Drivers of vegetative dormancy across herbaceous perennial plant species

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Drivers of vegetative dormancy across herbaceous perennial plant species

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RH: Drivers of dormancy

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Data accessibility. Should the manuscript be accepted, we will upload supporting data to Dryad and will include the data DOI.

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Abstract. Vegetative dormancy, i.e. the temporary absence of aboveground growth for ≥1 year, is paradoxical, because plants cannot photosynthesize or flower during dormant periods. We test ecological and evolutionary hypotheses for its widespread persistence. We show that dormancy has evolved numerous times. Most species displaying dormancy exhibit life history costs of sprouting, and of dormancy itself. Short-lived and mycoheterotrophic species have higher proportions of dormant plants than long-lived species and species with other nutritional modes. Herbivory and foliage loss are associated with higher future dormancy levels, suggesting that carbon limitation promotes dormancy. Maximum dormancy duration is lower under higher precipitation and at higher latitudes. Study length affects estimates of some demographic parameters. Our results identify both life historical and environmental drivers of dormancy. We also highlight the importance of the little understood costs of sprouting and growth, latitudinal gradients in stress, and mixed nutritional modes, in the evolution of herbaceous perennials.

INTRODUCTION

Many herbaceous perennial plant species renew their aboveground parts annually, using resources accumulated during previous growing seasons, and stored in belowground perennating structures such as bulbs and rhizomes. Although it is widely believed that all herbaceous perennials produce aboveground parts every year, detailed studies have shown that many plants in a large number of species from many families do not (Lesica & Steele 1994; Shefferson 2009; Reintal *et al.* 2010). In these species, plants that fail to emerge aboveground may reappear after ≥1 year of subterranean existence, and some plants cycle irregularly between years with and without aboveground parts. The temporary absence of aboveground growth for one or more years is known as vegetative dormancy, or prolonged dormancy (hereafter, 'dormancy') (Lesica & Steele 1994; Shefferson 2009). In this study, we present the first detailed analysis of the causes, ecological functions, and evolutionary significance of dormancy, using data from all published studies in which it has been recorded.

Previous attempts to understand dormancy have used case studies of individual populations or species to infer its biology across all dormancy-prone species. This approach implies that the causes and functions of dormancy are similar wherever it occurs. However, the mean proportion of plants in dormancy in any year, duration of dormancy, and transition rates between dormancy and other life states, vary widely across space, time, populations, and species (Kull & Tuulik 1994; Shefferson & Tali 2007; Brys *et al.* 2011). If dormancy evolved once in plant evolutionary history, it might be driven by similar factors in all or most species in which it occurs, whereas if it evolved numerous times, the driving mechanisms would probably differ depending on the genetic and evolutionary contexts on each occasion. Because most literature on dormancy assumes that its basis is the same across all plant taxa, we examine the prediction that dormancy has a common origin early in the evolution of herbaceous perennials (the **common background hypothesis**).

Dormancy appears paradoxical, because dormant plants forego reproduction and often suffer higher mortality risk than sprouting plants (Shefferson *et al.* 2014). However, depending on the costs and benefits associated with dormancy *vs.* sprouting (i.e. seasonal re-emergence from a perennating organ), natural selection can contribute to maintaining dormancy. Two major, mutually non-exclusive hypotheses have been proposed to explain this: certain life history costs contribute to the evolutionary maintenance of dormancy (the **trade-off hypothesis**), and dormancy reduces the negative impacts of environmental stress and variation on fitness (the **environmental stress hypothesis**). We propose four predictions about dormancy across the plant kingdom, derived from these hypotheses: 1) longer lifespan makes dormancy more adaptive (the **lifespan prediction**), 2) dormancy is more strongly expressed in species utilising non-photosynthesis-based carbon sources (the **nutritional mode prediction**), 3) commonly experienced weather cues promote dormancy (the **common weather prediction**), and 4) greater environmental stress at higher latitudes creates a latitudinal gradient of dormancy (the **latitudinal gradient prediction**). The basis for these hypotheses and predictions is explained below.

