# Supplementary Information for "Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale"

Appendix S1 - Reference list of data sources used for plant traits

Appendix S2 - Figure showing results of PCA on plant morphological trait data from which axes of trait variation were derived

Appendix S3 - Extended methods

Appendix S4 - Results of Bayesian Multi-Response Mixed Models without populations with annual life-cycles for comparison

Appendix S5 - Species list with associated plant forms, habitats and basic climate information

Appendix S6 - Table showing DIC values for all competing Bayesian Multi-Response Mixed Models

Appendix S7 - Full table of model coefficients for best fitting Bayesian Multi-Response Mixed Model

Appendix S8 – Discussion of the residual covariance of life-history metrics

Appendix S9 – Phylogenetic variance coefficients figure

#### Appendix S1 - Reference list of data sources used for plant traits

The majority of this data was sourced from the TRY – Plant Trait Database using their data request system. Trait data were selected from this data request using selection criteria given the main text.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., et al. (2011). TRY–a global database of plant traits. *Glob. Change Biol.*, *17*, 2905-2935.

Further data were added to this dataset where available from literature sourced via the https://datadryad.org/

Original data source citations for trait data are given below.

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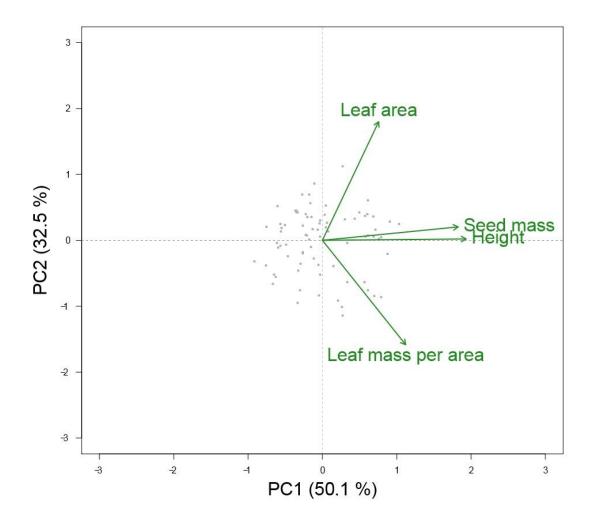
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# Other TRY datasets

Data within TRY was also sourced from the following datasets which are not, to our knowledge, currently published elsewhere.

| Dataset name  | Dataset author          |
|---|-------------------------|
| Cold Tolerance, Seed Size and Height of North American Forest<br>Tree Species | Hawkins, Bradford       |
| Dispersal Traits Database   | Higgins, Steve          |
| Meadow Plant Traits: Biomass Allocation, Rooting depth                        | Lanta, Vojtech          |
| Midwestern and Southern US Herbaceous Species Trait Database                  | Weiher, Evan            |
| Overton/Wright New Zealand Database   | Wright, Ian             |
| Plant Traits From Spanish Mediteranean shrublands                             | Gross, Nicholas         |
| The Netherlands Plant Height Database   | Ozinga, Wim             |
| Costa Rica Rainforest Trees Database  | Salgado, B. Finegan, B. |
| Herbaceous Plants Traits From Southern Germany                                | Roemermann, Christine   |
| Leaf Area, Dry Mass and SLA Dataset   | Schamp, Brandon         |
| Plant Traits in Pollution Gradients Database                                  | Anand, Madhur           |
| Leaf N-Retention Database   | de Vries, Franciska     |

Appendix S2 - Figure showing results of PCA on plant morphological trait data from which axes of trait variation were derived



### Appendix S3 – Extended methods

This appendix includes a more detailed version of the methods applied in 'Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale', Kelly et al. 2021. For associated code and data see: <a href="https://doi.org/10.5281/zenodo.4457447">https://doi.org/10.5281/zenodo.4457447</a> Any further questions regarding methods should be directed to Ruth Kelly at <a href="https://kelly@afbini.gov.uk">kelly@afbini.gov.uk</a>.

#### Overview

In order to examine the relationships between traits, climate, phylogeny and life-history strategies we integrated data from multiple data sources. We then used a Bayesian multi-response mixed modelling approach to predict life history response variables as a function of trait, climate and phylogeny and the residual covariance between life-history variables.

# Data collation and derivation Species selection

Species in this study were selected on the basis of the availability of high quality demographic matrix model data in the COMPADRE database of plant demography (Salguero-Gómez *et al.* 2015) and the availability of matching species trait data for key functional traits. A full species list of accepted names and accepted synonyms for the COMPADRE species set was created using the 'iPlant checker tool 'from the iPlant Collaborative Taxonomic Name Resolution Service vr. 4.0 (<a href="http://tnrs.iplantcollaborative.org/">http://tnrs.iplantcollaborative.org/</a> downloaded 2/11/2016). The resulting list of accepted species names and synonyms matching those in COMPADRE was then used to extract functional trait data from other sources.

