrix estimated by the phylogeny associated with our species[21]. We excluded two fern species that made up all ferns in our sample (*Asplenium*

adulterinum and *A. cuneifolium*), which were not present in the phylogeny. Consequently, 138 populations consisting of 71 species were included in our MCMCglmm analysis. Our response variable (correlation coefficients) was modelled using a Gaussian distribution. We determined the number of iterations, burn-in and thinning by visually assessing the mixing of three chains and formally using Gelman and Rubin's convergence diagnostic using R package coda[40]. We let the MCMC algorithm run for 800,000 iterations, with a burn in period of 80,000 and a sampling interval of 400. Each model generated ~1,800 independent samples of model parameters. Parameter-expanded proper diffuse priors were used for random effects (inverse Wishart distribution with V=1 and ν=0.001, alpha-μ=0 and alpha-V=100), and proper diffuse priors for residuals (inverse Wishart distribution with V=1 and ν=0.001). We confirmed results were not sensitive to the choice of prior by fitting multiple models. The adequacy of models with and without phylogeny was assessed by comparing the Deviance Information Criterion (DIC) of the two models[41]. The relative variance attributable to the phylogenetic random effect component was subsequently calculated as the ratio of variance explained by phylogeny to the sum of phylogenetic variance, species variance and residual variance.

To visualize evidence for demographic buffering through phylogeny we used the contmap function of the phytools R package[42]. The mapping of the degree of demographic buffering (represented by the mean correlation coefficient per species) is based on maximum-likelihood estimation of states at internal nodes and interpolation of the states along each edge[43,44].

Phylogeny

Study species were allocated to their currently recognised families under the Angiosperm Phylogeny Group classification[45,46] and guided by The Plant List

(http://www.theplantlist.org/). The full species list with corresponding families was then submitted to PHYLOMATIC (http://phylodiversity.net/phylomatic/[47]) to produce a topologically correct tree at family level. Further resolution was accomplished by reference to more specific phylogenetic studies. These more specific studies are listed in the Supporting Information (Electronic Appendix S5) of Salguero-Gomez, et al.[21]. For this purpose, the tree topology was manipulated in MESQUITE (http://mesquiteproject.wikispaces.com/[48]). Our priority was to produce a topologically accurate tree given expert knowledge on systematics of the taxa concerned including all the information available (e.g., genetic, morphological and chemical). In this respect, we followed the philosophy employed for the NCBI taxonomy, which is not generated directly from DNA sequence data, but from authoritative primary literature sources for nomenclature and classification[49]. Finally, in order to temporally calibrate this topologically acceptable tree, phylogenetic distances were interpolated with the *bladj* function of PHYLOCOM[50], using the node ages provided by Wikström, et al.[51].

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Competing Financial Interests statement The authors declare no competing financial interests.

Data Availability Empirical data is available from http://www.compadre-db.org/. Correspondence and requests for materials should be addressed to DH (D.J.Hodgson@exeter.ac.uk).

Figure legends

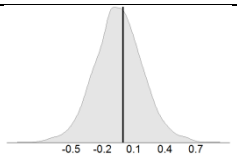
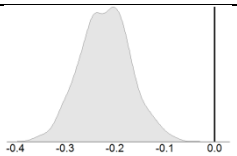
Figure 1. Distribution of correlation coefficients from uncorrected (sd, sensitivity) and corrected (variance standardised standard deviation, variance standardised sensitivity) Spearman correlations (N=141)

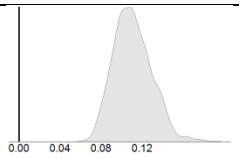
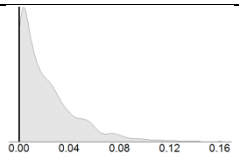
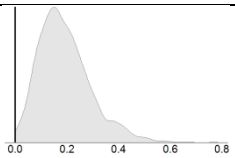
Figure 2: Posterior distributions of the correlation coefficient (at average number of stage classes) between sensitivity and standard deviation of vital rates, as predicted from MCMCglmm models that account for species identity and the number of stage classes. Posterior distributions are shown for a naïve uncorrected analysis, an uncorrected analysis with phylogenetic control, a variance standardised (vs) analysis and a vs analysis with phylogenetic control. Naïve analyses using unscaled sensitivities and standard deviations yield highly credible evidence for demographic buffering throughout the plant kingdom. Link-scaling, to remove mean-variance relationships, yielded no credible bias towards demographic buffering in the presence of phylogenetic control. **pMCMC<0.01; * pMCMC<0.05; ns not significantly different from zero (N=138)

Figure 3: Maximum likelihood ancestral state reconstruction of demographic strategy onto the phylogeny. Legend shows the colour range from blue-green (demographic buffering) to yellow-red (demographic lability).