Life history costs are negative, indirect consequences for life history traits, such as survival or reproduction, caused by optimising other life history traits (Stearns & Magwene 2003). These costs are often caused by patterns of allocation of scarce resources or by pleiotropy, and manifested as negative correlations between life history traits (de Jong & van Noordwijk 1992). In the case of dormancy, some life history costs will be evolutionary drivers of dormancy if they are associated with adverse effects on the fitness of sprouting plants, such as reducing future survival, sprouting, or flowering caused by sprouting, growth, or reproduction. If, for example, sprouting in a particular year were associated with a high risk of herbivory, or if rapid growth caused significant loss of limited resources, remaining dormant might be adaptive (Shefferson *et al.* 2014). The **trade-off hypothesis** suggests that dormancy-prone species should exhibit strong fitness-related costs caused especially by sprouting and growth (this does not preclude some trade-offs making dormancy less adaptive, as might happen if dormancy itself is associated with future increases in mortality or lower fecundity).

The impact of these trade-offs would be expected to depend on lifespan and nutritional mode. Lifespan may selectively influence dormancy because short-lived species have fewer opportunities to sprout and reproduce than long-lived species. Similarly, low costs of dormancy might select for longer lifespan if costs of sprouting are high, because longer lifespan provides more opportunities to reproduce. In one view of classical life history theory, such effects can also stem from recruitment interacting with a trade-off between survival and reproduction, where low or unpredictable recruitment favours long lifespans, while high recruitment favours short lifespans (Stearns 1976). We therefore predict that foregoing reproduction through dormancy will be less adaptive, or even maladaptive, in short-lived *vs.* long-lived species (the **lifespan prediction**). Trade-offs might also be very strong in mycoheterotrophs (achlorophyllous plants acquiring all their carbon from mycorrhizal fungi), because limitation of carbon from the mycorrhizal associate would impose a strong physiological cost on sprouting (Bruns *et al.* 2002; Shefferson *et al.* 2016). Mixotrophs (green species acquiring carbon from both mycorrhizal fungi and photosynthesis) may suffer intermediate carbon limitation relative to mycoheterotrophs and autotrophs (Selosse & Roy 2009; Merckx 2013). Thus, mycoheterotrophs should be more dormancy-prone than photosynthetic species (the **nutritional mode prediction**).

The **environmental stress hypothesis** proposes that temporal environmental variation causes sprouting to impose fitness costs. These might be triggered by disturbance or suboptimal growth conditions caused by factors such as weather, herbivory, drought, and disease, increasing mortality or reducing reproduction. Several studies have shown that the proportion of dormant plants in a population in any year is correlated with local weather conditions prior to, or during, the growing season (Shefferson *et al.* 2001; Miller *et al.* 2004; Hutchings 2010). Thus, common cues such as rainfall or temperature may determine the extent of dormancy (the **common weather prediction**). Furthermore, if abiotic stress is greater at higher latitudes, for example due to harsher winters and stronger fluctuations in weather during the growing season (Normand *et al.* 2009), dormancy would be predicted to increase with latitude (the **latitudinal gradient prediction**). At its extreme, the environmental stress hypothesis suggests that dormancy may be a “bet-hedging trait”, reducing short-term fitness while raising lifetime fitness by avoiding risks associated with sprouting in highly unfavourable years (Shefferson 2009; Gremer *et al.* 2012), as also proposed for seed and bud dormancy (Cohen 1966; Nilsson *et al.* 1996; Childs *et al.* 2010).

In this study, we test the hypotheses and predictions presented above. A wide range of data was collated on all herbaceous perennial species in which dormancy has been documented. We examine the relationships between the proportion of dormant plants in populations, the duration of dormancy, and the life historical properties of populations and the environmental contexts under which they were observed. For life historical properties, we examined the effects on dormancy of perennating structure, nutritional mode, life history costs, and evolutionary history. For environmental factors, we assessed the impacts on dormancy of the latitude and geographic locations of populations, climate, and herbivory.

MATERIALS AND METHODS

Dataset development

We examined the ecological and evolutionary contexts of dormancy by creating a dataset including a large number of characteristics about dormancy from every relevant literature source available, supplemented with demographic data from published and unpublished sources, and subjecting it to statistical and phylogenetic analyses. Here, we summarise the development of this dataset (hereafter, "main dataset"; full details in *Supplemental Methods*, and characteristics of the species and populations in *Supplemental Results*).

