The fast-slow continuum and reproductive strategies structure plant life history variation worldwide

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The identification of patterns in life history strategies across the tree of life is essential to our prediction of population persistence, extinction and diversification. Plants exhibit a wide range of patterns of longevity, growth, and reproductive strategies, but the general determinants of this enormous life history variation are poorly understood. We use demographic data from 418 plant species in the wild, from annual herbs to super-centennial trees, to examine how growth form, habitat and phylogenetic relationships structure plant life histories, and develop a framework to predict population performance. We show that 55% of the variation in plant life history strategies is adequately characterised using two independent axes: the *fast-slow* continuum, including fast-growing, short-lived plant species at one end and slow-growing, long-lived species at the other, and a *reproductive strategy* axis, with highly reproductive, iteroparous species at one extreme, and poorly reproductive, semelparous plants with a propensity to shrink at the other. Our findings remain consistent across major habitats, and are minimally affected by plant growth form, height or phylogenetic ancestry, suggesting that the relative independence of the fast-slow and reproduction strategy axes is general throughout the plant kingdom. Our findings have similarities with how life history strategies are structured in mammals, birds and reptiles. The position of plant species' populations in the two-dimensional space produced by both axes predicts their population growth rate and rate of recovery from disturbances. This life history framework could be used to complement trait-based frameworks on leaf and wood economics, which together may allow prediction of responses of plants to anthropogenic disturbances and changing environments.

Significance

Schedules of survival, growth and reproduction define life history strategies across species. Understanding how life history strategies are structured is fundamental to our understanding of the evolution, abundance and distribution of species. We found that life history strategies of 418 plant species worldwide can be explained by an axis representing the "pace of life" and an additional axis representing the wide range of reproductive strategies that plants employ. This framework predicts population growth rate and response to perturbations, showing great promise as a predictive tool for plant population responses to environmental change.

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Demographic schedules of survival, growth and reproduction, which comprise life history strategies, are fundamental to our understanding of a range of ecological and evolutionary processes, such as invasions and local extinctions (1-3), community structure (4, 5), and species diversification (6, 7). Consequently, the development and careful testing of theory on how organisms allocate resources to survival, growth and reproduction are important goals for evolutionary biology, ecology, and conservation biology (8). Indeed, calls for the development of a "periodic table" to classify species based on their life history strategies, and to predict population dynamics and community composition go back to the early development of evolutionary biology as a discipline (9).

A main axiom of life history theory is that trade-offs (*i.e.* budgetary compromises) between different aspects of an organism' demographic schedules, such as survival, growth and/or reproduction, constrain and optimise the range of possible life history strategies that can evolve across the tree of life (10, 11). Yet, the plant kingdom encompasses a vast amount of life history variation; plant longevity, for instance, ranges from weeks to millennia (12). Many plant species' life cycles include cryptic life stages such as seedbanks (13) or dormant adults (similar to animal hibernation) (14). Reproduction too can be highly variable among plants, with seed mass and per-capita seed production ranging six orders of magnitude (15). Previous classifications of plant life history strategies have been limited in geographic (16, 17), taxonomic and phylogenetic scales (17), as well as the inability to differentiate life history trade-offs (17-19).

Here we propose an analogous approach to that developed decades ago for (vertebrate) animals (20) to study the drivers behind plant life history variation. We combine demographic, phylogenetic and ecological data from natural populations of 418 plant species worldwide (Figure1; Supporting Information) to address the following questions: (i) what are the main axes of variation of plant life history strategies? and, (ii) to what extent do phylogenetic ancestry, habitat, growth form, and size constrain plant life-history variation? We then test (iii) whether the position of a species on these axes predicts two important metrics of population performance: population growth rate and speed of recovery from disturbances. If clear patterns emerge, they may form the basis for a satisfactory classification and predictive framework of plant responses to the changing environment, and to make cross-taxonomic comparisons.

We use the COMPADRE Plant Matrix Database (21) to address these questions, drawing from the demographic, biogeographic, anatomic and phylogenetic information of the 418 plant species covering 105 families (Supporting Information). Together, the selected species represent 825 natural populations worldwide across all major terrestrial habitats and vascular plant growth forms (Figure 1), and for which at least four years of high-resolution demographic field data exist. For each species, we use their population matrix models (22) to calculate a set of representative life history traits that inform on schedules of survival, growth and reproduction (11) (Table 1), and we then evaluate the variation in these traits along major axes using phylogenetically-corrected principal components analyses (PCA) (23).