#### **Functional traits**

Four commonly measured functional traits were chosen based on their availability across many taxa, and their relevance in describing functional strategies of plants: plant height (m), seed mass (mg), Leaf Mass per unit Area (LMA) and leaf area (mm2). These traits were chosen to align closely with the axes of variation in global plant form and function described by Díaz et al (2016). Plant height and seed mass were chosen to represent a spectrum of plant structure and size (from short species with low stem density with small seeds to larger species with high stem density and large seeds) (Díaz et al. 2016). Plant height is associated with the ability to compete for light resources, whole plant fecundity and plant dispersal (Moles 2018). Seed dry mass is associated with post germination establishment, seed longevity and dispersal (although its relationship with dispersal is strongly mediated by height) (Godoy et al., 2015; Tamme et al. 2014; Moles 2018). LMA was chosen for its relationship to leaf investment strategies described in the widely studied 'Leaf Economic Spectrum' (Westoby et al. 2002; Reich et al. 2003; Wright et al. 2004). High LMA values are correlated with low leaf nutrient concentrations and lower rates of photosynthesis, but longer leaf life-spans and higher tolerance of herbivory and abiotic stress (Wright, 2004). From a demographic perspective traits associated with high LMA, could be expected to benefit species with slower plant lifehistories which will be subject to greater biotic and abiotic stresses over the course of their life-cycles. Leaf area is a key ecological trait which has been previously shown to be relatively uncorrelated with the LMA (Laughlin 2014; Pierce et al. 2014; Díaz et al. 2016). Leaf area is associated with the surface area available for light-interception, thermodynamics, water-use efficiency and vulnerability to herbivory (Niinemets, Portsmuth, & Tobias, 2006; Moles 2018). Functionally, higher leaf area could be expected to be in associated with faster life-cycles due to greater photosynthetic capacity and lower stress tolerance. Data for these functional traits were obtained from the TRY Plant Trait Database (Kattge et al. 2011) and the Botanical Information and Ecology Network BIEN (Enquist et al. 2009) and further individual studies sourced from the literature and Dryad data repository. A full list of data sources is given in see (see Appendix S1 in Supporting Information).

#### Functional traits - calculation and criteria for inclusion

For each functional trait a mean value was calculated per species per location (or per study where no geographic information was supplied). In datasets where only minimum and maximum values were available, mean values were taken as the mean of these two values. A grand mean was then calculated as the mean value across locations for each species. Measurements were only included for healthy adult plants. Experimental conditions (e.g. greenhouse/climate chambers) were only included where these were designed to mimic field conditions. Modelled or extrapolated values were also excluded.

In order to derive two key axes of trait variation in our dataset we conducted a PCA on the natural log transformed functional trait metrics (Height, Leaf Area, Leaf Mass per unit Area and Seed Mass) (package 'vegan'; Oksanen et al. 2017). These axes very closely resemble those previously described in the literature by Díaz et al. (2016) (Appendix S2). These axes described a total of 82.5% of variation in the functional trait data, and are hereafter referred to as the "PC1 - Size and structure" (50%) and "PC2 – Leaf traits" (32.5%).

# **Demographic metrics**

Six demographic metrics were chosen to represent the core elements of variation in plant life-history strategies. Age at maturity, mature lifespan and generation time, were chosen to represent different but related aspects of the fast-slow continuum in plant life histories. Annual reproduction, inequality of reproduction across plant lifespan and distribution of mortality across lifespan are associated with the second major axis of life-history variation which relates to the reproductive rates of species and the variation in reproduction and mortality risk across the lifespan (Salguero-Gómez et al. 2016, Healy *et al.* 2019).

## Demographic metrics - criteria for inclusion

All demographic metrics were calculated from population level matrix population models in the COMPADRE database vr. 4.0.1 (Salguero-Gómez *et al.* 2015). Studies were included only from vascular plant species in unmanipulated outdoor environments. In addition, matrices were only included where: 1) they were separable into individual matrices representing growth/survival and fecundity (i.e. **U** and **F**), 2) did not include clonality (due to conceptual difficulties life-span and individuality in clonal reproducing species), and 3) were ergodic, primitive and irreducible. Where original authors provided individual matrices per year per location these matrices were selected by preference and pooled matrices across multiple populations were only used where no individual population matrices were available. The accuracy of all matrices was checked against the original sources, and corrections were made to the dataset to match the original publications (see associated code and datasets: https://doi.org/10.5281/zenodo.4457447).

# Preparation of matrices

Individual matrices were averaged across years within populations prior to the calculation of the demographic rates. In four species, matrix transitions were longer than 1 year in duration, and matrices were converted to annual time-steps prior to the calculation of life-history metrics. These annual matrices were obtained by taking the  $n^{th}$  root of the A (survival, growth and fecundity matrix) and U (growth/survival) matrices respectively where n = the transition interval in years, and then calculating the F matrix as A - U. All other species had annual transitions.

# Calculation of demographic metrics

Age at maturity was calculated as the mean age at which first reproduction occurs among individuals who survive to reproductive age (Caswell, 2001; p. 124). Mature lifespan was defined as the mean lifespan of individuals in the population conditioned on having survived to first reproduction, this metric is strongly correlated with measures of maximum life span, but is not influenced by high levels of juvenile mortality prior to maturity (Caswell, 2001; p. 118-120). Age at maturity and mature lifespan were calculated based on the function

