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

Roberto Salguero-Gómez²,³, Owen R. Jones⁴,⁵, Eelke Jongejans⁶, Simon P. Blomberg⁷, David Hodgson¹, Cyril Mbeau-Acè⁸, Pieter A. Zuidema³, Hans de Kroon⁴,⁷ & Yvonne M. Buckley⁸

*School of Biological Sciences. Centre for Biodiversity and Conservation Science. The University of Queensland. St. Lucia QLD 4072, Australia;²Evolutionary Demography Laboratory, Max Planck Institute for Demographic Research, Rostock 18057, Germany;³Max Planck Odense Center on the Biodemography of Aging, University of Southern Denmark, Odense M 5230, Denmark;⁴Department of Biology, University of Southern Denmark, Odense M 5230, Denmark;⁵Institute for Water and Wetland Research, Departments of Animal Ecology & Ecosystems and Experimental Plant Ecology, Radboud University Nijmegen 6500 GL, the Netherlands;⁶Centre for Ecology and Conservation, University of Exeter, Tremough TR10 9EZ, United Kingdom;⁷School of Biological Sciences, Plymouth University, Plymouth PL4 8AA, United Kingdom;⁸Forest Ecology and Forest Management Group, Wageningen University, Wageningen 6700 AA, the Netherlands;⁹School of Natural Sciences & Trinity Centre for Biodiversity Research, Zoology, Trinity College Dublin, University of Dublin, Ireland.§Joint senior authors

Submitted to Proceedings of the National Academy of Sciences of the United States of America

The fast-slow continuum is one of the most fundamental concepts in ecology, which describes how organisms allocate resources between growth and reproduction. This results in a continuous spectrum ranging from “fast” to “slow,” with the predominant strategies being semelparous (a single reproductive event) and iteroparous (repeated reproductive events), respectively. Understanding this continuum is crucial for predicting population responses to environmental change and for the development of conservation strategies.

In this study, the authors aimed to classify plant species based on their life history strategies and to predict population growth rate and response to perturbations. They used demographic data from 418 plant species worldwide, which allowed them to build a framework of life history strategies. The framework was used to predict population performance and population responses to environmental change.

The significance of this work lies in its ability to predict population responses to environmental change, which is crucial for conservation and management strategies. Understanding the fast-slow continuum in plants can help in the development of more effective conservation strategies, especially in the face of climate change and habitat loss.

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.

Reserved for Publication Footnotes

- Comparative biology | Life history strategy | Iteroparity | Generation time | Matrix population model

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’s 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 over 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 (Figure 1; Supporting Information) to address the following questions: (i) what are the main axes of variation in 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 response to 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.

www.pnas.org --- --- PNAS
the life history trait with greatest loading onto PCA 1 (Table 1), related to the fast-slow continuum (11): generation time (\(T\)) explain 21% of the variation in plant life history strategies, respectively. 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 (\(L_M\); 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, \(p\)) is negatively loaded onto PCA 2. Mature life expectancy (\(L_M\)), the period between age of sexual maturity (\(L_M\)) 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 2A). From negative to positive scores on the 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 hemicycrophytes) vs. trees (nano- to 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 throughout 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 (\(L_M\)) 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 hemicycrophytes (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; \(F_{3,395} = 34.88; P < 0.001\)). 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). Epi-

phytes (species growing upon other plants; e.g. forest babyboy
Table 1. Loadings of the life history traits grouped by their relation to turnover, and strategies to longevity, growth and reproduction onto the first two PCA axes. Loadings in bold (>|±0.50|) indicate high contribution of the life history trait to the PCA axis.

