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LETTER

Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale

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Abstract

Life history strategies are fundamental to the ecology and evolution of organisms and are important for understanding extinction risk and responses to global change. Using global datasets and a multiple response modelling framework we show that trait-climate interactions are associated with life history strategies for a diverse range of plant species at the global scale. Our modelling framework informs our understanding of trade-offs and positive correlations between elements of life history after accounting for environmental context and evolutionary and trait-based constraints. Interactions between plant traits and climatic context were needed to explain variation in age at maturity, distribution of mortality across the lifespan and generation times of species. Mean age at maturity and the distribution of mortality across plants' lifespan were under evolutionary constraints. These findings provide empirical support for the theoretical expectation that climatic context is key to understanding trait to life history relationships globally.

Keywords

Botany, climate, comparative demography, ecological strategies, ecology, evolution, lifespan, matrix population model, multivariate modelling, population dynamics.

INTRODUCTION

'Life history theory tries to explain how evolution designs organisms to achieve reproductive success. The design is a solution to an ecological problem posed by the environment and subject to constraints intrinsic to the organism'. Stearns (2000).

Life history theory is explicitly integrative, taking into account the environment as well as evolutionary, morphological and physiological constraints (Partridge & Harvey 1988; Stearns 1992). Lifetime reproductive success is determined by key life history elements such as age at reproduction, quantity of offspring and reproductive lifespan, which are themselves underpinned by vital rates such as survival, growth and reproduction. Trade-offs in energy and resource allocation between

these vital rates limit the range of viable life history strategies, meaning that there can be no 'Darwinian demon' which maximises growth, reproduction and survival simultaneously (Partridge & Harvey 1988; Stearns 1992). Classical life history theory focused on optimisation theory and suggested that there is a single optimal life history strategy in a given environment (Stearns 1992). More contemporary approaches, suggest that multiple life history solutions exist in a given environment, allowing stable co-existence of a diverse range of strategies (e.g. Evolutionarily Stable Strategies, Mirmirani & Oster 1978, and- adaptive performance landscapes, Arnold 2003). These theoretical frameworks are in keeping with the observation that very different life history strategies often occur together in natural environments, for example short-lived herbaceous species and long-lived trees in forests (Silvertown *et al.* 1993). This divergence in life history strategies also occurs between closely related species (Münzbergová 2013).

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Conversely, very different growth forms can give rise to similar life histories (Salguero-Gómez *et al.* 2016). Here we propose a framework that enables the explanation of life history strategy variation within and across environments from widely available species trait data within phylogenetic constraints.

Understanding how plant 'functional traits' such as plant size, leaf area and seed-size influence fitness through their effects on vital rates is a core aim of functional ecology (Violle *et al.* 2007; Laughlin *et al.* 2020; Swenson *et al.* 2020). The assumption that plant demographic performance can be predicted from functional traits is central to its application in community ecology and ecosystem dynamics (McGill *et al.* 2006; Westoby & Wright 2006; Salguero-Gómez *et al.* 2018). However, despite being a key foundation of trait-based ecology, evidence underpinning the relationships between plant traits and vital rates or life history is mixed (Yang *et al.* 2018; Laughlin *et al.* 2020; Swenson *et al.* 2020), with studies finding relatively weak relationships at global scales (Adler *et al.* 2014; Paine *et al.* 2015; Che-Castaldo *et al.* 2018; de Jonge *et al.* 2018; Yang *et al.* 2018).

Two potential reasons for weak trait-life history relationships at global scales are: (1) environmental context dependency and (2) the multivariate nature of both life history strategies and functional trait syndromes at an organismal scale. Life history evolution occurs in response to a given environmental context (Partridge & Harvey 1988; Stearns 1992); hence, the relationship between functional traits and life history or vital rates is likely to differ depending on the environmental context and may even change direction (Yang *et al.* 2018; Laughlin *et al.* 2020; Swenson *et al.* 2020). For example, high leaf mass per unit area (LMA) is considered adaptive in arid environments due to higher water use efficiency, but this represents a trade-off with N use efficiency and photosynthetic rates; meaning that lower LMA is more adaptive in wetter environments (Reich *et al.* 2003). Similarly, height may be adaptive in areas with high resource availability and competitors as it facilitates competition for light, but may reduce survival in freezing environments due to hydraulic failure in woody tissues (Zanne *et al.* 2014). While, the climate dependency of trait to vital rate relationships is fundamental to functional ecology (Reich *et al.* 2003), how this climatic contingency affects life history strategies at global scales is not well understood. Empirically, environmental context dependency of trait-life history relationships have recently been shown to be important in explaining the competitive dynamics of both annual plant species and trees under different climatic conditions (Zambrano *et al.* 2017; Pérez-Ramos *et al.* 2019), and rates of vegetative reproduction in different habitats across a broad range of plant taxa in botanic gardens (Pistón *et al.* 2019). At global scales climate differences are at their largest, and therefore incorporating interactions between traits and climate is likely to be fundamental to understanding trait to life history relationships at these scales.

As selection occurs at the level of the individual or phenotype (Lande & Arnold 1983) and strong covariances and trade-offs exist between life history elements (Franco & Silvertown 1996; Salguero-Gómez *et al.* 2016; Healy *et al.* 2019) multivariate response models are needed to properly reflect the underlying genetic and evolutionary processes (Blows 2007; Hadfield & Nakagawa 2010; Swenson *et al.* 2020). By contrast, linear regression models which implicitly assume a direct relationship between an individual functional trait and life history metrics (e.g. between seed-size and fecundity) cannot account for the strong trade-offs and covariances which exist between life-history metrics (Blows 2007; Swenson *et al.* 2020). Furthermore, the use of multiple functional traits as predictors of life history variables allows for there to be multiple solutions to the problem of optimising fitness in a single environment (Arnold 2003; Laughlin & Messier 2015; Swenson *et al.* 2020). This incorporation of the multidimensional nature of the phenotype-fitness relationship has recently been successfully demonstrated within habitats for forest and grassland species (e.g. Godoy *et al.* 2015; Rüger *et al.* 2018; Breitschwerdt *et al.* 2019; Pérez-Ramos *et al.* 2019).

Variation in life history strategies is constrained by phylogenetic history, and whilst this has been investigated (e.g. Burns *et al.* 2010; Salguero-Gómez *et al.* 2016; Che-Castaldo *et al.* 2018), it is rarely examined together with multivariate life history, traits and environmental context. This is particularly important as both life history and traits are phylogenetically constrained.