'lifeTimeRepEvents' in the R package 'Mage' (Jones & Salguero-Gómez, 2016). Generation time is a measure of how long it would take for a cohort to replace itself based on its asymptotic growth rate and net reproductive rate, and is thus a population level metric influenced by both survival and reproduction (package 'popbio'; Stubben & Milligan 2007). Mean annual reproductive rate was defined as the number of new aboveground individuals produced by a population at its stable stage distribution (SSD) in each year. For matrices with a seed stage the number of seeds was multiplied by the probability of a seed reaching the first aboveground stage to make appropriate comparisons between estimates from studies with and without seed stages. Inequality of reproduction across lifespan was measured using the Gini coefficient of inequality of annual reproductive output across the lifespan (package 'ineg', Zeileis, 2014). Reproductive output in each time step was based on age specific fecundity curves ('mx curves' calculated as per Caswell 2001, p. 118-121, using the function 'makeLifeTable' in the R package 'mage' with modification to allow reproduction in the first timestep). The Gini coefficient of inequality ranges from 0 to 1, with 0 representing an equal spread (e.g. iteroparous species that reproduces every year) and 1 being completely unequal (e.g. semelparous species with a single reproductive event). Populations with annual life-cycles species were assigned a Gini coefficient of 1 reflecting their semelparous life-cycles, as inequality could not be calculated for species with a single timestep. Models were tested with and without populations with annual life-cycles included in the dataset, and the results were not qualitatively different (Appendix S4). The distribution of mortality across lifespan was measured as the median/maximum lifespan of species, giving a range of values between 0-1 function 'exceptionalLife' (see https://github.com/healvke/Healv et al 2019 Animal Life History). These values can also be interpreted as reflecting the shape of the survivorship curve of the species. High values close to 1 indicate a convex Type I curve where mortality is low in juvenile stages and increases in old age, intermediate values close to 0.5 indicate a Type II curve where mortality is evenly distributed across the lifespan or centred around the median age, and low values indicate a concave Type III curve with increased mortality in juvenile stages.

All demographic metrics were calculated from the first above ground stage to allow appropriate comparison between studies with and without seed-stages. Following the calculation of each demographic metric at the population level, values for populations of the same species within studies in the same habitats and within 5 km were averaged to match the spatial scale of the environmental data.

After all data processing the final species overlap for which all data types were available was 80 (see Appendix S5, for species list with associated growth forms, habitats and basic climate information).

# Climate data

Two climatic variables representing key drivers of plant physiological rates, temperature and water availability, were derived for each population location. Whilst climatic influences on demography are likely to be much more complex, given collinearity of many climate variables, the size of the dataset (80 species), and the risk of losing generality through over-parameterization, we decided *a priori* that temperature and water availability were the most appropriate for this study. Similarly, other environmental parameters such as soil types, pH, microclimates, resource availability, biotic competition or disturbance regimes have been shown to be associated with plant traits and life-histories at smaller spatial scale (Teller *et al.*, 2016; Treurnicht *et al.*, 2016), it was not possible to include them in this model due to sample size considerations.

Temperature data at each location was extracted from (WorldClim Version 2.0 at 30 arcsecond resolution; Fick et al. 2017). Due to the high degree of collinearity between available temperature variables, we used a single composite temperature variable represented by the first PCA axis calculated from the temperature variables (Bio1-Bio7) in WorldClim. This

temperature axis explained 67% of the variation in temperature data at our sites and represents a gradient from cooler seasonably-variable temperate climates to hot, less-seasonal tropical climates.

To quantify moisture availability we used the Global Aridity Index, which quantifies precipitation deficit over atmospheric water demand and is a composite measure based on Precipitation, Temperature (T) and PET (Potential Evapotranspiration, a function of solar radiation, mean temperature and temperature range assuming a reference crop) (Trabucco et al. 2009). We log-transformed the Aridity Index as we expected the influence of water stress to be higher where water is limiting (i.e. at lower values) (Levine *et al.* 2008; Coutts *et al.* 2016). Hereafter, we refer to this variable as 'moisture availability' to reflect the direction of the variable (i.e. higher values indicate more humid conditions). Moisture availability and the temperature PCA were not significantly correlated in our dataset (non-parametric Spearman's Rho = 0.053, p = 0.639, n = 80).

Geographic locations were obtained for each population from COMPADRE v. 4.0.1. Where geographic coordinates were not supplied they were estimated based on the location described in the paper. Climate variables were extracted as a mean value from a 2.5 km radius around each study location to match the spatial scale of the study coordinates (package 'raster'; Hijmans, 2017).

# **Phylogeny**

Phylogenetic relationships between species were quantified used a time-calibrated phylogeny (downloaded 02/07/2018; Zanne et al. 2014). Twelve species which were present in our dataset but absent from the phylogeny were added to this tree by placing them in the location of the most closely related species in the same genera based on literature (Calviño et al., 2007; Conti et al. 1999; Jacquemyn et al. 2011; Jin et al, 2014; Simon et al. 2016). For seven of these species a detailed phylogeny for the genus could not be found and the species location was assigned randomly to the location of another unused species in the same genus. All species present in the phylogeny, but absent from our dataset were dropped from the phylogeny (package 'ape', Paradis et al. 2014).

#### Statistical analysis

## **Bayesian Multi-Response Mixed Modelling**

In order to investigate the complex relationships between functional traits, climate, phylogeny and the life-history strategies a Bayesian Multi-Response General Linear Model framework was used. This approach allows for the explicit incorporation of both phylogenetic structure and the estimation of covariances between the multiple demographic response variables, in tandem with the estimation of the fixed effects (i.e. coefficients for traits and climate). Given both the theoretical and empirical evidence of covariances and trade-offs inherent in plant life-history strategies (Partridge & Harvey, 1988; Stearns, 1992; Franco & Silvertown, 1996; Salguero-Gómez et al. 2016), the estimation of life-history covariances was considered crucial from both a statistical and theoretical perspective.

To satisfy the normality assumptions of this analysis, and reduce the influence of extreme values, all demographic metrics (except the Gini Index of inequality of reproduction across lifespan) were natural log transformed based on inspection of histogram plots. The Gini Index was square root transformed for the same reasons. All variables were then rescaled to a mean of 0 and expressed in units of standard deviation.