Results

Two life history axes: the fast-slow continuum and reproduction

The repertoire of life histories among vascular plants is satisfactorily captured by the first two PCA axes, which together explain 55% of the variation. Following the Kaiser criterion (24), we retain PCA axes 1 and 2 in our global analyses because only for these axes the associated eigenvalues are >1, followed by a sharp drop in amount of variance explained with the third and further axes (Supporting Information). PCA 1 and 2 explain 34% and 21% of the variation in plant life history strategies, respectively. The life history traits most closely aligned with PCA axis 1 are related to the fast-slow continuum (11): generation time (T) is the life history trait with greatest loading onto PCA 1 (Table 1), closely followed by the mean sexual reproduction (φ) and the rate of growth of individual plants (progressive growth, γ). The positive loading of T onto PCA 1 had an opposite sign to the negative loadings for both growth and mean sexual reproduction, supporting the well-established trade-off between fast growing, highly reproductive species, and population turnover (11, 25). Two additional life history traits that inform on longevity and mortality schedules also loaded positively onto PCA 1, *i.e.* the shape of the survivorship curve (H), and mean age at maturity (L_α; Table 1; Figure 2). The majority of the traits closely aligned with PCA axis 2 represent dimensions of a plant's reproductive strategy not captured by mean sexual reproduction: the net reproductive rate (R_0), and frequency of reproduction throughout an individual's life expectancy (*i.e.* degree of iteroparity; S) are positively loaded onto PCA 2. The rate of shrinking individual plants (retrogressive growth, ρ) is negatively loaded onto PCA 2. Mature life expectancy (L_ω), the period between age of sexual maturity (L_α) and mean life expectancy (21), is a poor contributor to PCA 1 or 2, and is the main driver of PCA 3 (loading = -0.84; Supporting Information).

From negative to positive scores on PCA 1 (*fast-slow axis*, hereafter), plants increase investment in longevity-related life history traits and decrease in population turnover (*i.e.* greater generation time), at the expense of growth and production of new recruits (Figure 2). From negative to positive scores on PCA 2 (*reproductive strategy axis*, hereafter), plants attain greater lifetime reproductive success and frequency of reproduction, and tend to shrink less. The fact that size is typically measured differently in herbs (helophytes, geophytes and hemicryptophytes) *vs.* trees (nano-/meso-/megaphanerophytes) (21, 22, 26, 27) does not appear to be responsible for the orientation of retrogressive growth in the PCA space, as this pattern remains consistent in analyses for either group separately (Supporting Information). More generally, a robust and consistent association and loadings of the life history traits described above emerges when different subsets of plant growth forms (27), major habitats (28), and taxonomic classes are considered separately (Supporting Information), suggesting that this is a global pattern thoughout the plant kingdom. Interestingly, PCA 3 is retained (its associated eigenvalue > 1 (24)) only in certain groups, *i.e.* herbs, but not others (shrubs or trees), and for species in the Liliopsida and Magnoliopsida (Supporting Information). In these groups, mature life expectancy L_ω is the main driver of PCA 3. Randomisation tests suggest that the pattern is robust to spurious correlations that might have been expected from coercing life history traits onto sequentially orthogonal axes with the PCA (24) (Supporting Information).

Major habitat is alone a weak predictor of the position of plant species along the reproductive strategy axis ($F_{3,395}$ = 2.46; P = 0.06), but a significant predictor for the fast-slow axis ($F_{3,395}$ = 4.83; P = 0.003). Tropical and subtropical species seem to attain greater longevities than species in arid, temperate, and alpine or arctic regions, a result that may be due to the dominance of long-lived trees in tropical communities (29) and/or the non-random sampling of demographic studies in these habitats (16, 21; S5 Table). Tall plants such as megaphanerophytes (> 25 m; e.g. Canadian hemlock, *Tsuga canadensis*) and mesophanerophytes (10-25 m maximum height; e.g. black pine, *Pinus nigra*) tend to have greater fast-slow axis scores than smaller species like hemicryptophytes (whose shoot apical meristems are at ground level; e.g. Mead's milkweed, *Asclepias meadii*) and geophytes (whose shoot apical meristems are belowground; e.g. garlic, *Allium sativum*; Figure 2.B; $F_{7,395} = 34.88$; $P < 0.001$). Growth form is also significantly associated with the reproductive strategy axis ($F_{7,395} = 17.43$; $P < 0.001$), whereby PCA scores also increase sequentially with growth form size, from helophytes (shoot apical meristems resting below water) and geophytes having the lowest reproductive scores, to phanerophytes (shrubs and tall succulent cacti) having the highest reproduction scores (Figure 2.B). Epiphytes (species growing upon other plants; e.g. forest babyboot orchid, *Lepanthes rubripetala*) do not differ in their reproductive strategy axis scores from the rest of herbs.

Phylogenetic relationships play a rather weak role in explaining the repertoire of life history strategies. In our analysis, Pagel's λ, a scaling parameter for the correlation in traits between species ranging from 0 (no correlation) to 1 (the correlation expected under Brownian motion) (30), is 0.20 ± 0.09 (95% CI), suggesting a rather minor role of overall phylogenetic ancestry in our analyses. However, some exceptions exist: species in the Magnoliopsida have lower fast-slow scores (shorter lives, higher growth) than Cycadophyta and Pinopsida (Supporting Information). The phylogenetic signal of species within the same taxonomic class (Liliopsida: 0.18 ± 0.02, Magnoliopsida: 0.20 ± 0.04) is greater than those grouped by growth forms (herbs: 0.03, shrubs: 0.00 or trees: 0.00; Supplementary Information), implying some infra-class structuring of life history strategies.