First, we conducted a Google Scholar literature search for published data on dormancy, using several relevant search terms (details in *Supplemental Methods*). Next, we analysed demographic datasets to increase the statistical power to address questions about dormancy. From these datasets, we assessed relationships between vital rates (probabilities of survival, sprouting, size transitions, flowering, and fruiting), and numbers of flowers and fruits produced, and characteristics including size, sprouting status (sprouting *vs*. dormant), flowering status (flowering vs. not flowering), individual life history, and year. Among these relationships, trade-offs were identified as significant negative slopes associated with size, sprouting, flowering, or fruiting in either of the previous two years *vs.* survival, sprouting, flowering, or fruiting in the current year. Costs of reproduction, sprouting, growth, size, and dormancy were noted as binomial variables in the main dataset. All these analyses were performed as generalized linear mixed models (GLMMs) compared with AICc using the packages *lme4* (Bates, Maechler & Bolker 2012) and *MuMIn* (Bartoń 2014) in *R* 3.4.1 (R Core Team 2016). Inference proceeded *via* the best-fit model and equally parsimonious models (ΔAICc $\leq$ 2.0), and *via* Akaike weights for each independent factor summed across all models, which relate the strength of a factor from 0 (no support) to 1.0 (complete support) (Burnham & Anderson 2002).

Next, for each population in each year, the GLMMs obtained were used to create either high-resolution historical (3yr) population projection matrices, or standard ahistorical (2yr) matrices when years of data were too limited for construction of historical matrices. Historical population projection matrices are second-order matrix models, in which transition probabilities represent the probability that an individual in state *i* in year *t*-1 and state *j* in year *t* transitions to state *k* in year *t*+1 (Ehrlén 2000). In ahistorical matrix models, transition values represent the probability that an individual in state *j* in year *t* transitions to state *k* in year *t*+1 (Ehrlén 2000). Projection matrices were used to estimate the mean life expectancy of individual plants (Steiner *et al.* 2012), which was used to examine the influence of lifespan on dormancy.

Finally, we estimated the mean proportion of plants in each population that were dormant each year as the complement of the resighting probability estimated by Cormack-Jolly-Seber mark-recapture modeling in program MARK (White & Burnham 1999; Shefferson *et al.* 2001). We also determined the frequency distribution of the duration of dormancy episodes per population, and median and maximum durations. These metrics were incorporated into our main dataset, together with metrics describing the studies and study sites.

Phylogenetic analyses: testing the common background hypothesis

We conducted a phylogenetic analysis to infer a hypothetical evolutionary history for dormancy, and to assess whether it exhibits phylogenetic signal (i.e. the tendency for more closely-related species to share more similar trait values, Cadotte & Davies 2016). First, we developed a phylogenetic tree of the 114 species known to exhibit dormancy, based on the Open Tree of Life (Hinchliff *et al.* 2015) using package *rotl* (Michonneau *et al.* 2016) for *R* (R Core Team 2016). We also included 261 herbaceous plant species from the COMPADRE database which, from detailed demographic studies, appear incapable of dormancy (Salguero-Gómez *et al.* 2015). The original publications were examined for each of these species, to confirm that dormancy had not been recorded. Onto this tree we plotted maximum recorded values per species for mean proportion of dormant plants and for duration of dormancy (see *Statistical analyses* below), and used the resulting character evolution reconstructions to test the **common**

background hypothesis. We reconstructed ancestral character states *via* maximum likelihood with the *R* package *phytools* (Revell 2012).

We hypothesized that the capacity for dormancy would yield significant phylogenetic signal if dormancy is constrained by a common genetic background, whereas lack of phylogenetic signal would suggest macroevolutionary lability and/or strong environmental determination of trait values. As species-level measures of the capacity for dormancy, we used the maximum values per species of the mean proportion of dormant plants, and duration of dormancy. We analyzed phylogenetic signal in both metrics using Blomberg's *K* and bootstrapping to determine significance in *R* package *picante* (Kembel *et al.* 2010) for *R* (R Core Team 2016). See *Supplemental Methods* for further details.

Statistical analyses: tests of the trade-off and environmental stress hypotheses

The linear models, matrices, and derived metrics described above, were used to construct the main dataset. This was then analysed evidence of the effects of different life historical characteristics within each population on the mean proportion of plants that were dormant, and maximum duration (years) of dormancy. Although mean or median values might be considered better measures of duration of dormancy, they were rarely reported. Data on maximum duration of dormancy were available from approximately twice as many studies as data on median length of dormancy.