#### Model construction and selection

Four candidate models of life history variation were constructed based on *a priori* hypotheses about the potential roles of climate, traits and their interactions (Fig. 1). The most complex model included the two PCA axes representing plant functional traits (PC1 – Size and

structure, and PC2 – Leaf traits) and the two climate variables (Temperature PCA1 and Moisture availability), and the pairwise interaction of each functional trait axis with each climate variable. In all models, phylogeny was fitted as a random variable with a separate estimate for each response trait, and a residual covariance matrix was fitted to account for the covariance between demographic metrics and residual variation within demographic metrics. This residual covariance matrix was fully parameterised, such that variance explained could differ both within demographic metrics and between pairs of metrics (Hadfield *et al.*, 2010). Model fitting was conducted using the function 'MCMCglmm' in the package 'MCMCglmm' (Hadfield, 2010), with priors for multivariate responses and phylogeny based on Hadfield, (2017). Alternative models were compared using Deviance Information Criteria (DIC), a hierarchical generalization of the Akaike Information Criteria.

As the candidate model with lowest DIC value was the most complex of our alternative hypotheses 'Traits in interaction with climate', we further improved final model parsimony by removing individual interaction terms between trait axes and climate variables in a stepwise manner until the removal of further terms no longer reduced the DIC.

Model DIC values can vary slightly for individual chains of Bayesian models, therefore the model selection procedure was conducted three times to ensure that the overall ranking of models was consistent (see Hadfield, 2010). DIC is suitable for use in cases where response variables are approximately Gaussian (Hadfield, 2010), and because it was necessary to set some criterion for model simplification given the complexity of the full model and size of the dataset.

#### Model validation

Model validation was conducted using a combination of visual inspection of trace and posterior density plots. Number of iterations, thinning and the burn-in period for the global model were assessed by inspecting trace plots and posterior density plots, and calculating autocorrelation metrics and effective sample sizes using the R package 'coda' (Plummer *et al.*, 2006). Models were run with 1,000,000 iterations, a burnin of 200,000 and a thinning rate of 1000. Effective sample sizes for all estimated parameters in the final model were > 400 (min = 483, max = 1,668). The final model was run 3 times and convergence was assessed for both fixed and random variables in using the Gelman-Rubin statistic (multivariate potential scale reduction factors were 1.02 and 1.01 respectively) (Gelman & Rubin, 1992). Convergence of the covariance matrix was assessed by visualisation of combined trace plots for the three chains.

#### Variance explained

The variance in life-history metrics explained by the final model (i.e. traits, climate and phylogeny), was calculated as described in for conditional R2 values in Nakagawa & Schielzeth, 2013.

Specifically, the proportion of variance described by the model was calculated as:

fixed effects variance + phylogenetic variance fixed effects variance + phylogenetic variance + residual variance + residual covariance

Where the 'fixed effects variance' was the sum of the variances in the fitted values for each response metric, calculated from the fixed effects coefficients of the fitted model. The phylogenetic variance, is the sum of the variances explained for each response trait as reported by mcmcGLMM, and in the residual covariance is the sum of the residual covariance matrix fitted by mcmcGLMM. For more details on variance calculations in mcmcGLMM see: Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. J. Stat. Softw., 33, 1–22.

All statistical analysis was conducted in R 3.5.0 (R Core Team). R scripts and datasets are available at  $\frac{https://doi.org/10.5281/zenodo.4457447}{https://doi.org/10.5281/zenodo.4457447}$ 

# Appendix S4 - Results of Bayesian Multi-Response Mixed Models without populations with annual life-cycles for comparison

Bayesian estimates of posterior means, upper and lower credible intervals and effective sample sizes for fixed effects for each life-history metric in fitted multi-response General Linear Mixed Model when annual species were excluded. Refer to main text for details of model fitting.

| Life history metric | Explanatory variable   | Posterior<br>mean | Lower<br>95% CI | Upper<br>95% CI | Effective sample size |
|---------------------|------------------------|-------------------|-----------------|-----------------|-----------------------|
| Age at maturity     | Structure and size     | 0.58              | -0.14           | 1.39            | 800.00                |
|                     | Leaf traits            | 0.05              | -0.41           | 0.52            | 883.38                |
|                     | Temperature PCA        | -0.22             | -0.56           | 0.16            | 800.00                |
|                     | Moisture availability  | 0.03              | -0.17           | 0.22            | 719.72                |
|                     | Size * Temperature PCA | 0.76              | 0.34            | 1.28            | 651.06                |
|                     | Size * Moisture        | 0.35              | -0.05           | 0.81            | 989.73                |
| Annual reproduction | Structure and size     | -0.31             | -0.99           | 0.41            | 625.23                |
|                     | Leaf traits            | 0.25              | -0.18           | 0.75            | 800.00                |
|                     | Temperature PCA        | 0.22              | -0.14           | 0.58            | 800.00                |
|                     | Moisture availability  | -0.04             | -0.26           | 0.21            | 941.76                |
|                     | Size * Temperature PCA | -0.24             | -0.71           | 0.23            | 800.00                |
|                     | Size * Moisture        | -0.25             | -0.79           | 0.27            | 800.00                |
| Generation time     | Structure and size     | 0.60              | 0.02            | 1.14            | 800.00                |
|                     | Leaf traits            | -0.31             | -0.77           | 0.06            | 800.00                |
|                     | Temperature PCA        | -0.14             | -0.41           | 0.16            | 800.00                |
|                     | Moisture availability  | 0.17              | -0.04           | 0.36            | 939.28                |
|                     | Size * Temperature PCA | 0.58              | 0.17            | 0.96            | 800.00                |
|                     | Size * Moisture        | -0.07             | -0.54           | 0.31            | 632.96                |
| Mature lifespan     | Structure and size     | 0.39              | -0.17           | 0.97            | 800.00                |
|                     | Leaf traits            | -0.41             | -0.79           | 0.08            | 715.00                |
|                     | Temperature PCA        | 0.11              | -0.16           | 0.41            | 800.00                |
|                     | Moisture availability  | 0.19              | -0.02           | 0.38            | 812.35                |
|                     | Size * Temperature PCA | 0.41              | -0.01           | 0.82            | 800.00                |
|                     | Size * Moisture        | -0.17             | -0.59           | 0.27            | 800.00                |
| Distribution of     | Structure and size     | -0.13             | -0.89           | 0.56            | 800.00                |
| mortality           | Leaf traits            | 0.15              | -0.36           | 0.64            | 698.66                |
|                     | Temperature PCA        | 0.16              | -0.16           | 0.51            | 800.00                |
|                     | Moisture availability  | -0.11             | -0.31           | 0.09            | 800.00                |
|                     | Size * Temperature PCA | -0.77             | -1.26           | -0.28           | 800.00                |
|                     | Size * Moisture        | 0.41              | -0.06           | 0.88            | 800.00                |
| Inequality of       | Structure and size     | 0.54              | -0.08           | 1.18            | 811.46                |
| reproduction        | Leaf traits            | 0.46              | 0.04            | 0.90            | 607.27                |
|                     | Temperature PCA        | -0.03             | -0.36           | 0.29            | 800.00                |
|                     | Moisture availability  | 0.11              | -0.11           | 0.34            | 800.00                |
|                     | Size * Temperature PCA | -0.07             | -0.48           | 0.39            | 800.00                |
|                     | Size * Moisture        | -0.16             | -0.63           | 0.24            | 602.38                |