Understanding the extent to which life history strategies are explained by traits, environment and evolutionary factors is also of great practical importance. The quantification of life history is inherently data hungry, and deriving plant population matrices from which life history metrics are derived requires intensive longitudinal fieldwork (Salguero-Gómez *et al.* 2018). The recent collation of detailed life history information in the form of plant population matrices for several hundred species greatly advances the scope for comparative analyses (Salguero-Gomez *et al.* 2015). However, functional trait data remain much more widely available with data on key traits now available for hundreds of thousands of species (e.g. Enquist *et al.* 2016; Kattge *et al.* 2020). Thus, robust models of life history from functional traits, phylogeny and environmental context, could facilitate the estimation of life history metrics for many more species.

Here, we propose a model framework that specifically tests how climate influences trait to life history relationships at global scales (Fig. 1), whilst accounting for the relationships between individual components of life history strategies (e.g. reproduction, age at maturity, lifespan) and the phylogenetic relationships between species. Whilst relationships between functional traits and climate, and the covariation of functional traits are well documented (e.g. Wright *et al.* 2004; Chave *et al.* 2009; Zanne *et al.* 2014; Díaz *et al.* 2016; Moles 2018; Boonman *et al.* 2020), the novelty of our work lies in the application of a multidimensional holistic framework to understand how traits and climate relate to life history strategies across a diverse range of plant growth forms at global scales. Specifically, we provide a global test of this framework using data compiled from the largest available databases of plant traits (TRY, BIEN and primary literature), plant demography (COMPADRE) and broad-scale climate variables (Worldclim and CGIAR) for 80 plant species of worldwide. From previous work we expect phylogeny to structure plant life history strategies (Burns *et al.* 2010; Salguero-Gómez *et al.* 2016; Che-Castaldo *et al.* 2018). We expect
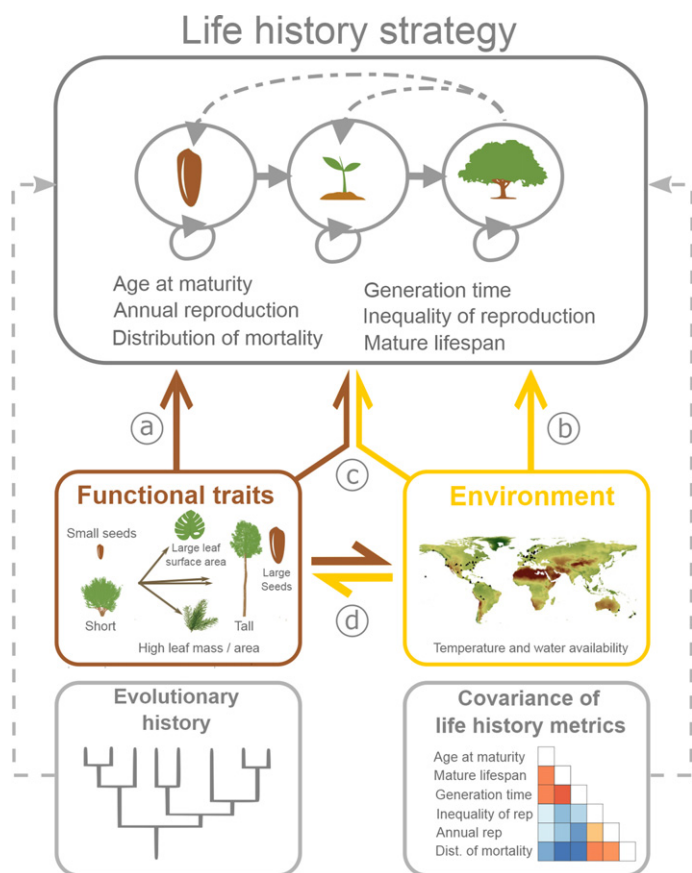
Life history strategy

FIGURE 1 Conceptual illustration of model framework and alternative hypotheses. Four candidate models were compared based on *a priori* hypotheses: (a) traits only (traits explain life history strategies in the absence of climate information), (b) climate only (climate explains life history strategies in the absence of trait information), (c) traits and climate (traits and climate additively predict life history but do not interact) and (d) traits interact with climate (life history strategies are predicted by the interaction between traits and climate, that is, the effect of traits depend on climatic conditions). Grey boxes below show the random effects which were included in all models, these were the phylogenetic relationships between species, and the residual covariance structure between life history metrics. Images are for illustrative purposes only.

relatively weak relationships with climate variables and functional traits when these are considered separately or additively in the model (Paine *et al.* 2015; Coutts *et al.* 2016; Yang *et al.* 2018). The absence of an interaction between climate and functional traits would be consistent with the idea that there is a single global relationship between functional traits and life history strategies, meaning that relationships between functional traits and life history (e.g. taller species have slower life history strategies) could be generalised to other locations irrespective of differences in climate. We expect that including an interaction between traits and climate will improve our capacity to explain life history strategies, because of underlying differences in functional trait to vital rate and life history relationships along environmental gradients. This interaction would indicate that the relationship between functional traits and emergent life history strategies differs between climatic contexts at the global scale.

MATERIAL AND METHODS

Overview

To examine the relationships between traits, climate, phylogeny and life history strategies we integrated data from multiple data sources. Climate and life history metrics were matched for location at a 5 km scale, but due to a lack of co-location of trait data with demographic data, traits were used as species mean values. We then used a Bayesian multi-response mixed modelling approach to predict life history response variables as a function of traits, climate and phylogeny, together with the residual covariance between the life history response metrics. This multivariate model is based on the statistical framework for comparative biology presented by Hadfield & Nakagawa (2010), which to our knowledge has not been previously applied in the context of global plant life history evolution.

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-Gomez *et al.* 2015) together with matching species trait data for key functional traits (see details below).

Functional traits
Four commonly measured functional traits were chosen based their relevance to describing life history strategies of plants and on their availability across taxa: mean adult height (m), seed mass (mg), leaf dry mass per unit area (LMA; mg/mm^2) and leaf area (mm^2) (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 and 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 (Tamme *et al.* 2014; Moles 2018). LMA was chosen for its relationship to leaf investment strategies described in the 'Leaf Economics 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 lifespans and greater protection against abiotic stress (Wright *et al.* 2004). From a life history perspective high LMA could confer advantages to species with slower life-histories as these are more likely to benefit from more conservative allocation of energy and resources. Leaf area is associated with the surface area available for light-interception, thermodynamics, water-use efficiency and vulnerability to herbivory (Niinemets *et al.* 2006; Moles 2018), and has been previously shown to be relatively uncorrelated with LMA and the Leaf Economics Spectrum (Laughlin 2014; Díaz *et al.* 2016). Functionally, higher leaf area could be expected to be associated with faster life-histories due to

greater photosynthetic capacity and lower stress tolerance. Furthermore, plant height, woodiness, leaf area and seed dry mass tend to be positively related across species because of allometric constraints (Cornelissen 1999; Díaz *et al.* 2016). Data for functional traits were obtained from the TRY Plant Trait Database (Kattge *et al.* 2011, 2020) and the Botanical Information and Ecology Network BIEN (Enquist *et al.* 2016) and further individual studies sourced from the literature and the Dryad data repository (see Appendix S1 in Supporting Information for a full list of data sources).