We tested the **trade-off hypothesis** and **environmental stress hypothesis** by analysing the impacts of life history and environmental variables on dormancy across populations. Firstly, we created two global GLMMs differing only in response term: the first included the logit-transformed mean proportion of plants in dormancy in each population (normally distributed). The second included the maximum duration of dormancy observed in each population (Poisson distributed). Fixed factors tested in both models were one geographic variable (absolute latitude for each population's location), two environmental variables (mean annual precipitation and mean annual temperature throughout the years of each study, obtained from the nearest weather station to the site), five biological variables (nutritional mode, perennating structure, mean life expectancy [years], and any reproductive and sprouting costs [binomial]), and two study description variables (length of study [years] and number of plants recorded). Species was included as a random factor in both models. We also included geography more fully by creating sets of models in which either continent, or longitude varying linearly within continent, was included as a random factor. Significant relationships with biological variables, particularly with costs of sprouting or reproduction, would be evidence supporting the trade-off hypothesis, and significant relationships with geographic and environmental variables would support the environmental stress hypothesis. These models were developed using the *lme4* package (Bates *et al.* 2015) for *R* (R Core Team 2016), as before. Although herbivory might be an important driver of dormancy, few studies reported on it, preventing its inclusion in the main mixed models.

We also compared factors associated with high *vs.* low mean proportions of plants in dormancy (defined, respectively, as having means of >20% and ≤10% of plants dormant per population), and long *vs.* short maximum dormancy durations (defined as >3 and ≤2 years, respectively), as additional tests of the trade-off hypothesis and lifespan prediction. Category limits were chosen to clearly separate high *vs.* low levels of dormancy, while preserving statistical power. Populations with values between these categories were omitted from the analysis, leaving 128 and 163 populations (66 and 98 species) available for the analysis of proportions and durations of dormancy, respectively. We predicted that populations with short dormancy duration would exhibit short mean life expectancy and high incidence of sprouting, growth, and reproductive costs, whereas the opposite would be true of populations with long dormancy duration.

To examine the role of trade-offs further, we also assessed the impacts of different factors on costs of reproduction, sprouting, growth, and dormancy, using GLMMS as before. The same fixed and random factors were included, together with the presence of costs themselves. To assess the prediction that longer-lived would be more dormancy-prone (the lifespan prediction), we examined the relationships between mean life expectancy and the same fixed and random factors, excluding mean life expectancy itself, using GLMMs as before.

Dormancy has been widely reported in terrestrial orchids. This may reflect more demographic data having been amassed for Orchidaceae than for other plant families (Reintal *et al.* 2010). To examine whether orchids behave differently from other families, we repeated all of the mixed modeling described above, first with only the Orchidaceae species in our dataset, and then with only non-orchids.

RESULTS

Phylogenetic analyses and the common background hypothesis

Maximum duration of dormancy and mean proportion of dormant plants varied strongly across plant families (Figure S1). Ancestral state reconstructions of maximum duration dormant and mean proportion dormant suggested complex evolution with a minimum of, respectively, 22 gains with 32 losses, and 18 gains with 20 losses (Figure S2). In both cases, the most recent common ancestor of the ferns and the angiosperms also appears to be dormancy-prone. We found no evidence of phylogenetic signal in either dormancy metric (proportion: $K = 0.245$ vs. $K_{random} = 0.153 \pm 0.004$, $P = 0.928$; duration: $K = 0.192$ vs. $K_{random} = 0.153 \pm 0.005$, $P = 0.908$).

Trade-offs and life history

There was strong support for dormancy being driven by trade-offs (i.e. significant negative correlations between life history traits). Of 81 species for which trade-off data were available, some form of life history cost was found in 94.0%. Among 236 populations with data available to test for the presence of at least one cost, only 43 (18.2%) showed no trade-offs. 51.3% of populations exhibited reproductive costs, 58.1% exhibited costs of sprouting, and 27.1% exhibited costs of growth. Costs of reproduction most commonly involved costs to future size (25.0%), and least commonly involved costs to fruiting (8.1%). Sprouting most commonly exerted costs upon survival (49.6%), seen as increased mortality in the following two years. It affected future fruiting in only 5.5% of cases. Costs of growth most commonly affected survival (19.5%), and least commonly affected sprouting (2.5%). Intriguingly, 35.2% of all populations exhibited a life history cost associated with large size, most often expressed through lower future survival (25.0% of cases), or decreased flowering (23.7%).