Bayesian variance estimates for the phylogenetic effects on each life-history metric in fitted Multi-response General Linear Model fitted WITHOUT ANNUAL SPECIES (see main text for details).

| Life history metric        | Posterior mean | Lower 95% CI | Upper 95% CI | Effective sample size |
|----------------------------|----------------|--------------|--------------|-----------------------|
| Age at maturity            | 2.20           | 1.08         | 3.40         | 800.00                |
| Annual reproduction        | 0.03           | 0.00         | 0.13         | 800.00                |
| Generation time            | 0.04           | 0.00         | 0.14         | 800.00                |
| Mature lifespan            | 0.22           | 0.00         | 0.59         | 800.00                |
| Distribution of mortality  | 1.51           | 0.00         | 2.38         | 570.40                |
| Inequality of reproduction | 0.16           | 0.00         | 0.69         | 800.00                |

# **Appendix S5 - Species list**

Full list of species included in the final analysis, with information on life-forms and the habitats in which demographic parameters were measured. Basic climate information are given to provide some context, and are derived based on the study locations at which demographic parameters were measured. Species are listed in ascending order of mean annual temperature at the study locations. Growth forms show the predominant growth forms for each species based on scientific literature and floras. \* Indicates that the species was added to our phylogeny during analyses based on the location of the closest species in that genera available in the literature (see methods in main text for details).

| Species                     | Growth form    | Habitat<br>(Demography) | Mean annual<br>temperature<br>(Bioclim1) | Temperature<br>Annual Range<br>(Bioclim 7) | Aridity Index |
|-----------------------------|----------------|-------------------------|--|--|---------------|
| Saxifraga aizoides          | Perennial forb | Alpine moraine          | -3.64                                    | 22.39                                      | 5.09          |
| Silene acaulis              | Perennial forb | Scree                   | -3.09                                    | 35.70                                      | 1.78          |
| Epipactis<br>atrorubens*    | Perennial forb | Forest                  | -0.79                                    | 38.06                                      | 1.30          |
| Sarracenia<br>purpurea      | Perennial forb | Bog/fen wetland         | -0.64                                    | 45.75                                      | 1.53          |
| Minuartia<br>obtusiloba*    | Perennial forb | Alpine fellfields       | -0.23                                    | 29.63                                      | 1.21          |
| lpomopsis<br>aggregata      | Perennial forb | Grassland               | 0.01                                     | 39.56                                      | 0.71          |
| Pinguicula alpina           | Perennial forb | Heath                   | 0.26                                     | 29.57                                      | 1.07          |
| Pimpinella<br>saxifraga     | Perennial forb | Unmanaged roadverge     | 1.35                                     | 25.30                                      | 2.46          |
| Geranium<br>sylvaticum      | Perennial forb | Grassland               | 5.34                                     | 30.51                                      | 1.18          |
| Primula farinosa            | Perennial forb | Grassland               | 5.70                                     | 26.00                                      | 0.97          |
| Heracleum<br>mantegazzianum | Perennial forb | Grassland               | 5.70                                     | 24.24                                      | 1.21          |
| Digitalis purpurea          | Perennial forb | Grassland               | 5.91                                     | 22.75                                      | 3.14          |
| Agrimonia<br>eupatoria      | Perennial forb | Road verge              | 6.24                                     | 27.46                                      | 0.96          |
| Succisa pratensis           | Perennial forb | Grassland               | 6.36                                     | 26.37                                      | 0.92          |
| Plantago media              | Perennial forb | Grassland               | 6.44                                     | 25.99                                      | 0.90          |
| Cirsium palustre            | Perennial forb | Grassland               | 6.47                                     | 25.72                                      | 0.89          |
| Actaea spicata              | Perennial forb | Deciduous forest        | 6.53                                     | 25.06                                      | 0.87          |
| Ranunculus<br>peltatus      | Perennial forb | Aquatic                 | 6.59                                     | 23.24                                      | 0.86          |
| Lathyrus vernus             | Perennial forb | Grassland               | 6.74                                     | 27.21                                      | 0.90          |
| Trollius laxus              | Perennial forb | Forested fen            | 6.76                                     | 36.71                                      | 1.27          |
| Hieracium<br>floribundum    | Perennial forb | Grassland               | 6.92                                     | 36.89                                      | 1.06          |
| Sanicula<br>europaea*       | Perennial forb | Forest                  | 7.04                                     | 25.25                                      | 0.86          |
| Fumana<br>procumbens        | Shrub          | Grassland               | 7.33                                     | 25.97                                      | 0.86          |
| Pinus strobus               | Tree           | Forest                  | 7.55                                     | 27.70                                      | 0.87          |
| Arenaria<br>serpyllifolia   | Annual forb    | Grassland and scree     | 8.08                                     | 28.98                                      | 0.85          |