Functional traits – calculation and criteria for inclusion. Measurements of functional traits were only included from healthy adult plants in datasets. Experimental conditions (e.g. greenhouse/climate chambers) were only included where these were designed to mimic field conditions. Modelled or extrapolated values were excluded. For each functional trait the final mean value for each species used in further analyses was calculated by taking the mean value across all study locations of that species. This prevented the individual studies or locations with many records from having a disproportionate effect.

In order to derive two key axes of trait variation for further analyses 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). This step was necessary to reduce the number of explanatory variables in the model given our sample size, while maintaining information from all four functional trait variables of interest. These axes closely resemble those previously described for the entire TRY database in Díaz *et al.* 2016 (Appendix S2). These axes described a total of 82.5% of variation in the functional trait data, and hereafter are referred to as the 'PC1 - Size and structure' (50.1%) and 'PC2 – Leaf traits' (32.5%).

Life history metrics

Six life history metrics were chosen to represent the core elements of variation in plant life history strategies (Salguero-Gómez *et al.* 2016). Age at maturity, mature lifespan and generation time were chosen to represent different, but related, aspects of the pace of plant life-histories (slow-to-fast life-histories). While, annual reproduction, inequality of reproduction across lifespan and distribution of mortality across lifespan represent variation in reproduction and mortality risk across the lifespan (Salguero-Gómez *et al.* 2016; Healy *et al.* 2019).

Life history metrics – criteria for inclusion. All life history metrics were calculated from population level matrix population models in the COMPADRE database vr. 4.0.1 (Salguero-Gomez *et al.* 2015). Studies were included only from vascular plant species in unmanipulated outdoor environments. In addition, matrices were only included where they: (1) were separable into individual matrices representing growth/survival and fecundity (i.e. **U** and **F** sub-matrices), (2) did not include clonality (due to conceptual difficulties in calculating lifespan and individuality in clonally reproducing species), and (3) were primitive, irreducible and ergodic.

Where original authors provided individual matrices per year per location these matrices were used 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 where there were differences between the COMPADRE data and the original publications the data in the original publications was used.

Preparation of matrix population models. To produce one matrix per population, individual matrices were averaged across years within populations prior to the calculation of the life history metrics. In four species, matrix transitions were longer than one year in duration, and matrices were converted to annual time-steps prior to the calculation of life history metrics (Appendix S3). All other species had annual transitions.

Calculation of life history metrics. Age at maturity was calculated as the mean age at which first reproduction occurs among individuals that survive to reproductive age (Caswell 2001). Mature lifespan was defined as the mean lifespan of individuals in the population conditional on having survived to mean sexual maturity (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). Annual reproduction was defined as the mean number of new aboveground individuals produced annually by a population at its stable stage distribution (SSD). Inequality of reproduction across lifespan was measured using the Gini coefficient of inequality of annual reproductive output across the lifespan (package 'ineq'; Zeileis 2014). The Gini coefficient of inequality ranges from 0 to 1, with 0 representing an equal spread (e.g. iteroparous species that reproduce every year) and 1 being completely unequal (e.g. semelparous species with a single reproductive event). Populations with annual life-cycles were assigned a Gini coefficient of 1 reflecting their semelparous life-cycles (model results were not qualitatively different when populations with annual life-cycles were omitted, Appendix S4). Reproductive output in each time step was based on age specific fecundity curves ('m_x curves', function 'makeLifeTable', R package 'Mage' with modification to allow reproduction in the first time step). The distribution of mortality across lifespan was measured as the median/maximum lifespan of species, giving a range of values between 0 and 1. Values close to 1 indicate that juvenile mortality is low relative to the lifespan of the species, while low values indicate high mortality in juvenile stages relative to lifespan (see Appendix S3 for details).

All life history metrics were calculated from the first aboveground stage to allow appropriate comparison between studies with and without seed-stages. Following the calculation of each life history 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 climate data and enable the modelling of demographic

metrics as a function of climate. Where populations were > 5km apart or from different habitats (13 species) the life history metrics were not averaged, and instead a single population was chosen at random.

Climate data

Two climate variables representing key drivers of plant physiological rates, temperature and water availability, were derived for each population location. Climate variables were extracted as a mean value from a 2.5 km radius around each COMPADRE study location (package 'raster'; Hijmans 2017). Given collinearity of many climate variables, the size of the dataset (80 species), and the risk of losing generality through over-parameterisation, we decided *a priori* that temperature and water availability were the most appropriate climate variables for this study.

Temperature data were extracted from WorldClim Version 2.0 at 30 arc-second resolution (Fick & Hijmans 2017). 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 68.0% 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 (following Coutts *et al.* 2016).

We used the Global Aridity Index to quantify moisture availability. The Global Aridity Index quantifies precipitation deficit over atmospheric water demand (Trabucco & Zomer 2009). We log-transformed the Aridity Index as we expected the influence of water stress to be higher where water is limiting (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, $p = 0.639$, $n = 80$).

Data on all variables were available for 80 species (Fig. 2). Mean annual temperatures of the study sites ranged from −3.6 to 28.1, and the moisture availability included arid, semi-arid, dry sub-humid and humid zones (Trabucco & Zomer 2009). See Appendix S5 for species list with associated plant growth forms, habitats and basic climate information from demographic study locations.

Phylogeny

Phylogenetic relationships between species were quantified using a time-calibrated phylogeny of 32 223 vascular land plant species (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 genus based on literature (Conti *et al.* 1999; Calviño & Downie 2007; Jacquemyn *et al.* 2011; Jin *et al.* 2014; Simon *et al.* 2016, see Appendix S5). For seven of these species a detailed phylogeny for the genus could not be found and the species location was assigned randomly within the genus. All species which were absent from our dataset were dropped from the phylogeny (package 'ape'; Paradis & Schliep 2018).