68.2% of populations also exhibited some cost of dormancy, typically expressed as a cost to future sprouting (48.7% of cases) or flowering (36.9%).

Trade-offs were most often influenced by latitude and annual precipitation, and by sample size and study duration (Table S2). Reproductive costs were more common in populations from higher latitudes, in those experiencing lower precipitation, and in studies involving more plants (Table S3). Sprouting costs were more common at lower latitudes, under lower precipitation, in mycoheterotrophs, and in longer studies recording more plants (Table S4). Some models that were as parsimonious as the best-fit model suggested that such costs were more common in shorter-lived species (Tables S2 and S4). Growth costs were most common in rhizomatous species and least common in taprooted species, and more common at lower latitudes and under lower precipitation (Table S5). Costs of both growth and dormancy were more common in longer studies (Tables S5 and S7). Costs of large size were more common at higher latitudes, under lower precipitation, in short-lived species, and in shorter studies (Table S6). Finally, studies of ≥10yrs duration were twice as likely as studies of ≤5 years to reveal historical costs of sprouting on survival (0.114 ± 0.031 vs. 0.059 ± 0.029, respectively).

Populations with high mean proportions of dormant plants had significantly lower mean life expectancies than populations with low mean proportions dormant ($t_{73.7} = -4.264$, $P < 0.0001$), contradicting the lifespan prediction. These populations were significantly more likely to exhibit costs of sprouting ($t_{107.7} = 2.499$, $P = 0.014$), but not costs of reproduction ($t_{94.9} = 0.324$, $P = 0.747$) or size ($t_{75.9} = 1.873$, $P = 0.065$) (Figure 1a-d). Counterintuitively, populations with longer maximum dormancy duration also had significantly shorter mean life expectancies than those with shorter dormancy ($t_{65.3}$ = -2.430, P = 0.018), and were more likely to exhibit costs of sprouting ($t_{104.7}$ = 3.186, P = 0.002) and size ($t_{105.1}$ = 2.797, P = 0.006), but not reproduction ($t_{114.3}$ = 0.857, P = 0.393) (Figure 1e-h).

The best-fit mixed model of mean life expectancy indicated significant influences of type of perennating structure, nutritional mode, costs of sprouting, and study duration, although the last parameter was not included in some models that were as parsimonious as the best-fit model (Tables S2 and S8). The longest life expectancies were found in rhizomatous, autotrophic species with no sprouting or reproductive costs (the longest estimated mean life expectancy was 522 years in *Caladenia orientalis* [Orchidaceae], and the longest estimated mean life expectancy for a non-orchid species was 169 years in *Lathyrus vernus* [Fabaceae]). Shortest mean life expectancies were in mycoheterotrophic species with sprouting costs. Study duration had a small but significant impact on mean life expectancy (+0.160 ± 0.057 years per year of study), suggesting that study length affects matrix-estimated life history traits (Figure S3; Table S8).

Life historical and environmental drivers of dormancy

Our best-fit mixed model of the mean proportion of dormant individuals included significant effects of sprouting costs, nutritional mode, and perennating structure, with the latter two factors not occurring in some equally parsimonious models (Table S9). In particular, the mean proportion of dormant plants was lowest in mixotrophs, and highest in mycoheterotrophs (Figure 2a). Mean proportion dormant was also lower in species with taproots than in rhizomatous species (Figure 2b). Species with sprouting costs also had higher proportions of dormant plants (Figure 2; Table S9).

Our best-fit model of maximum duration of dormancy included significant effects of study length, sprouting costs, type of perennating structure, precipitation, and absolute latitude, with the latter two factors absent in some models that were as parsimonious as the best-fit model (Tables S2 and S10). Rhizomatous species had the longest maximum dormancy values, whereas those with corms or bulbs had the shortest. On average, species with sprouting costs had maximum duration of dormancy roughly twice that of species without (Figure 3). Higher precipitation was associated with lower proportions of plants in dormancy (Figure 3a). Across all populations and species, the relationship between maximum duration of dormancy and absolute latitude was negative (Figure 3b). Maximum observed dormancy duration also increased by 0.217 ± 0.017 years per year of study (Figure 3c).