| Myosotis<br>ramosissima     | Annual forb            | Grassland and scree             | 8.08  | 28.98 | 0.85 |
|-----------------------------|------------------------|---------------------------------|-------|-------|------|
| Saxifraga<br>tridactylites* | Annual forb            | Grassland and scree             | 8.08  | 28.98 | 0.85 |
| Veronica arvensis           | Annual forb            | Grassland and scree             | 8.08  | 28.98 | 0.85 |
| Trillium<br>grandiflorum    | Perennial forb         | Forest                          | 8.23  | 36.53 | 1.19 |
| Trollius europaeus          | Perennial forb         | Abandoned wet grassland         | 8.60  | 24.21 | 0.98 |
| Alliaria petiolata          | Perennial forb         | Forest                          | 8.75  | 40.15 | 0.94 |
| Cirsium                     | Perennial forb         | Grassland                       | 8.77  | 29.24 | 0.71 |
| pannonicum*                 |                        |                                 |       |       |      |
| Dipsacus fullonum           | Perennial forb         | Grassland                       | 8.84  | 37.72 | 0.92 |
| Cirsium acaule*             | Perennial forb         | Grassland                       | 8.89  | 29.55 | 0.69 |
| Scorzonera<br>hispanica     | Perennial forb         | Grassland                       | 8.91  | 29.47 | 0.69 |
| Linum tenuifolium           | Perennial forb         | Grassland                       | 9.02  | 29.21 | 0.68 |
| Tsuga canadensis            | Tree                   | Forest                          | 9.12  | 32.47 | 1.27 |
| Gentiana<br>pneumonanthe    | Perennial forb         | Heath                           | 9.24  | 23.09 | 1.16 |
| Himantoglossum<br>hircinum* | Perennial forb         | Grassland                       | 9.31  | 25.58 | 0.80 |
| Armeria maritima            | Perennial forb         | Mine spoil                      | 9.47  | 22.99 | 1.29 |
| Primula vulgaris            | Perennial forb         | Forest                          | 9.64  | 20.96 | 0.82 |
| Pinus nigra                 | Tree                   | Grassland                       | 9.67  | 25.28 | 0.80 |
| Cynoglossum<br>officinale   | Perennial forb         | Dune Grassland                  | 9.75  | 18.73 | 0.97 |
| Orchis purpurea*            | Perennial forb         | Grassland                       | 9.89  | 23.32 | 1.16 |
| Molinia caerulea            | Perennial<br>graminoid | Heathland                       | 10.23 | 21.66 | 1.14 |
| Paeonia officinalis         | Perennial forb         | Woodland                        | 10.26 | 24.29 | 0.85 |
| Primula elatior             | Perennial forb         | Forest                          | 10.39 | 22.44 | 1.08 |
| Acer saccharum              | Tree                   | Forest                          | 10.89 | 39.88 | 0.91 |
| Cytisus scoparius           | Shrub                  | Urban grasslands<br>and prairie | 10.92 | 22.44 | 1.20 |
| Abies concolor              | Tree                   | Forest                          | 11.12 | 30.29 | 0.89 |
| Pinus ponderosa             | Tree                   | Forest                          | 11.12 | 30.29 | 0.89 |
| Carduus nutans              | Perennial forb         | Grassland                       | 12.52 | 18.53 | 1.28 |
| Allium vineale              | Perennial forb         | Grassland                       | 12.72 | 38.45 | 0.85 |
| Cerastium<br>fontanum       | Perennial forb         | Grassland                       | 12.72 | 38.45 | 0.85 |
| Rosa multiflora             | Shrub                  | Forest                          | 12.72 | 38.45 | 0.85 |
| Ratibida<br>columnifera     | Perennial forb         | Grassland                       | 12.94 | 41.90 | 0.49 |
| Sphaeralcea<br>coccinea*    | Perennial forb         | Grassland                       | 12.94 | 41.90 | 0.49 |
| Lupinus arboreus            | Shrub                  | Grassland                       | 12.96 | 17.42 | 0.93 |
| Nothofagus fusca            | Tree                   | Forest                          | 13.35 | 18.17 | 1.02 |
| Banksia ericifolia          | Shrub                  | Shrubland/Forest                | 17.16 | 19.09 | 1.08 |
| Petrophile<br>pulchella*    | Shrub                  | Shrubland/Forest                | 17.16 | 19.09 | 1.08 |
|                             |                        |                                 |       |       |      |