Statistical analysis

Multi-response mixed modelling

To model the relationships between functional traits, climate, phylogeny and life history strategies a Bayesian Multi-response generalised linear model framework was used (Fig. 1). This approach allows for the explicit incorporation of both phylogenetic structure and the estimation of covariances between the multiple response variables, in conjunction with the estimation of the fixed effects (i.e. functional traits and climate).

To satisfy the normality assumptions all life history metrics (except the Gini Index of inequality of reproduction across lifespan) were natural log transformed. The Gini Index was square-root transformed for the same reasons. All variables were 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
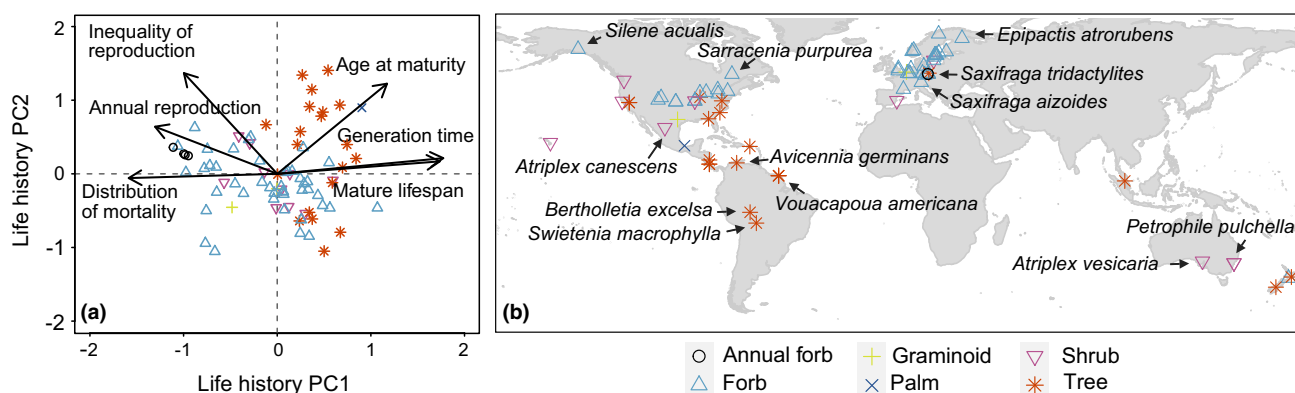

FIGURE 2 Locations of life history studies in (a) life history PCA space and (b) geographic space. Colours and point types represent the predominant growth form of each species. The life history PCA is for visualisation of the life history metrics and species' growth forms and is not used in the model. The PCA was conducted on the natural log of all life history metrics, except for 'Inequality of reproduction' which was square root transformed for normality. All metrics were standardised to units of deviation and mean centred prior to PCA. Named species in b) are those mentioned in the main text.

their interactions (Fig. 1). The most complex model included two PCA axes representing plant functional traits (PC1 – Size and structure, and PC2 – Leaf traits) and 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 variance estimated for its association with each life history metric, and a residual covariance matrix was fitted to account for the covariance between life history metrics and residual variation within life history metrics (Hadfield 2010). This residual covariance matrix was fully parameterised, such that variance explained could differ both within life history metrics and between pairs of metrics. Model fitting was conducted using the R package 'MCMCglmm', with priors for multivariate responses and phylogeny based on Hadfield (2010). Alternative models were compared using Deviance Information Criteria (DIC), a hierarchical generalisation of the Akaike Information Criteria for Bayesian models (Spiegelhalter *et al*. 2002).

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 to reach the final model with the lowest DIC. For further details on model selection and validation, which followed Gelman & Rubin 1992; Plummer *et al*. 2006; Hadfield 2010, see Appendix S3.

The variance in life history metrics explained by the final model (i.e. traits, climate and phylogeny), was calculated as described for conditional R^2 values in Nakagawa & Schielzeth, 2013. The residual covariance between life history metrics was included in the residual variance component of the calculation, and as such is not included as part of the reported variance explained by the model (see Appendix S3).

All statistical analysis was conducted in R 3.5.0 (R Core Team) (for further details see Appendix S3). R scripts and datasets available at https://doi.org/10.5281/zenodo.4457447

RESULTS

The model which best explained the life history metrics included interactions between climate and functional traits, indicating climate dependency in the relationship between traits and life history strategies (DIC = 643.5). This model had a much lower DIC than the null model containing only phylogeny and residual covariance structure (DIC = 838.6; ΔDIC = 195.1). By contrast, models which included as fixed effects only traits (DIC = 852.2), only climate (DIC = 866.3) or traits and climate without an interaction (DIC = 849.0) performed worse than the null model (Appendix S6). Estimates of model coefficients differed slightly between competing models, but the overall direction of the coefficients did not.

The most parsimonious model contained interactions between the Size and structure trait axis (PC1) and each of the climate variables (Temperature PCA and Moisture availability), together with a main effect of the Leaf traits axis (PC2). Although the Leaf traits axis was retained in the final

model (ΔDIC 3.35), all credible intervals of model coefficients overlapped zero (Fig. 3). Inferences about the importance of variables from model coefficients in Fig. 3 are difficult because of the complexity of the model framework, for more inferences about the relative importance of variables in the model see DIC model selection tables (Appendix S6). The variance in life history strategies explained by the final model including traits, climate and phylogeny was 69.7%.

Traits and climate

The utility of functional traits and climate for predicting life history metrics differed depending on the life history metric. Posterior mean coefficients for traits with credible intervals not overlapping zero were observed for biological timing metrics (age at maturity, generation time, mature lifespan) and for the distribution of mortality across lifespan, but not for fecundity related metrics (annual reproduction and inequality of reproduction across lifespan; Fig 3). For a full list of model coefficients and credible intervals see Appendix S7.

The plant size and structure axis was particularly important as a predictor of biological timings, with later age at maturity, longer generation times (i.e. the expected number of years taken for a population to replace itself) and longer mature lifespan associated with larger plant size. A positive interaction between the size and structure axis and the temperature PCA was evident for age at maturity and generation time (Fig. 4). Larger species were older at maturity and had longer generation times in hotter less seasonal climates, but this relationship was flatter in cold and seasonal climates (β = 0.55, CI (0.08, 1.01), and β = 0.37, CI (0.02, 0.80)) for this interaction in age at maturity and generation time respectively, compare contours in Fig. 4a and b at cool seasonal vs. hot stable conditions). In our dataset this relationship relates to the capacity of short species in very cold climates to exhibit very slow life histories similar to those of tall species in warmer climates. For example, *Epipactis atrorubens* and *Sarracenia purpurea* had ages at maturity above the 75th percentile in the dataset (13.0 and 13.3 years repectively), and the high Arctic and tundra cushion plant *Silene acaulis* had generation times above the 75th percentile (295.8 years). Mean annual temperatures in the demographic study locations for each of these three species were −0.8, −0.6 and −3.1 °C respectively. In hot stable climates, similar ages at maturity and generation times were seen in the tree species *Avicennia germinans* (age at maturity 10.4 years) and *Vouacapoua americana* (generation time of 295.5 years). Mean annual temperatures in the demographic study locations for each of these species were 24.1 and 25.3 °C respectively.