Life history strategies may overlap regardless of plant growth form and size

While Raunkiær's growth forms (27) take somewhat different positions along the fast-slow axis and reproductive strategy axis, the overlap is considerable such that species with different growth forms may occupy the same life history space. Similar survival, growth and reproduction schedules can be realised through different anatomic structures. For example, shorter-lived trees and shrubs (like *Cecropia obtusifolia*, *Acer saccharum*; Figure 2.B) occupy a life history space on the fast slow axis that overlaps with herbaceous perennials (particularly helophytes, geophytes, and epiphytes Figure 2.B). The life history strategies of herbs range from short-lived ephemerals to the tree-like lifestyles of the cushion pink (*Silene acaulis*) or thyme (*Thymus vulgaris*).

Strikingly, the amount of variation shown on the reproductive strategy axis for herbs and trees is similar. Both groups display a similar range of life histories in the timing of reproduction (iteroparity) and lifetime reproductive potential, regardless of their position on the fast-slow axis (Figure 2). For example, the reproductive strategy axis values of short-lived herbs, such as goldenrod (*Solidago mollis*) or scarlet monkeyflower (*Mimulus cardinalis*), are similar to those of woody species like black pine, scotch broom (*Cytisus scoparius*) or hoop pine (*Araucaria cunninghamii*).

In contrast to comparative animal demography (11, 25), a uniform measure of "body size" does not exist for plants across the plant kingdom. We have therefore presented the results (Fig. 2, Table 1) without allometric scaling. Yet, Raunkiær growth forms clearly differ in size, amongst other crucial functional attributes. By using Raunkaier growth form height thresholds, we have attempted to more explicitly include size in the analyses (Supplementary Information). When life history traits are rescaled by plant height, the results do not change qualitatively. The amount of variation explained by PCA 1 (32.99%) and PCA 2 (19.73%), which also corresponds to the fast-slow continuum and to reproductive strategies, respectively, adds to *ca.* 53%. This suggests that either plant size does not have a strong effect in the structuring of plant life histories, or that using Raunkiær growth form height thresholds as our proxy of plant size is not accurate enough. Compared with the results with no allometric scaling (Fig. 2, Table 1), the phylogenetic signal is completely lost (Pagel's $\lambda = 0.00$), likely due to the fact that Raunkiær's growth forms are phylogenetically conserved in our data ($\lambda = 0.96 \pm 0.02$, $P < 0.001$).

Two orthogonal axes to predict population performance

The fast-slow/reproductive strategy framework predicts population performance, including both short-term response to perturbation and long-term asymptotic dynamics (Fig. 3). While many metrics of short-term (transient) dynamics are available (31, 32), we use the damping ratio here to illustrate the predictive capacity of our life history framework. Damping ratio can be thought of as the rate at which transient responses to disturbance fade away, or its rate of recovery to asymptotic dynamics (22). A species' rate of recovery is associated with its scores on the fast-slow ($F_{1,384} = 96.99$, $P < 0.001$) and the reproductive strategy axis ($F_{1,384} = 53.3$, $P < 0.001$). Natural populations with faster recovery are found on the top-left and bottom of Figure 3.A, suggesting that rapid recovery can be attained via a fast growth, high reproduction, short generation time strategy, or alternatively via a strategy of low reproduction and frequent shrinkage (33). Asymptotic population growth rates ($r = \log(\lambda)$) are strongly differentiated along both axes (fast-slow axis: $F_{1,374} = 145.79$, $P < 0.001$; reproductive strategy axis: $F_{1,374} = 177.80$, $P < 0.001$), with high population growth rates for fast-growing (γ), iteroparous, highly reproductve species (Φ, R_0) (Figure 3.B). Lower population growth rates are typical of species that delay maturity (L_α), have low senescence associated with their survivorship curve (H) and/or undergo frequent shrinkage (ρ).

Discussion

Quantifying life history strategies

The diversity of growth forms, functions and ecological roles of species have long puzzled biologists. A key question has been whether there are key combinations of survival, growth, and reproduction strategies that can only exist in certain habitats but not others (9), or whether nature is a random trait assemblage (34). To address these questions, several frameworks have been developed that aim to classify and predict species' responses to biotic and abiotic agents (9). Perhaps the most widely acknowledged framework in this respect is the fast-slow continuum (11), which states that, because trade-offs between reproduction and survival are pervasive, the repertoire of life history strategies are constrained and can thus be accurately described along a single axis of high allocation to reproduction on one end, and high allocation to survival on the other. While the fast-slow continuum has received substantial empirical support, explaining 60-80% of the variation among mammals (25, 35, 36), birds (37), and reptiles (38), analyses going back over 30 years have also pointed out the existence of a secondary axis related to reproductive strategies. For instance, Stearns (20) found that while 68-75% of covariation in life history traits of 162 mammals is explained the first axis, corresponding to the fast-slow continuum, an important second axis describing a continuum from altricial to precocial species, explains an additional 12-20%. Gaillard et al. (39) found for 80 mammals and 114 birds that 74-85% of variation is explained by the fast-slow axis, but that a second important axis related to iteroparity absorbs 5-15%.