| Thymus vulgaris                | Shrub                  | Rocky<br>escarpment     | 17.47 | 25.45 | 0.46 |
|--------------------------------|------------------------|-------------------------|-------|-------|------|
| Atriplex vesicaria             | Shrub                  | Arid open<br>shrublands | 17.63 | 26.70 | 0.18 |
| Sapium<br>sebiferum*           | Tree                   | Forest                  | 18.15 | 30.10 | 1.02 |
| Bothriochloa<br>ischaemum      | Perennial<br>graminoid | Grasslands              | 19.16 | 32.62 | 0.54 |
| Fagus grandifolia              | Tree                   | Forest                  | 19.39 | 30.10 | 0.98 |
| Atriplex canescens             | Shrub                  | Grassland               | 20.34 | 33.07 | 0.16 |
| Syzygium jambos                | Tree                   | Forest                  | 21.55 | 11.82 | 2.16 |
| Clidemia hirta                 | Shrub                  | Forest                  | 21.79 | 11.42 | 2.43 |
| Astrocaryum<br>mexicanum       | Palm                   | Forest                  | 24.11 | 15.75 | 2.08 |
| Vochysia<br>ferruginea         | Tree                   | Tropical Forest         | 25.33 | 9.19  | 2.60 |
| Swietenia<br>macrophylla       | Tree                   | Forest                  | 25.56 | 15.16 | 0.57 |
| Dicorynia<br>guianensis        | Tree                   | Forest                  | 25.67 | 9.72  | 1.88 |
| Oxandra asbeckii               | Tree                   | Forest                  | 25.74 | 9.69  | 1.85 |
| Vouacapoua<br>americana        | Tree                   | Forest                  | 25.74 | 9.69  | 1.85 |
| Pentaclethra<br>macroloba      | Tree                   | Forest                  | 26.04 | 10.57 | 2.53 |
| Stryphnodendron microstachyum* | Tree                   | Forest                  | 26.04 | 10.57 | 2.53 |
| Shorea leprosula               | Tree                   | Forest                  | 26.75 | 10.82 | 1.17 |
| Bertholletia<br>excelsa        | Tree                   | Forest                  | 26.91 | 13.24 | 0.93 |
| Avicennia<br>germinans         | Tree                   | Tropical<br>mangrove    | 28.14 | 10.20 | 0.36 |

# Appendix S6 - DIC values for all competing Bayesian Multi-Response Mixed Models

Summary of candidate Generalised Multi-response Mixed Models of the relationships between traits, climate, phylogeny and life-history metrics. Phylogeny was fitted as a random effect in all models with separate coefficients calculated for each response trait. A fully flexible residual covariance matrix was fitted between response traits in all models. Models were compared by Deviance Information Criterion values (DIC), with a lower DIC indicating a more parsimonious model. Each model was run three times as DIC values change slightly on each model run due to the stochasticity inherent in the MCMC model fitting process.

| Candidate model  | Explanatory variables  | <b>DIC</b> (mean ± s.d.) |
|--|--|--------------------------|
| Null model   | None   | 838.6 ± 0.3              |
| Traits only  | PC1 (Size and structure)<br>PC2 (Leaf traits)  | 852.2 <b>±</b> 0.8       |
| Climate only   | Temperature PC1 Log moisture availability  | 866.3 ± 0.2              |
| Climate and traits (no interactions)   | PC1 (Size and structure) PC2 (Leaf traits) Temperature PC1 Log moisture availability   | 849.0 ± 0.4              |
| Climate and traits<br>(with interactions)  | PC1 (Size and structure) PC1 (Size and structure) * Temperature PC1 PC1 (Size and structure) * Log moisture availability PC2 (Leaf traits) PC2 (Leaf traits) * Temperature PC1 PC2 (Leaf traits) * Log moisture availability Temperature PCA Log moisture availability | 643.5 ± 3.3              |
| Final model  Reached by removing individual terms from the "Climate and traits (with interactions)" model using backwards stepwise selection | PC1 (Size and structure) PC1 (Size and structure) * Temperature PC1 PC1 (Size and structure) * Log moisture availability PC2 (Leaf traits) Temperature PCA Log moisture availability   | 636.0 ± 1.2              |

# Appendix S7 - Full table of model coefficients for best fitting Bayesian Multi-Response Mixed Model

Bayesian estimates of posterior means, upper and lower credible intervals and effective sample sizes for fixed effects for each life-history metric in fitted multi-response General Linear Model. Refer to main text for details of model fitting including phylogenetic and residual covariance structures.