There was an additive effect of the size and structure axis and moisture availability on generation time with plants in areas with greater moisture availability having longer generation times (β = 0.22, CI (0.03, 0.41)). Moisture availability was also important in determining the mature lifespan of species and showed an additive effect with size and structure, meaning that both greater moisture availability and larger size and structure were associated with longer mature lifespans (β = 0.22, CI (0.03, 0.43), β = 0.66, CI (0.13, 1.25)) for moisture availability and the size and structure axis respectively; Fig. 3).
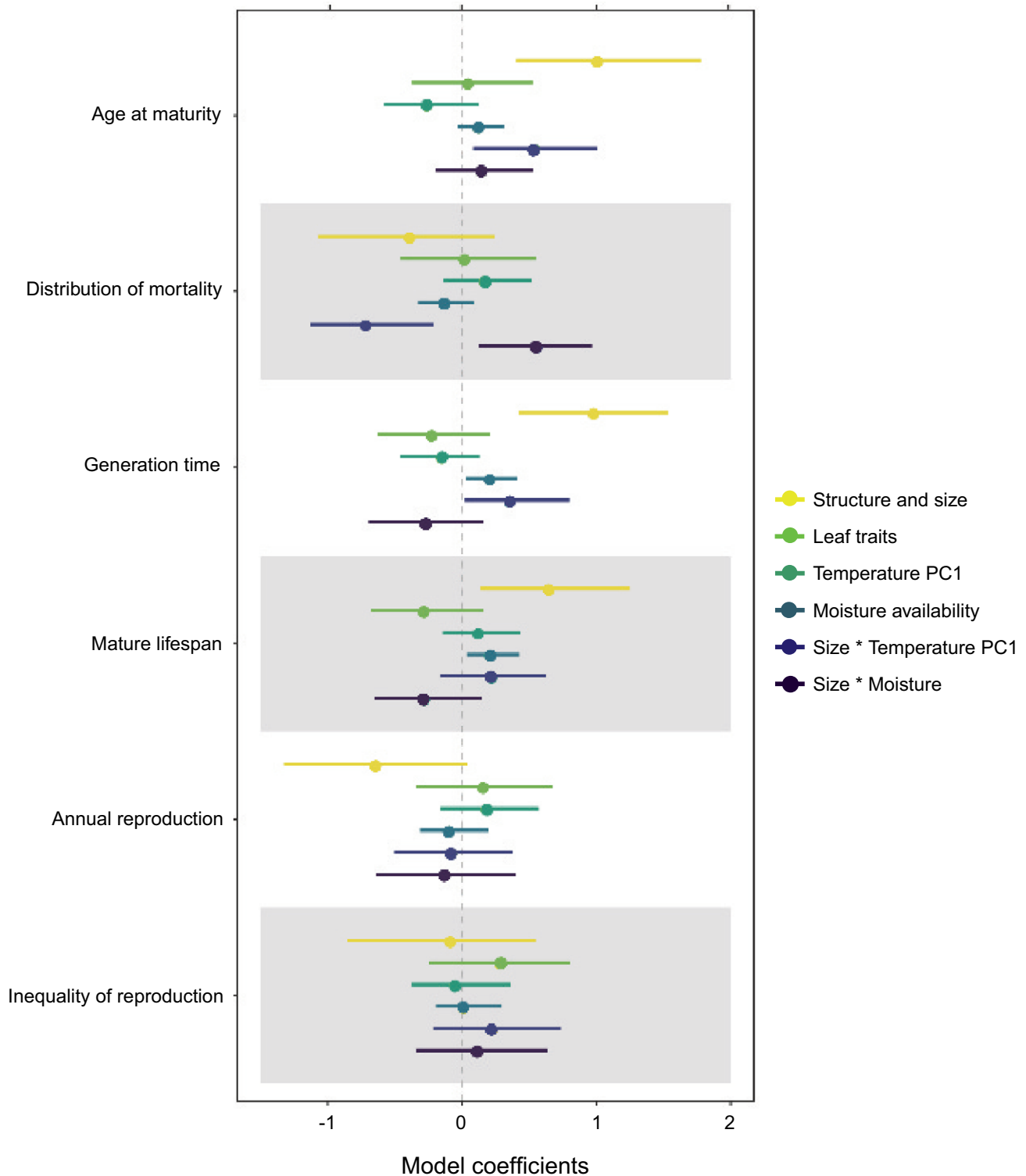
FIGURE 3 Model coefficients of fixed effects from the final Bayesian multi-response model. Filled circles indicate posterior mean model coefficients and solid lines indicate 95% credible intervals. The vertical dashed line indicates effect size of zero. Trait variables include two PCA axes aligned with 1) structure and size and 2) leaf traits; climate variables include moisture availability and the PCA temperature axis, *Indicates an interaction between trait and climate variables. Where an interaction exists between a trait axis and climate variable, the coefficient value of the trait variable represents the relationship between that trait and the associated life history metric when the climate variable is at its mean value in the dataset. Similarly, the coefficients of climate variables in the presence of an interaction with a trait variable represent the relationship of climate with life history at the mean value of that trait variable.
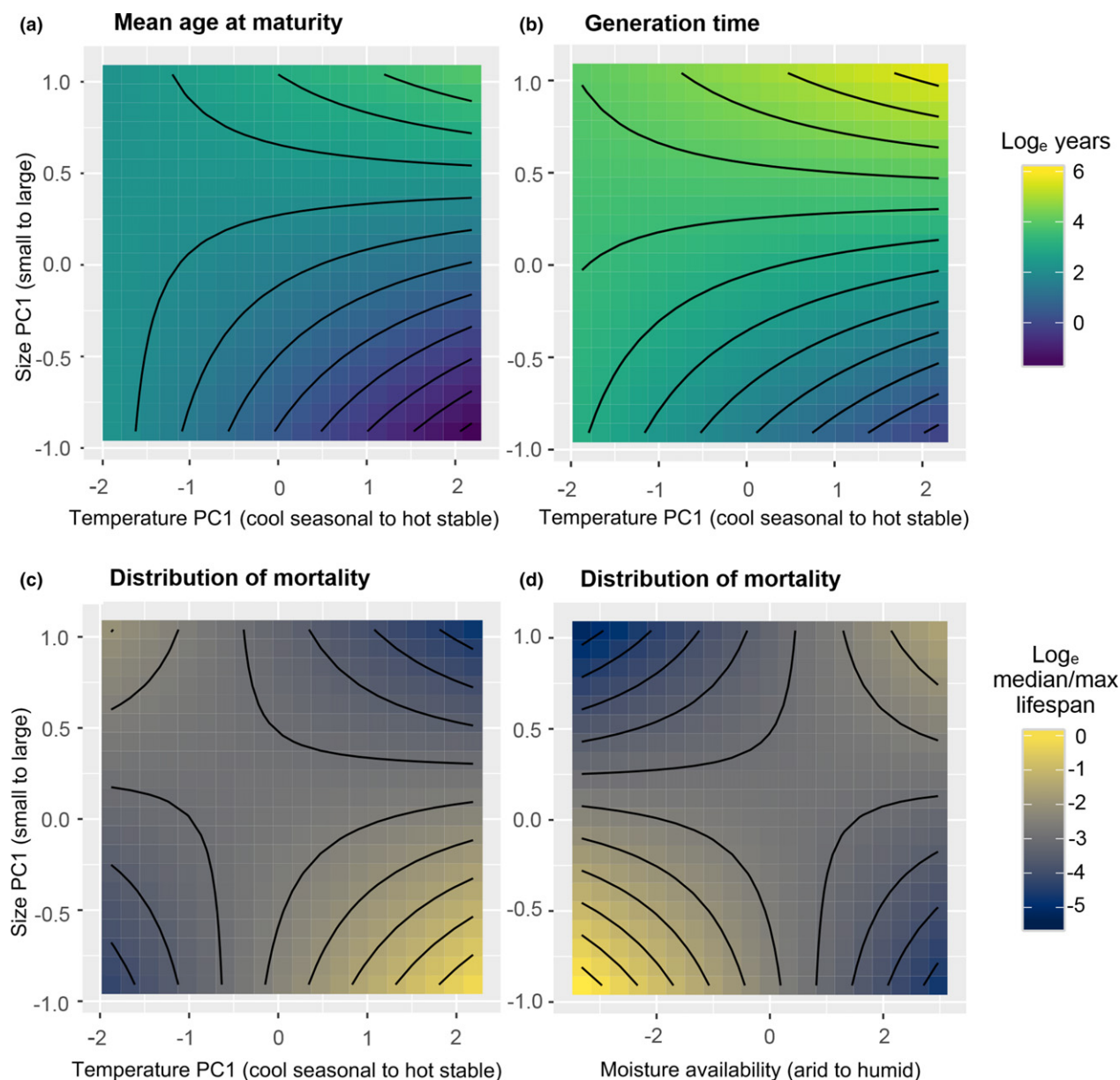
FIGURE 4 Contour plots illustrating interactions between plant traits and climate, and their association with life history metrics (a) 'Age at maturity' (b) 'generation time' (c) and (d) 'distribution of mortality'. Colour scales show marginal estimated mean predictions for each response variable across the range of trait ('Size and structure PC1', y axis) and climate data ('Temperature PC1' or 'Moisture availability', x axes) observed in the dataset. All other variables were set at their mean value for marginal predictions. On the plotted log scale, 'distribution of mortality' values of zero indicate species with a median lifespan equal to the maximum lifespan (e.g. annuals), and increasingly negative values indicate lower median lifespans relative to the maximum (e.g. higher juvenile mortality). Only response variables with trait-climate interaction coefficients with credible intervals not overlapping 0 are plotted.