Our analysis of over 400 globally distributed plants finds qualitatively similar results to these studies for vertebrates (20, 35-40), albeit suggesting greater relative importance of the reproductive strategy axis. We find two independent axes of life history variation in plants: one corresponding to the fast-slow continuum and another to characteristics of reproductive strategy not captured by mean sexual reproduction. When we account for the potential allometric effects of size in these relationships, the percent variation explained only decreased minimally (1.1% for PCA 1, and 1.6% for PCA 2), and the phylogenetic signal remained low. In contrast to analogous comparative approaches for animals (20, 39, 40), we find very little phylogenetic signal in our results, nor indications for a structurally important role of adult size.

Typically around 80% of the variation in animal life history strategies can be captured with two axes, whereas here we captured just over 50% of the observed variation. The reason for this difference might be that plants are typically characterised by more complex life cycles than vertebrates. For instance, plants often have dormant stages (14), and long-term seedbanks (13) whereas animals usually do not. Furthermore, in contrast to many of the species considered in these animal-based studies, all plants are indeterminate growers (42), whereby cellular fate is not determined early in life, so the allocation of meristems to survival (*e.g.* wood), growth (leaf) or reproduction (flower) can be continuously adjusted, as well as overall plant size. This totipotency has resulted in strategies such as resource-dependent sex-switching (43), and the rejuvenating abilities of some trees (44, 45). Furthermore, all vascular plants are modular constructions based on the repetition of basic units (46-48) enabling some plants to shrink in adverse conditions (33, 48), or reproduce clonally (49). We find that retrogressive growth (shrinkage) correlates negatively with reproductive traits, which is in agreement with the frequent increase in reproductive output with plant size (42). However, these complex life history traits are not exclusive to the plant kingdom; many animals experience dormancy (*i.e.,* hibernation (50), diapause (51), estivation (52) or brumation (53), clonal reproduction (54), organ/tissue regeneration (55), or modular growth forms (*e.g.*, corals (56)). Demographic comparative analyses including complex life history traits across both plant and animal kingdoms will help determine whether, and for which taxa, multiple axes are needed to capture inter-specific patterns of life history variation.

Life history analyses and population performance

The life history traits analysed here are derived from natural populations examined in the field, and these studies therefore capture population performance as a product of life history strategy and the particular a/biotic conditions experienced by that population over the course of the study. Clearly, no species can persist with populations operating at a population growth rate $\log(\lambda) < 0$ indefinitely. Furthermore, some areas of life history space remain unfilled; in the 418 plant species of our data set there are no species with low scores on both the fast-slow axis and the reproductive strategy axis (bottom left; Fig. 3B), or with high fast-slow scores but low reproductive strategy scores (bottom right), suggesting that such combinations of life history traits are unsustainable. Interestingly, we have found species with high scores on both axes (top right). Rather than defying basic life history trade-offs, these species likely represent very successful cases of expanding populations. Several of these species correspond to invasive plants such as black pine in New Zealand (57), or scotch broom in Australia (58). The reproductive strategy axis includes populations of invasive species at the top, where the population growth rate $\log(\lambda) >> 0$ (Figure 3.B), and endangered species like the fragrant prickly apple (*Harrisia fragrans*) or Mead's milkweed *Asclepias meadii* at the low end (Figure 2.B). Given the restricted spatial replication of plant demographic studies (21), we are unable to discern how much of the values on the reproductive strategy axis, and low population growth rates, are driven by habitat quality or other conditions favouring population growth, and this remains a promising avenue of research. Also, future steps in the applicability of this framework need to focus on the classification of endangered and invasive species along this axis, and to take advantage of open access resources (15, 59) to discern the role of propagule quantity *vs.* quality (e.g. seed mass (60)) in structuring the reproduction strategy axis.

Population responses to future environmental change and anthropogenic disturbances depend on the species-specific life history strategy (61, 62). Our analyses reveal that populations from even distantly related plant taxa worldwide can have similar combinations of life history traits, with a modest influence of habitat and growth form. Therefore, the framework of life histories presented here is a necessary addition to current plant trait-based concepts such as the leaf (63) and wood (64) economics spectra, since traits can only be considered *truly functional* if they affect the critical fitness components of reproduction and survival (66). This framework, based on the fast-slow continuum and reproductive strategies, presents strong empirical support for the expansion of classical quantification and classifications of life history strategies of animals well into the plant kingdom. Furthermore, it provides a sound basis for future work untangling the associations in plant *and* animal functional traits with demographic processes and among physiological and life history trade-offs.