<table>
<thead>
<tr>
<th>Life history trait</th>
<th>Symbol</th>
<th>Definition</th>
<th>PCA 1</th>
<th>PCA 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turnover</td>
<td>T</td>
<td>Number of years necessary for the individuals of a population to be fully replaced by new ones</td>
<td>0.85</td>
<td>0.17</td>
</tr>
<tr>
<td>Longevity</td>
<td>H</td>
<td>Shape of the age-specific survivorship curve $l_i$, as quantified by Keyfitz’ entropy ($\eta$). $H$ values $&gt;1$, $=1$, $&lt;1$ correspond to survivorship curves types I, II and III, respectively</td>
<td>0.55</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Number of years that it takes an average individual in the population to become sexually reproductive</td>
<td>0.71</td>
<td>0.29</td>
</tr>
<tr>
<td>Growth</td>
<td>$\gamma$</td>
<td>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)</td>
<td>-0.73</td>
<td>-0.05</td>
</tr>
<tr>
<td></td>
<td>$\rho$</td>
<td>Mean probability of transitioning back to a smaller/less developed stage in the life cycle of the species, SSD-weighted</td>
<td>0.07</td>
<td>-0.77</td>
</tr>
<tr>
<td>Reproduction</td>
<td>$\Phi$</td>
<td>Mean per-capita number of sexual recruits across stages in the life cycle of the species, weighted by the SSD</td>
<td>-0.83</td>
<td>0.30</td>
</tr>
<tr>
<td>Degree of iteroparity</td>
<td>$S$</td>
<td>Spread of reproduction throughout the lifespan of the individual as quantified by Demetrius’ entropy ($S$). High/lower $S$ values correspond to iteroparasitosemelparous populations</td>
<td>-0.23</td>
<td>0.51</td>
</tr>
<tr>
<td>Net reproductive rate</td>
<td>$R_n$</td>
<td>Mean number of recruits produced during the mean life expectancy of an individual in the population</td>
<td>0.04</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Number of years from the mean age at sexual maturity ($l_m$) until the mean life expectancy ($n_b$) of an individual in the population</td>
<td>0.15</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Percentage of explained variation</td>
<td>34.06%</td>
<td>21.23%</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cumulative percentage of explained variation</td>
<td>34.06%</td>
<td>55.38%</td>
</tr>
</tbody>
</table>

*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 $\lambda$, 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 $0.20 \pm 0.09$ (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: $0.18 \pm 0.02$, Magnoliopsida: $0.20 \pm 0.04$) is greater than those grouped by growth forms (herbs: 0.03, shrubs: 0.00 or trees: 0.00; Supplementary Information), implying some infraclass 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 2B) occupy a life history space on the fast slow axis that overlaps with herbaceous perennials (particularly helophytes, geophytes, and ephiphytes Figure 2B). 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 Raunkiær 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%.

Two orthogonal axes to predict population performance
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. 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 3A, 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 (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%. Guillard et al. (39) found for 80 species...
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 save 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 analyzed 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 \( \lambda < 0 \) indefinitely. Furthermore, some areas of life history space remain unvisited; 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 defining 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 3B), and endangered species like the fragrant prickly apple (Harrisia fragrans) or Mead's milkweed Asclepias meadii at the low end (Figure 2B). Given the restricted spatial replication of plant demographic studies (21), we are unable to discern how much of the variation in 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, as it is because these concepts are not always informed by 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 418 plant species. For this list, we included all species from the vascular plant database of the world’s largest land plant family (67). We reduced this 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.onezooom.org/FWhf3b3e840f46) with branch length transformations applied to simultaneously estimate and account for phylogenetic signal, estimated by Pagel’s \( \lambda \) (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.thepplantlist.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). This allows us 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 initial topology was resolved, the integrative phylogenetic information was obtained, branch lengths were interpolated employing the function ‘bias’ of PHYLOCOM (70) given node ages in (73).

Analysis. From each species–axis–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

Footnote Author
in the Supplementary Materials. The corresponding life history traits (LHTs), composed to overall population turnover (T), longevity (T and L0), growth (v and p), and reproduction (q, S, R0, Lp; 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 gastrointestinal and maternal 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 classification via 2-way ANOVAs with PCA 1 and 2 scores as explanatory factors. We used Raukiaer's growth form classification (27), indicating the distance of the plant type (herbaceous perennials, shrubs and trees), major habitat (temperate, tropical & sub-tropical) and taxonomic class (Pinopsida, Liliopsida, Magnolopsida); 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 detailed 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) \( \log(\lambda) \) 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.

ACKNOWLEDGEMENTS. M. Franco provided the phylogenetic tree. We thank H. Possingham, D. Koons, and F. Colchoro for feedback, and the COMPADRE Plant Matrix Database team for data digitalisation and error-checking. This work was supported by the Max Planck Institute for Demographic Research and the Australian Research Council DE140100505 (R.S.-G.) and Marie-Curie Career Integration Grant (Y.M.B.).

6. West GB, Enquist BJ, & Brown JH (2009) Scaling, 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 classification via 2-way ANOVAs with PCA 1 and 2 scores as explanatory factors. We used Raukiaer's growth form classification (27), indicating the distance of the plant type (herbaceous perennials, shrubs and trees), major habitat (temperate, tropical & sub-tropical) and taxonomic class (Pinopsida, Liliopsida, Magnolopsida); 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 detailed 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) \( \log(\lambda) \) 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.

ACKNOWLEDGEMENTS. M. Franco provided the phylogenetic tree. We thank H. Possingham, D. Koons, and F. Colchoro for feedback, and the COMPADRE Plant Matrix Database team for data digitalisation and error-checking. This work was supported by the Max Planck Institute for Demographic Research and the Australian Research Council DE140100505 (R.S.-G.) and Marie-Curie Career Integration Grant (Y.M.B.).
24(4):817-831.