The distribution of mortality across lifespan was associated with size and structure in interaction with both the temperature PCA axis and moisture availability. In hotter less seasonal climates low median/max ratios (i.e. high juvenile mortality relative to the lifespan) were observed in plants with larger size and structure, whilst in cooler seasonal climates low values were observed in smaller plants ($\beta = -0.70$, CI $(-1.13, -0.21)$, Fig. 4c). This effect is primarily driven by the high maximum lifespans associated with these species, and less variance was evident in the median lifespans. This is exemplified in the dataset by high juvenile mortality in large long-lived trees in hot climates such as *Avicennia germinans* and

Bertholletia excelsa (median/max = 0.003 and 0.030 respectively), and the comparably low median/max ratios observed in the small long-lived herbaceous plant species *Silene acaulis* or the alpine *Saxifraga aizoides* in very cold climates (median/max = 0.007 and 0.023 respectively).

In the case of the interaction between 'size and structure' and moisture availability, low median/max values (i.e. high juvenile mortality relative to the lifespan) were associated with small plants in environments with high moisture availability, whereas larger plants had lower median/max ratios in drier environments ($\beta = 0.57$, CI $(0.13, 0.97)$, Fig. 4d). Trees measured in drier environments such as *Swietenia macrophylla*

(median/max = 0.02) had lower ratios than similarly sized trees measured in wetter climates such *Vouacapoua americana* (median/max = 0.05), although both have relatively low ratios characteristic of longer-lived species. Among medium sized shrub species there was no clear pattern in median/max ratios with moisture availability. For example, the arid shrubland species *Atriplex vesicaria* and *Atriplex canescens* exhibited the second and third lowest med/max ratios of shrub species (both 0.04), but the lowest ratio was exhibited by the temperate shrub species *Petrophile pulchella* (0.02). In small herbaceous species the pattern was reversed with the lowest ratios observed in long-lived species in areas of high moisture availability, with for example the moist alpine *Saxifraga aizoides* having a much lower ratio than its congener *Saxifraga tridactylites* in drier areas (median/max = 0.007 and 0.500 respectively).

Residual covariance of life history metrics

The final model indicated strong residual covariance of life history metrics after accounting for functional traits, climate and phylogeny. Indeed, of the 15 pairwise combinations of life history metrics only two pairs had credible intervals for residual covariance which overlapped with zero (Fig. 5, Appendix S8).

Phylogeny

Phylogenetic constraints on life history metrics were evident for age at maturity and distribution of mortality across lifespan, indicating that values for these metrics are conserved between closely related species ($\beta = 2.4$, CI (1.5, 3.6), and $\beta = 1.5$, CI (0.7, 2.8) respectively). Estimates of the variance explained by phylogeny for all other life history metrics were small with lower credible intervals approaching zero (Appendix S9).