Materials and Methods

COMPADRE. We used the COMPADRE Plant Matrix Database (21) to obtain demographic, biogeographic, and growth form data from an initial list of over 1,000 plant species. The demographic data therein are compiled as state-structured population models, which incorporate accurate information on the rates of survival, growth, and reproduction from natural populations where individuals are typically classified by stage and/or size (22). We only considered whole individual (genet) demography, and omitted studies that treated different parts of the genetic individual as independent units (ramets). Non-natural vegetation types such as forestry plantations and crop fields were not included. Only size-based matrices were chosen, or ontogeny-based models for which higher stages of development would also correspond to larger sizes. Due to these and other strict selection criteria used to allow comparative analyses (Supplementary Information), we narrowed down our initial list to 418 plant species. For each of these species, we calculated the arithmetic element-by-element mean of all available matrices under non-manipulated conditions, resulting in a single matrix that summarises the population dynamics of that species under natural conditions.

Phylogeny. We constructed a species-level phylogenetic tree for the species in our dataset (http://www.onezoom.org/FWifhj38wjf/Salguero-Gomez_et_al_2014.htm (66)) with branch length transformations applied to simultaneously estimate and account for phylogenetic signal, estimated by Pagel's λ (30). To do so, first, the identity of each individual species and its corresponding taxonomic family was validated in The Plant List website (http://www.theplantlist.org/). The specific names used by the authors, however, have been retained to facilitate the replicability, testing and usage of the fast-slow, reproductive strategy framework (See Extended Data). Second, we obtained an approximate phylogeny with PHYLOMATIC (67). Resolution below the level provided by phylomatic, which varies from family to family, was achieved by manually sorting individuals species in MESQUITE (68) by reference to published sources of phylogenetic information (See a full reference list for each taxonomic family in Supplementary Methods 2). This is because many species did not have information in GenBank to allow us to construct a phylogeny from DNA data. Moreover, closely related species that could be used as temporary surrogates could often not be obtained. Also, because “the ultimate authoritative source for the nomenclature and classification is the primary taxonomic literature itself" (69), we followed Federhen's practice at NCBI and use the available published information to determine the topological position of each species in the tree. Once the maximally resolved topology that we produced with the available information was obtained, branch lengths were interpolated employing the function *bladj* of PHYLOCOM (70) given node ages in (73).

Analysis. From each species' matrix population model, we derived nine basic life history traits typically used in comparative analyses of life histories grouped *a priori* according to their quantification of the timing and magnitude of turnover, longevity, growth and reproduction (11, 16, 22, 35-41). We calculated these with methods described in detail elsewhere (22) and in the Supplementary Materials. The corresponding life history traits (*LHTs*, below) broadly correspond to overall population turnover (T), longevity (H and L_α), growth (γ and ρ), and reproduction (φ, S, R_0, L_ω; see Table 1). LHTs were log-transformed to fulfill normality assumptions in posterior analyses. After the allometric size correction, LHTs were scaled to mean = 0 and S.D. = 1 for PCA (24). We then carried out a phylogenetically-informed PCA (23, 72) on these LHTs to determine the primary axes of demographic variation while simultaneously taking into account and assessing non-independence of lineages. We used the Kaiser criterion (23) after optimisation through varimax rotations to determine the number of axes necessary to explain a substantial amount of variation. To explore the role and possible interactions growth form, matrix dimension (73) and habitat, we used a three-way ANOVA (Supplementary Information) followed by post-hoc Tukey's honest significant difference (HSD) tests on the phylogenetically-informed PCA scores of the species. The major habitat classification (28) informs on the abiotic conditions to which populations are exposed while the growth form information describes potential anatomical constraints. We used Raunkiær's growth form classification (27), indicating the distance of the plant's shoot apical meristems to the ground. Matrix dimension was positively correlated with both axes PCA 1 (t_{417} = 85.51, $P <$ 0.001, R^2 = 16.85%) and PCA 2 (t_{417} = 17.72, $P <$ 0.001, R^2 = 3.85%); however, this effect was driven by the fact that long-lived trees achieve larger sizes (29) and thus require larger matrices to accommodate their dynamics: the ordered ranks of Raunkiær growth forms successfully predicted PCA scores on both PCA 1 ($F_{7,410}$ = 34.40, $P <$ 0.001, R^2 = 35.93%) and PCA 2 ($F_{7,410}$ = 12.13, $P <$ 0.001, R^2 = 15.74%). We checked for the consistency of our results by re-running the analyses on subsets of the data. We defined subsets by plant type (herbaceous perennials, shrubs and trees), major habitat (temperate, tropical & subtropical) and taxonomic class (Pinopsida, Liliopsida, Magnoliopsida); other subsets and levels were not tested because of the large data requirements for the model to converge (Supplementary Information). We also tested for the robustness of the results to spurious correlations using randomisation tests with two approaches described in the Supplementary Information.

Finally, we derived the damping ratio (rate at which populations recover from disturbance (22, 31)) and the rate of change of the population (22) ($r = \log(\lambda)$) to test the usefulness of the suggested framework for plant species classification via 2-way ANOVAs with PCA 1 and 2 scores as explanatory variables.