Tables

Table 1: Phylogenetic MCMCglmm model on predictors of demographic buffering across plant populations (N=138) with dimension standardised.

	Estimate	95% CRIs	Posterior Density
fixed term			
Intercept	-0.04	(-0.49,0.44)	
number of stage classes	-0.22	(-0.31,-0.11)	

random terms			
residual variance	0.11	(0.08,0.15)	
species variance	0.02	(0.00,0.07)	
phylogenetic variance	0.19	(0.00,0.39)	

To account for phylogenetic non-independence, models included a phylogenetic random effect derived from the Angiosperm phylogeny associated with our species[21]. Provided are the posterior means and 95% credible intervals of fixed and random effects, with number of stage classes as the fixed variable, and species and phylogeny as random variables. After accounting for species, the phylogenetic signal, estimated as heritability[52], was $H^2 = 0.57$ (95% CRI: 0.17–0.81).

Figure 1

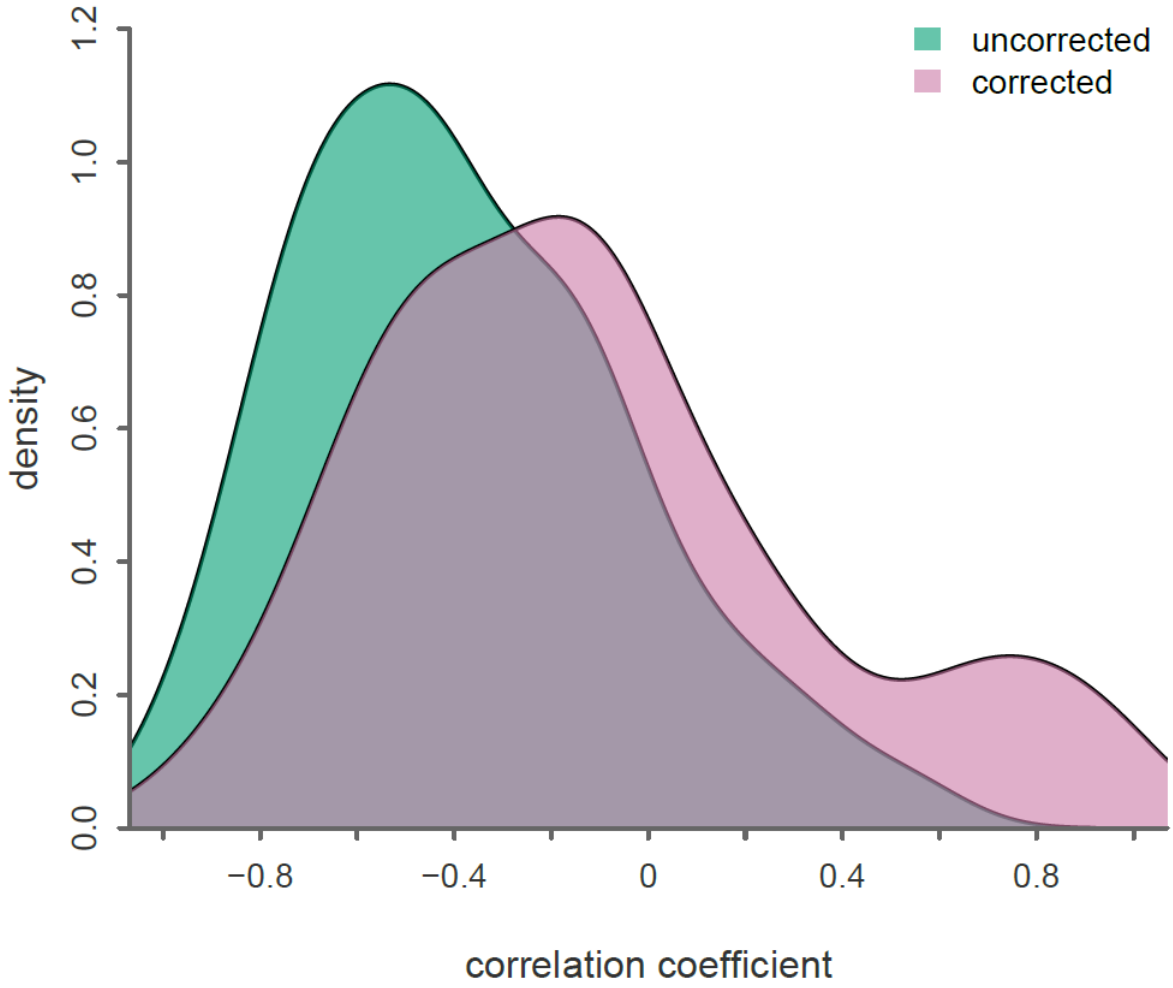

uncorrected
corrected
density
0.0
0.2
0.4
0.6
0.8
1.0
1.2
−0.8
−0.4
0
0.4
0.8
correlation coefficient

Figure 2

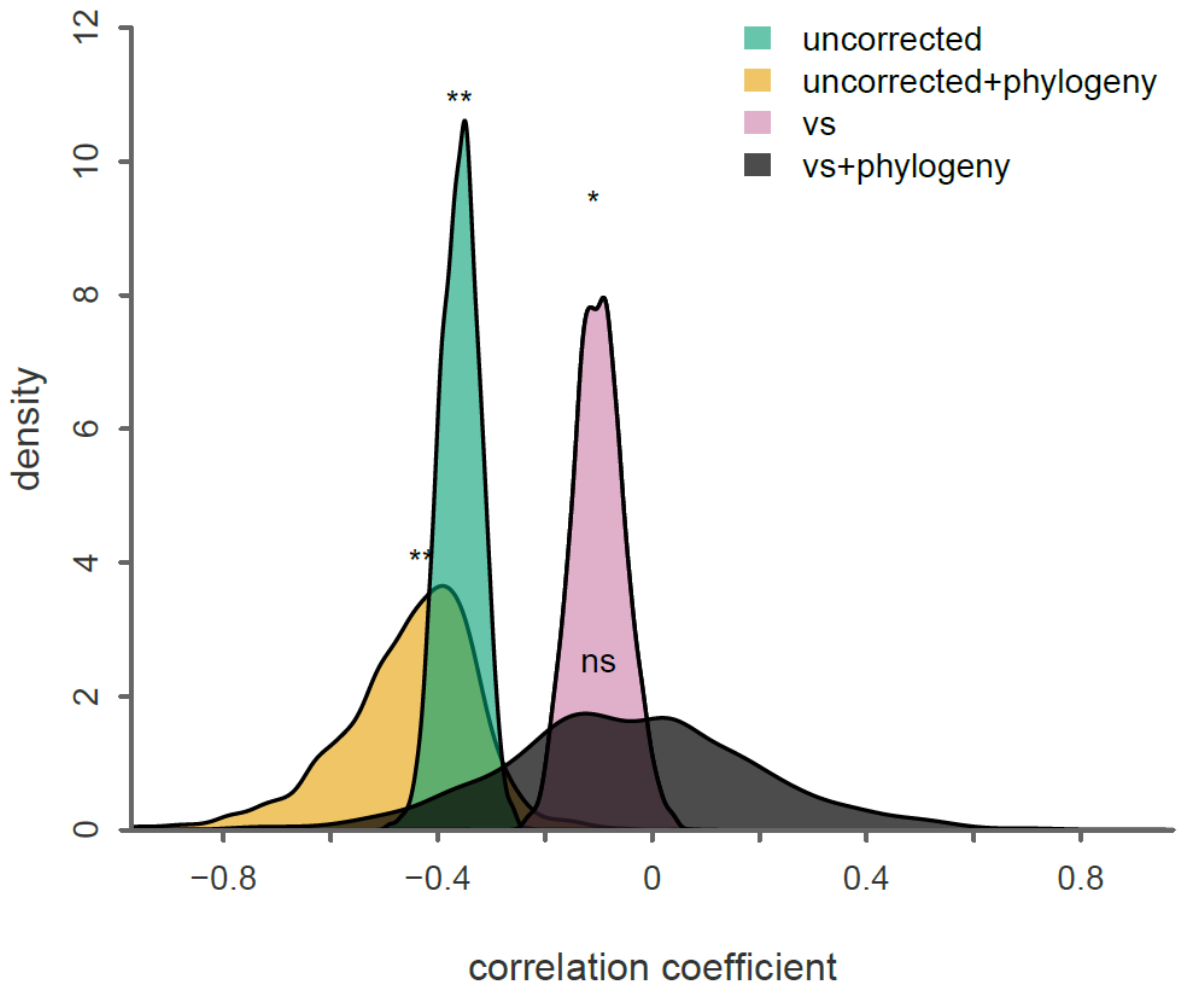
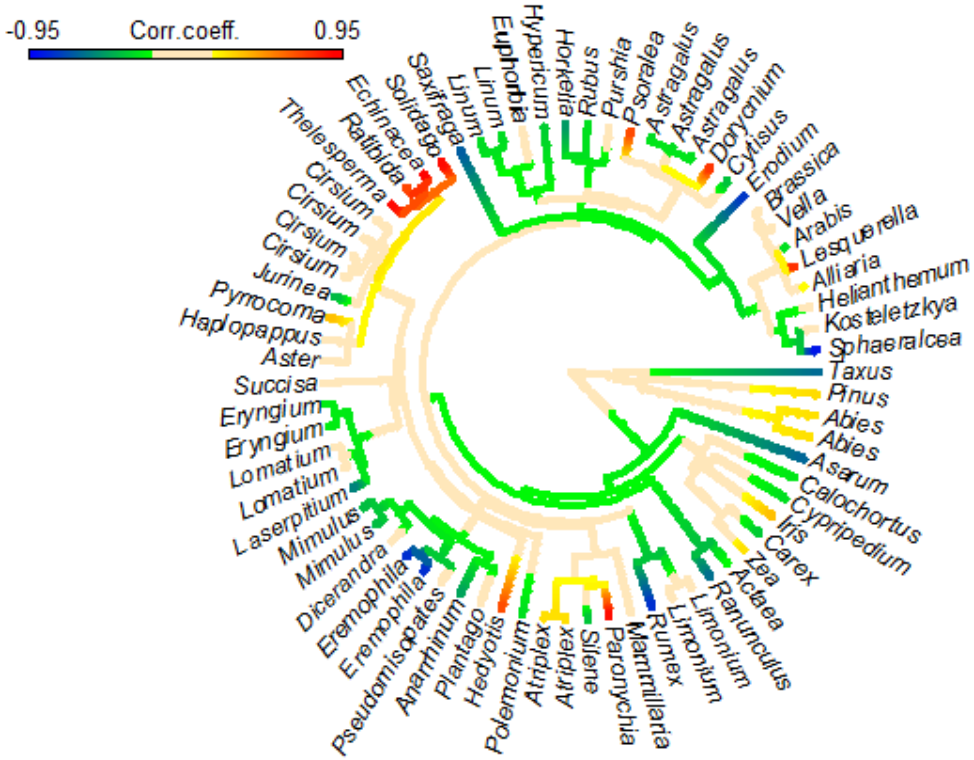