| Life history metric | Explanatory variable    | Posterior<br>mean | Lower<br>95% CI | Upper<br>95% CI | Effective sample size |
|---------------------|-------------------------|-------------------|-----------------|-----------------|-----------------------|
| Age at maturity     | Structure and size axis | 1.02              | 0.40            | 1.78            | 1144.26               |
|                     | Leaf traits axis        | 0.06              | -0.37           | 0.53            | 800.00                |
|                     | Temperature PCA         | -0.25             | -0.58           | 0.13            | 800.00                |
|                     | Moisture availability   | 0.14              | -0.03           | 0.31            | 800.00                |
|                     | Size * Temperature PCA  | 0.55              | 0.08            | 1.01            | 800.00                |
|                     | Size * Moisture         | 0.16              | -0.20           | 0.53            | 800.00                |
| Annual reproduction | Structure and size axis | -0.63             | -1.33           | 0.04            | 800.00                |
|                     | Leaf traits axis        | 0.17              | -0.34           | 0.67            | 720.58                |
|                     | Temperature PCA         | 0.20              | -0.16           | 0.57            | 800.00                |
|                     | Moisture availability   | -0.08             | -0.31           | 0.19            | 800.00                |
|                     | Size * Temperature PCA  | -0.06             | -0.50           | 0.37            | 800.00                |
|                     | Size * Moisture         | -0.12             | -0.64           | 0.40            | 920.76                |
| Generation time     | Structure and size axis | 0.99              | 0.42            | 1.54            | 800.00                |
|                     | Leaf traits axis        | -0.21             | -0.63           | 0.21            | 800.00                |
|                     | Temperature PCA         | -0.14             | -0.46           | 0.13            | 800.00                |
|                     | Moisture availability   | 0.22              | 0.03            | 0.41            | 800.00                |
|                     | Size * Temperature PCA  | 0.37              | 0.02            | 0.80            | 800.00                |
|                     | Size * Moisture         | -0.25             | -0.69           | 0.16            | 914.30                |
| Mature lifespan     | Structure and size axis | 0.66              | 0.13            | 1.25            | 800.00                |
|                     | Leaf traits axis        | -0.27             | -0.68           | 0.16            | 819.20                |
|                     | Temperature PCA         | 0.13              | -0.14           | 0.43            | 800.00                |
|                     | Moisture availability   | 0.22              | 0.03            | 0.43            | 800.00                |
|                     | Size * Temperature PCA  | 0.23              | -0.17           | 0.63            | 716.38                |
|                     | Size * Moisture         | -0.27             | -0.65           | 0.15            | 800.00                |
| Distribution of     | Structure and size axis | -0.38             | -1.07           | 0.24            | 800.00                |
| mortality           | Leaf traits axis        | 0.03              | -0.46           | 0.56            | 800.00                |
|                     | Temperature PCA         | 0.18              | -0.14           | 0.52            | 800.00                |
|                     | Moisture availability   | -0.12             | -0.32           | 0.09            | 892.64                |
|                     | Size * Temperature PCA  | -0.70             | -1.13           | -0.21           | 800.00                |
|                     | Size * Moisture         | 0.57              | 0.13            | 0.97            | 897.83                |
| Inequality of       | Structure and size axis | -0.07             | -0.86           | 0.55            | 826.55                |
| reproduction        | Leaf traits axis        | 0.30              | -0.25           | 0.81            | 800.00                |
|                     | Temperature PCA         | -0.04             | -0.37           | 0.36            | 800.00                |
|                     | Moisture availability   | 0.03              | -0.19           | 0.29            | 800.00                |
|                     | Size * Temperature PCA  | 0.24              | -0.21           | 0.74            | 800.00                |
|                     | Size * Moisture         | 0.13              | -0.34           | 0.64            | 914.51                |

Bayesian variance estimates for the phylogenetic effects on each life-history metric in fitted Multi-response General Linear Model.

| Life history metric        | Posterior mean | Lower 95% CI | Upper 95% CI | Effective sample size |
|----------------------------|----------------|--------------|--------------|-----------------------|
| Age at maturity            | 2.45           | 1.49         | 3.62         | 1149.99               |
| Annual reproduction        | 0.04           | 0.00         | 0.16         | 500.61                |
| Generation time            | 0.02           | 0.00         | 0.07         | 800.00                |
| Mature lifespan            | 0.10           | 0.00         | 0.35         | 800.00                |
| Distribution of mortality  | 1.64           | 0.71         | 2.77         | 604.42                |
| Inequality of reproduction | 0.15           | 0.00         | 0.60         | 800.00                |

### Appendix S8 – Discussion of the residual covariance of life-history metrics

The majority of life-history metrics showed residual covariances, after accounting for phylogenetic history, morphological traits and climate (Fig. 5), supporting the theoretical understanding that trade-offs and energetic constraints limit the life-history strategies of plant species (Partridge & Harvey 1988; Stearns 1992; Franco & Silvertown 1996; Salguero-Gómez et al. 2016). From an evolutionary perspective, species with older ages at maturity should benefit by having longer mature lifespans, higher mean reproduction and/or decreased variance in reproduction, in order to offset the fitness costs of late maturity (Partridge & Harvey 1988). We observed a positive association between age at maturity and mature lifespan indicating that a longer reproductive period may be associated with later maturation in plant species. However, we found no evidence that older age at maturity is associated with either higher annual reproduction or lower variance in reproduction across the lifespan. We also observed a negative covariance for both mature lifespan and generation time (two indicators of slow life-histories) with both annual reproduction and inequality in reproduction (Fig. 5) suggesting that species with longer mature lifespans and longer generation times have lower annual reproduction rates and a more even spread of reproduction across their life-cycles. However, care must be taken in the interpretation of these residual correlations as they could relate to other unmeasured covariates, and strong evidence for trade-offs or constraints are difficult to determine using broad scale comparative methods.

# Appendix S9 - Phylogenetic variance coefficients figure

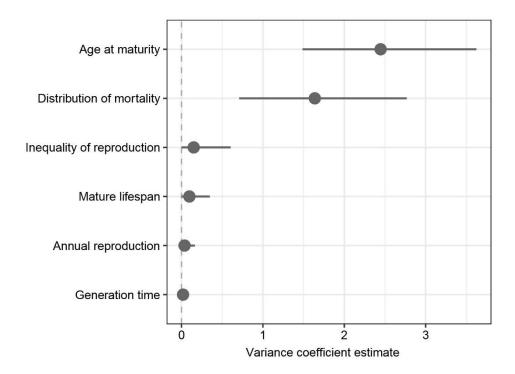


Figure shows model outputs of estimated variance coefficients for each individual life history metric explained by phylogeny in the Bayesian Multiple-response Model described in main text. Filled circles represent the posterior mean and lines indicate 95% credible intervals.