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Table 1. Symbols, definitions and loadings of the life history traits used in this study grouped by their relation to turnover, and strategies to longevity, growth and reproduction onto the first two PCA axes. Life history traits are calculated from the matrix population models (Supplementary Information). Absolute values of loadings >0.50 appear in bold, indicating a high contribution of the life history trait to the PCA axis under examination.

	Life history trait	**Symbol**	**Definition**	**PCA 1**	**PCA 2**
Turnover	Generation time	T	Number of years necessary for the individuals of a population to be fully replaced by new ones	**0.85**	0.17
Longevity	Survivorship curve type	H	Shape of the age-specific survivorship curve l_x as quantified by Keyfitz' entropy (H). H values >1, =1, <1 correspond to survivorship curves types I, II and III, respectively	**0.55**	0.23
	Age at sexual maturity	L_α	Number of years that it takes an average individual in the population to become sexually reproductive	**0.71**	0.29
Growth	Progressive growth	γ	Mean probability of transitioning forward to a larger/more developed stage in the life cycle of the species, weighted by the stable stage distribution (SSD)	**-0.73**	-0.05
	Retrogressive growth	ρ	Mean probability of transitioning back to a smaller/less developed stage in the life cycle of the species, SSD-weighted	0.07	**-0.77**
Reproduction	Mean sexual reproduction	Φ	Mean per-capita number of sexual recruits across stages in the life cycle of the species, weighted by the SSD	**-0.83**	0.30
	Degree of iteroparity	S	Spread of reproduction throughout the lifespan of the individual as quantified by Demetrius' entropy (S). High/low S values correspond to iteroparous/semelparous populations	-0.23	**0.51**
	Net reproductive rate	R_o	Mean number of recruits produced during the mean life expectancy of an individual in the population	0.04	**0.75**
	Mature life expectancy	L_ω	Number of years from the mean age at sexual maturity (L_α) until the mean life expectancy (η_e) of an individual in the population	0.15	0.27
			Percentage of explained variation	34.06%	21.23%
			Cumulative percentage of explained variation	34.06%	55.38%

Figure 1 Coverage of the studied species. The 418 vascular plant species represent (**A**) all major terrestrial habitats and (**B**) growth forms; the latter scheme categorises vascular plants according to the position of its shoot apical meristems in relation to ground level. Tissue in gray is typically renewed every year, whereas black is perennial.

Figure 2 Life history variation in vascular plants is characterised by a high degree of independence of life history traits associated with the fast-slow continuum and reproductive strategies. Phylogenetically corrected principal component analyses (PCA) of the life history traits described in Table 1 with population turnover (black arrow), and traits related to longevity (gray arrows), growth (dark blue), and reproduction (red). Arrow length indicates the loading of each life history trait onto the PCA axes. Points represent the position of species along the first two PCA axes, are colour-coded according to (**A**) major habitat, and (**B**) Raunkiær's growth form. Box-and-whisker plots on the top and right of each panel represent median (thick bar), upper and lower quartiles (edge of rectangle) maximum and minimum (outer bars) excluding outliers (empty circles; >3/2 of absolute value of quartile) of the PCA axis 1 and 2, respectively. Groups with different letters are statistically significant.

Figure 3 The value of any species along the fast-slow continuum, together with its reproduction strategy, predicts population performance including (**A**) damping ratio, the rate at which a population returns to equilibrium after disturbance, and (**B**) population growth rate (r = log(λ)), the rate of population size change through time. Redder tones mean higher value of population metrics. Bluer colours of r reflect population decline. It is not always possible to calculate the damping ratio (n = 389 species).