DISCUSSION

Our results demonstrate the importance of climate dependency in trait to life history relationships across plant species at the global scale. Models containing trait-climate interactions in addition to phylogeny performed better than those containing only phylogeny, but models with only main effects of traits and climate without this interaction did not perform better than a model with phylogeny alone. As expected, life history metrics showed residual covariances after accounting for phylogenetic history, morphological traits and climate (Fig. 5). This provides further empirical support for the use of multivariate frameworks in life history analyses, and supports the view that simple-one-to-one matching of functional traits to individual life history metrics or vital rates is biologically unrealistic (Blows 2007; Laughlin & Messier 2015; Swenson *et al.* 2020). Phylogenetic constraints were also important for age at maturity and the distribution of mortality across lifespans.

The observed interaction between traits and climate is evident in the relationship of plant size and structure (height and seed size) with life history metrics related to biological
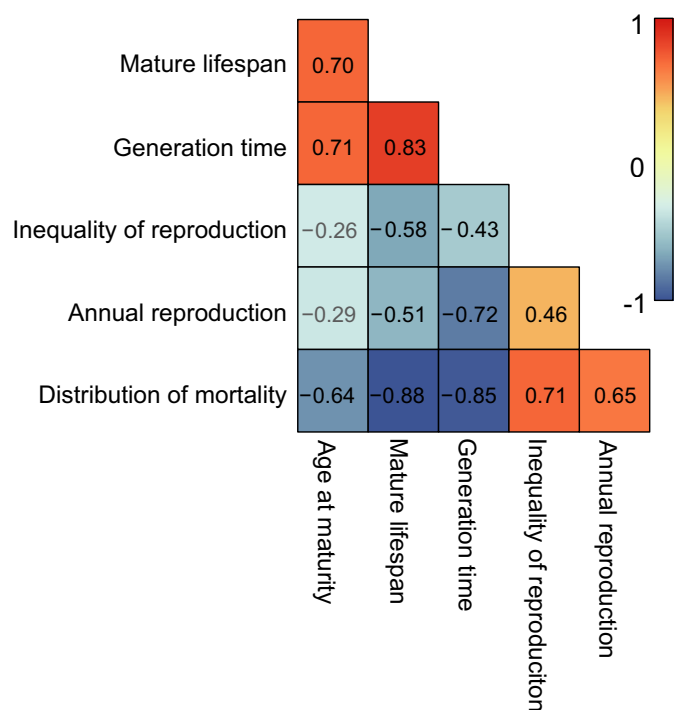

FIGURE 5 Residual correlation structure of life history metrics after accounting for traits, climate and phylogeny in the Bayesian multi-response model. Numbers in light grey indicate correlations where credible intervals overlapped zero in the fitted model. Life history metrics are ordered in plot according to the similarity of their correlation coefficients using hierarchical clustering for interpretive purposes.

timings and the distribution of mortality. Slower life history strategies, with older ages at maturity and longer generation times, were positively correlated with plant height and seed size in hotter more stable climates, but in cold seasonal climates this correlation was not evident. Slower life-histories were also associated with lower median/max lifespans (i.e. higher juvenile mortality relative to maximum lifespan), which was primarily driven by the greater variation in maximum lifespan across plant species. High plant height and large seed size are adaptive in hot, moist, resource rich environments where biotic competition is high (Moles 2018; Boonman *et al.* 2020), height is important in competing for light, and larger seeds show higher establishment under biotic competition and shade (Westoby *et al.* 2002). However, both height and seed size have associated resource costs (Chave *et al.* 2009; Moles 2018), and in freezing environments woodiness and height are associated with loss of hydraulic function (Zanne *et al.* 2014). Conversely, herbaceous species in extreme cold environments survive by senescing cheaper non-woody tissues, exhibiting long periods of below-ground dormancy, and/or avoiding extreme air temperatures beneath a snow layer (Zanne *et al.* 2014; Alahuhta *et al.* 2017). The novelty of our findings is in linking these trait-climate patterns to life history strategies and demonstrating that shorter species characteristic of colder regions can exhibit slow life-histories more usually associated with larger woody plants in warmer regions.

Previous authors have demonstrated a correlation between LMA and life history in plant species, suggesting that species with low LMA tend to have faster life-histories (Adler *et al.* 2014; Rüger *et al.* 2018). Our results are ambiguous on this point. The leaf-traits PCA axis was retained in the model after model selection by DIC, suggesting that leaf-traits do contribute to the explanation of multivariate variation in life history strategy. However, the credible intervals overlapped with zero for all individual life history metrics meaning that these relationships must be interpreted with caution. Despite this caveat the direction of the model coefficients for leaf-traits is in keeping with prior findings, with negative coefficients for generation time and mature lifespan indicating that faster life-histories are weakly correlated with higher leaf-area and lower LMA in our dataset. Larger sample sizes may be needed to investigate this further. The use of PCA axes to represent functional traits in our model has the effect of separating the effects of plant size (PCA 1) from those of leaf traits LMA and leaf area (PCA 2). Both leaf area and LMA are positively correlated with size (Appendix S2, Díaz et al 2016). Hence, previous univariate approaches may find stronger associations between high LMA and slower life histories because the effect of plant size has not been accounted for separately (Adler *et al.* 2014). Results of multivariate approaches in tropical forests may suggest that this association between leaf traits and life-history strategies is stronger within similar environmental conditions (Rüger *et al.* 2018).

The predictability of life history metrics differed greatly between the types of metrics used, with biological timings and distribution of mortality being more predictable from traits, climate and phylogeny than those related to fecundity. In particular, we did not observe any significant association between annual fecundity and inequality of reproduction across the lifespan and our trait and climate variables. Plant fecundity, in general, shows high-levels of intraspecific and inter-annual variation (Burns *et al.* 2010; Che-Castaldo *et al.* 2018); whereas biological timing metrics, such as age at maturity may be more conserved within species (Healy *et al.* 2019). Previous research has reported associations between plant height and both seed size and number, leading to an expectation that fecundity metrics would be linked to plant size (Pierce *et al.* 2014; Moles 2018). However, the relationships between large seed-size and survival in different environments are strongest in the establishment phase, and do not necessarily translate into higher survival at maturity. Furthermore, advantages of large seed size are traded off against the numeric advantages of having many small seeds (Moles & Westoby 2004; Moles 2018). As the fecundity metrics in this study are calculated from the first above ground stage, and thus implicitly include seed survival, germination and establishment, differences in size-survival relationships at each stage together with trade-offs in seed-number may obscure any overall pattern in our dataset.