uncorrected
uncorrected+phylogeny
vs
vs+phylogeny
**
*
**
ns
density
0
2
4
6
8
10
12
−0.8
−0.4
0
0.4
0.8
correlation coefficient

Figure 3


-0.95
Corr.coeff.
0.95
Euphorbia
Hypericum
Linum
Saxifraga
Solidago
Echinacea
Ratibida
Thelesperma
Cirsium
Cirsium
Cirsium
Cirsium
Jurinea
Pyrrocoma
Haplopappus
Aster
Succisa
Eryngium
Eryngium
Lomatium
Lomatium
Laserpitium
Mimulus
Mimulus
Diecrandra
Eremophila
Eremophila
Pseudomisopates
Anarrhinum
Plantago
Hedyotis
Polemonium
Atriplex
Atriplex
Silene
Paronychia
Mammillaria
Rumex
Limonium
Limonium
Ranunculus
Aclaea
Zea
Carex
Iris
Cypripedium
Celochortus
Asarum
Abies
Abies
Pinus
Taxus
Sphaeralcea
Kosteletzkya
Helianthemum
Alliaria
Lesquerella
Arabis
Vella
Brassica
Erodium
Cytisus
Dorycnium
Astragalus
Astragalus
Psoralea
Pursh ia
Rubus
Horkelia