Figure 1

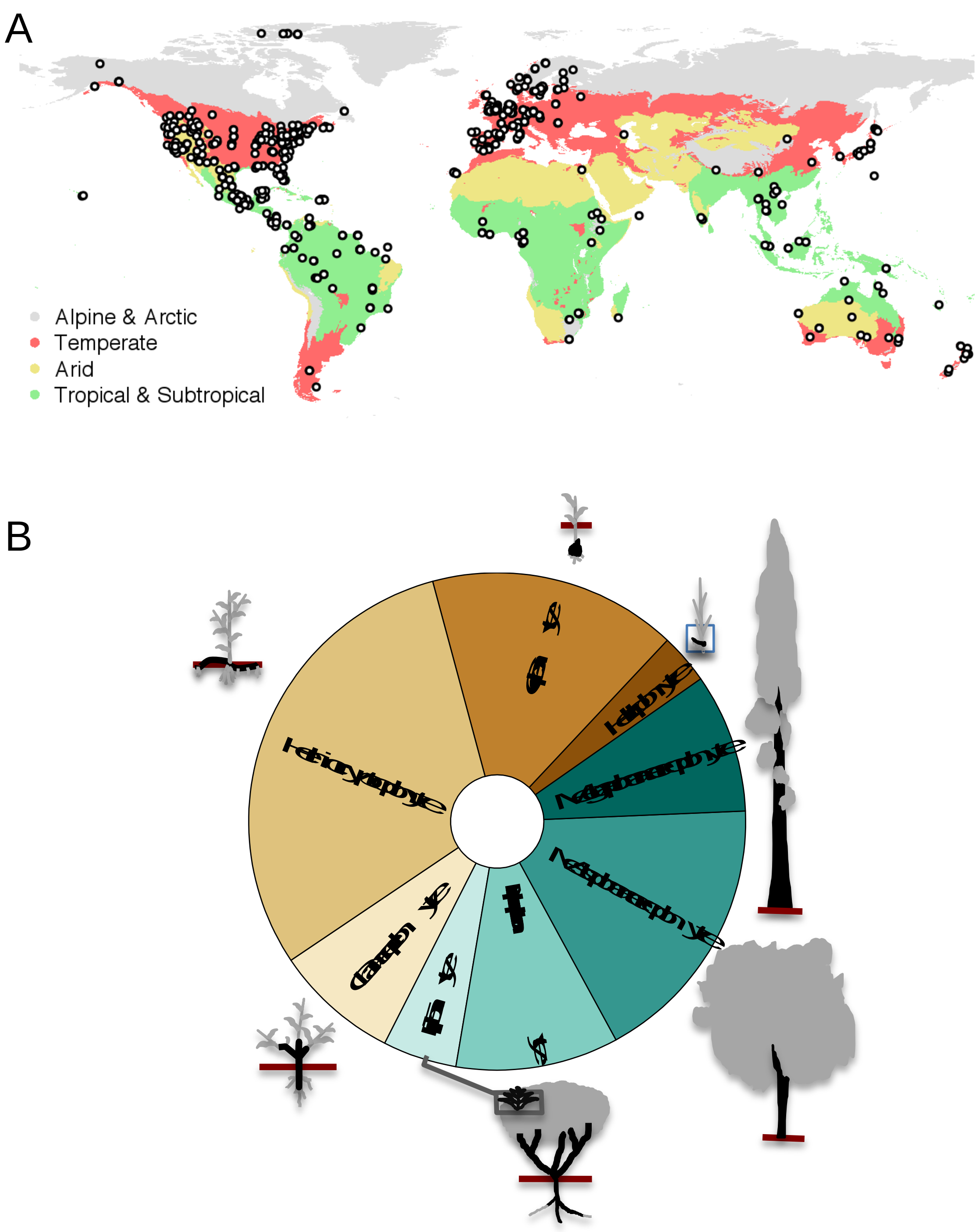
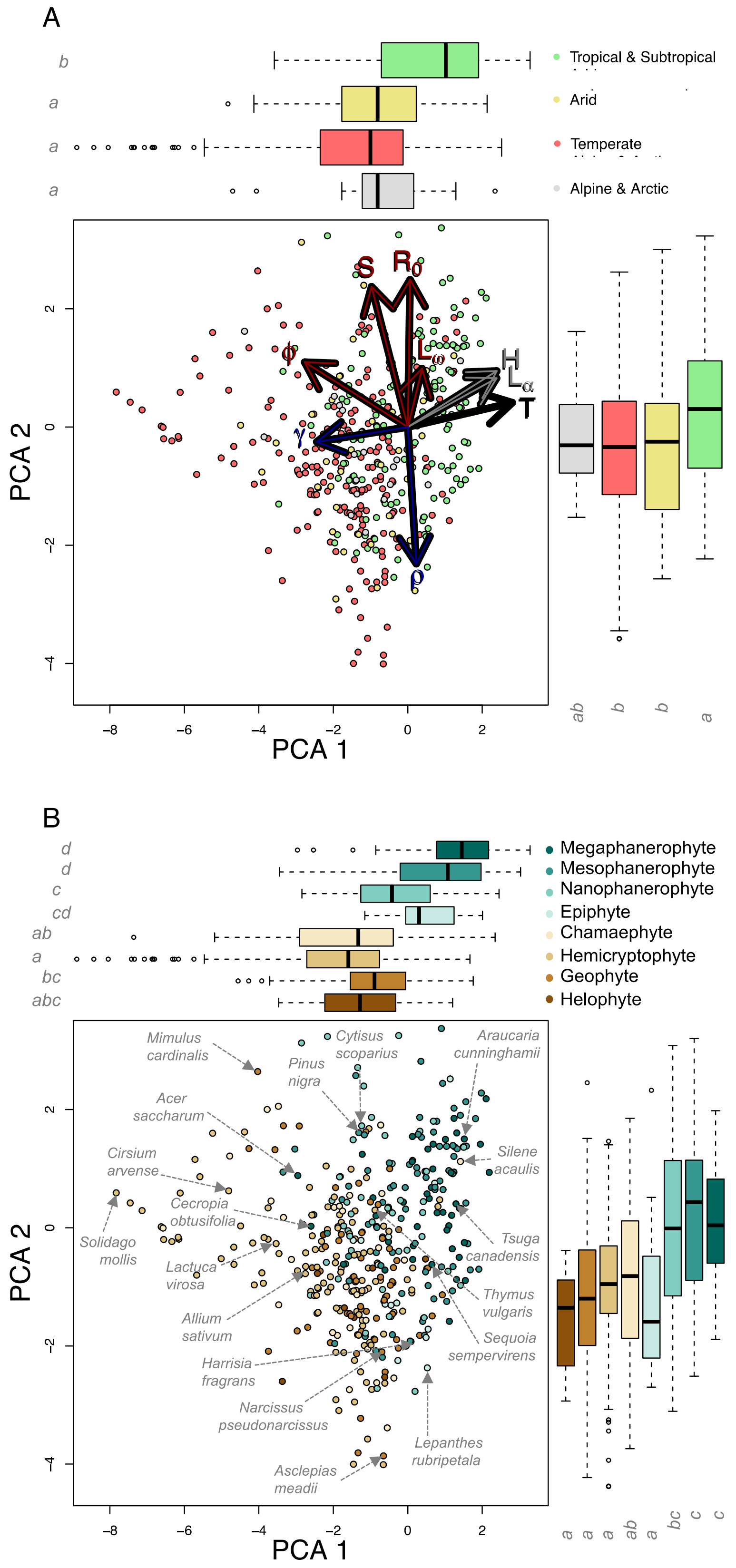
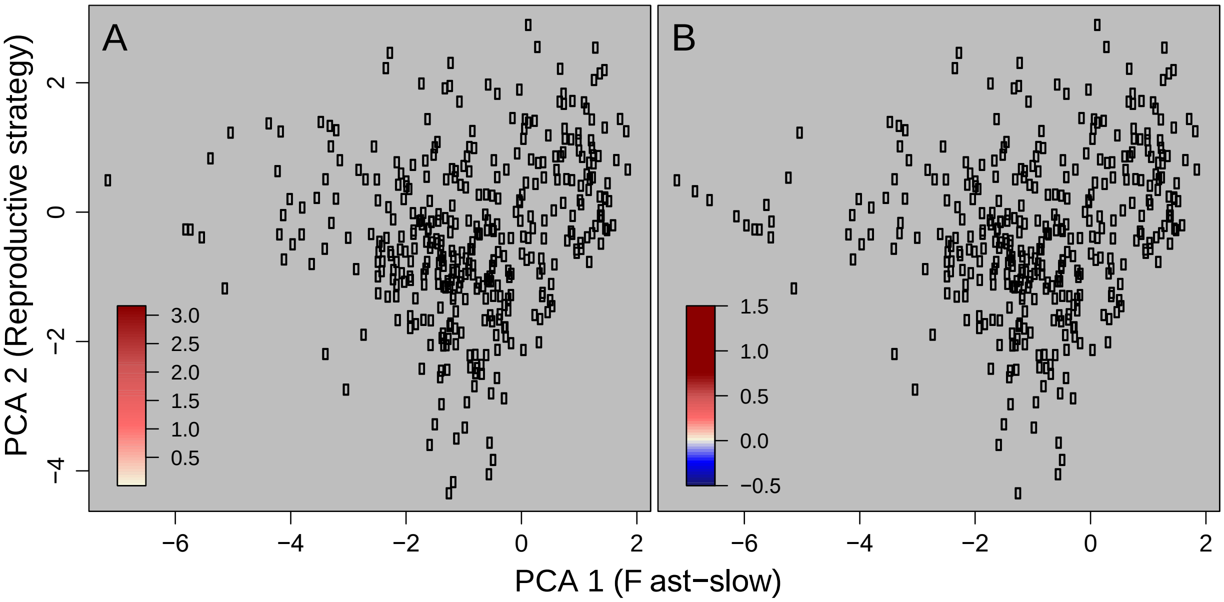