Despite the lack of explanatory power for annual reproduction, our models are useful for explaining generation time. Generation time in this analysis is a compound metric, describing the length of time taken for a population to replace itself under asymptotic dynamics. This duration is influenced by the joint effects of annual reproduction, survival rates and age at maturity (Caswell 2001). Generation time is useful for understanding the potential recovery rates of populations following disturbance, and, in combination with age at maturity, is useful in predicting species recovery trajectories. We demonstrate that combining phylogenetic information with the size and structure of species may be useful in inferring generation times, but only when used in combination with climatic information.

Limitations and ways forward

Our approach to modelling multivariate life history variation provides useful insights into the relative importance of traits, climate and evolutionary history influencing life history strategies across a global suite of plant species. However, despite using the largest available dataset of plant matrix models (COMPADRE), we were limited to 80 species for which both reliable matrix models and corresponding trait data were available. Increasing overlap between global datasets on life history and functional traits is crucial to further explore relationships between life history, traits, environment and evolutionary relatedness.

In order not to over-parameterise our model we chose not to include more environmental parameters such as soil types, pH, microclimates, land-use, habitat, intra and interspecific competition and disturbance regimes which are also likely to influence plant life history strategies (Silvertown *et al.* 1993; Kunstler *et al.* 2016; Liu *et al.* 2016; Teller *et al.* 2016; Treurnicht *et al.* 2016; Miedema *et al.* 2019; Pérez-Ramos *et al.* 2019; Pistón *et al.* 2019). For similar reasons, we focused on the most frequently measured plant traits (Díaz *et al.* 2016; Moles 2018), however, the inclusion of physiological and chemical traits (Funk *et al.* 2016) and morphological traits from other plant organs such as roots and floral structures (Laughlin 2014; Pistón *et al.* 2019), would be likely to increase the explanatory power of the model. A strength of our model framework is that these additional variables can be easily added as explanatory variables to test novel hypotheses as more data become available.

Our dataset is primarily composed of trees, shrubs and herbaceous perennials, with only two graminoid species, four annuals and one palm, and no data on other plant growth forms such as lianas, epiphytes, parasitic plants, mosses, liverworts, ferns and algae (Fig. 2). Our life history metrics span a wide range of climates, with mean temperatures ranging from −3.6°C to 28.1°C, and the moisture availability included arid, semi-arid, dry sub-humid and humid zones (Trabucco & Zomer 2009). However, geographically, our dataset shows similar biases to many biodiversity datasets (Collen *et al.* 2008; Stephenson *et al.* 2017; Tydecks *et al.* 2018), with the best coverage in Europe and North America, a few studies from Australia, New Zealand and South America, only one study from Asia and none from Africa. Combined, these taxonomic and geographic biases suggest that data is most needed for species from arid environments (only 2 species from arid zones), and larger species in very cold environments. These limitations are unlikely to affect the main pattern of the data which relates to the trend towards slower life histories in small species in colder climates, but they do limit our ability to

draw inferences about larger species very cold environments, and all species in very hot arid environments. Therefore, as with many areas of ecology the highest priority for increasing geographic data coverage should be in equatorial regions which support the highest richness of plant species, arid areas and throughout the continents of Africa, Asia and South America. This will require better ongoing investment and integration of biodiversity studies in these regions (Collen *et al.* 2008; Stephenson *et al.* 2017; Tydecks *et al.* 2018).

Functional traits vary across species ranges (Albert *et al.* 2010; Siefert *et al.* 2015) and are important in mediating plant fitness responses to climate (Henn *et al.* 2018), but trait data is rarely available from the same locations as detailed life history studies (Salguero-Gómez *et al.* 2018). For this reason we used species-level means for functional traits in this study. The overlap between life history and functional trait data is primarily limited by the time intensive nature of creating population matrix models. Therefore, targeted measurements of key plant traits for species and locations for which demographic population matrix models already exist or are being conducted are could lead to rapid gains in the prediction of life history strategies by providing population specific estimates of plant traits (Salguero-Gómez *et al.* 2018). In parallel, long term demographic studies with spatial replication across climates will enable a greater understanding of the extent of intraspecific variation in life history strategies (e.g. Smith *et al.* 2020). Alternatively, sources of information on key life history metrics such as lifespan, age at maturity and annual reproduction, compiled data from floras, forestry, horticulture and/or botanical gardens could also provide rapid gains. However, this will require a trade-off in terms detail and type of life history metrics which can be obtained.

CONCLUSION

Our framework integrates traits, climate, evolutionary history and emergent life history strategies into a single model at the global scale, in a way which is compatible with the fundamental principles of life history theory. Thus, it enables us to explicitly test how multivariate life history strategies are related to functional traits in ecological contexts, whilst incorporating phylogenetic history and the multivariate trade-offs between life history metrics. Our findings provide empirical support for the expectation that climatic context is key to understanding trait to life history relationships, and that the expectation of simple relationships between functional traits and life history across environments is unrealistic. Importantly, the inclusion of this interaction between traits and climate enabled the explanation of life history strategies, even though neither functional traits nor climate alone were useful in explaining life history after phylogeny had been accounted for.

At present the generality of our findings, particularly in very hot arid areas, remains limited by the availability of overlapping data on detailed life history metrics and less studied functional traits, particularly from key climatic regions and taxonomic groups. Therefore, we second the call of previous authors for greater collaboration between trait ecologists, demographers and evolutionary biologists to increase the overlap between trait and demographic databases, particularly

for understudied regions and taxa (Reich *et al.* 2003; Coutts *et al.* 2016; Moles 2018; Salguero-Gómez *et al.* 2018; Swenson *et al.* 2020). These collaborations will be essential in answering fundamental questions of both trait-based ecology and life history evolution at the global scale.

AUTHOR CONTRIBUTIONS

The study was initially conceived and designed by YMB, RS-G and RK. RK performed the data analysis and wrote the first draft. Advice on analyses was provided by AJ, KH, RSG and YMB. Data were contributed through TRY by MA, M Bahn, BC, JHC, JK, UN, & SP, and through COMPADRE by RS-G. Data were initially interpreted by YMB, KH, RK and RS-G with advice from all other authors. All authors provided intellectual input and edited the MS.

OPEN RESEARCH BADGES

This article has earned Open Data badge and Open Materials Badge. Data is available at (DOI: 0.5281/zenodo.4457447)

DATA AVAILABILITY STATEMENT

All data and R code necessary to reproduce the analyses presented herein is publicly available at https://doi.org/10.5281/zenodo.4457447.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.