Figure 2



A
b
a
a
a
Tropical & Subtropical
Arid
Temperate
Alpine & Arctic
S
R0
Lω
H
Lα
T
ϕ
γ
ρ
PCA 2
PCA 1
2
0
−2
−4
−8
−6
−4
−2
0
2
ab
b
b
a
B
d
d
c
cd
ab
a
bc
abc
Megaphanerophyte
Mesophanerophyte
Nanophanerophyte
Epiphyte
Chamaephyte
Hemicryptophyte
Geophyte
Helophyte
Mimulus cardinalis
Cytisus scoparius
Araucaria cunninghamii
Pinus nigra
Acer saccharum
Cirsium arvense
Silene acaulis
Cecropia obtusifolia
Solidago mollis
Tsuga canadensis
Lactuca virosa
Thymus vulgaris
Allium sativum
Sequoia sempervirens
Harrisia fragrans
Narcissus pseudonarcissus
Lepanthes rubripetala
Asclepias meadii
PCA 2
PCA 1
2
0
−2
−4
−8
−6
−4
−2
0
2
a
a
a
ab
a
bc
c
c

Figure 3


A
B
PCA 2 (Reproductive strategy)
PCA 1 (F ast−slow)
2
0
−2
−4
−6
−4
−2
0
2
−6
−4
−2
0
2
3.0
2.5
2.0
1.5
1.0
0.5
1.5
1.0
0.5
0.0
−0.5