With few exceptions (see *Supplemental Results*), the results of mixed model analyses of mean life expectancy, mean proportion dormant, and maximum duration of dormancy were robust when repeated with either orchids or non-orchids excluded from the analyses.

Impacts of herbivory or defoliation on future dormancy were reported in 37 of 39 populations from 13 studies. In 35 of these populations involving 9 species (*Castilleja mollis*, *Cephalanthera longifolia*, *Cleistesiopsis bifaria*, *Cypripedium calceolus*, *Cypripedium reginae*, *Dactylorhiza lapponica*, *Lathyrus vernus*, *Solidago missouriensis*, *Trillium grandiflorum*), a higher proportion of plants were dormant in years following severe herbivory or defoliation.

Herbivory was associated with increased sprouting in only one population, of *Liparis loeselii*.

DISCUSSION

Diverse backgrounds

Phylogenetic analyses showed that dormancy has evolved numerous times, refuting the common background hypothesis. Although this result suggests that dormancy has probably proved adaptive under many ecological circumstances, we also identified common drivers of dormancy in the form of life history costs and environmental interactions, suggesting that it may evolve repeatedly in response to common evolutionary and genetic contexts. Although data on this subject are not available, the frequency with which dormancy has evolved suggests that it can be achieved with only a small number of mutations at few loci. For example, if dormancy were linked in some clades to climatic stress caused by strong seasonality, its evolution in those clades might be rooted in mutations at loci involved in the physiological breaking of winter dormancy. The genes responsible might be those involved in the ABA-signalling pathway (Footitt *et al.* 2011), or in the growth of vegetative rhizomes, the latter of which are also engaged in the expression of winter dormancy (Paterson *et al.* 1995).

Mycoheterotrophy is also associated with an effect on the mean annual proportion of plants in dormancy. Carbon provisioning from mycorrhizal fungi makes sprouting largely superfluous except for the purpose of flowering (Shefferson *et al.* 2016). Some of the structural carbon in the perennating structures of mixotrophs is also provided by fungi (Roy *et al.* 2013) while growth of the shoot is mainly supported by photosynthesis (Gonneau *et al.* 2014). Since mixotrophy and mycoheterotrophy have evolved in at least three plant families (Ericaceae, Ophioglossaceae, Orchidaceae), dormancy and mycoheterotrophy may have common evolutionary contexts to both dormancy and mycoheterotrophy, at least within these clades.

Life history relationships

We found strong evidence of certain life history costs, particularly costs of sprouting, being associated with higher levels of dormancy (the trade-off hypothesis). While none of the trade-offs examined (costs of flowering, fruiting, sprouting, growth, size, and dormancy itself) was significant in all populations, almost every population exhibited at least one trade-off. Populations with higher mean proportions of plants in dormancy, and longer maximum durations of dormancy, were more likely to exhibit costs of sprouting (Figures 2 and 3). Furthermore, mycoheterotrophic species had higher mean proportions of dormant plants than autotrophic or mixotrophic species, supporting the nutritional mode prediction (Figure 2a).

Although greater growth and larger size are often considered indicators of higher fitness (Salguero-Gómez & Casper 2010), this study showed that they were associated in many species with lower probabilities of future sprouting and survival, respectively. Since our analyses separated the effects of size from those of reproduction, the significant effects observed are unlikely to have been a reflection of reproduction being a costly activity occurring only in larger plants. Instead, large size and greater growth appear to inflict costs beyond the physiological impacts of previous reproduction (Bierzychudek 1982). One possible explanation is that species displaying such costs, e.g. *Asarum arifolium*

(Aristolochiaceae), *Ophrys sphegodes* (Orchidaceae), and *Corallorhiza odontorhiza* (mycoheterotrophic Orchidaceae), exhibit strong evidence of senescence; large plants are old plants, subject to higher mortality risk. Alternatively, the trade-offs documented may be stronger when environmental conditions deteriorate severely, causing plants that invest in growth under good conditions to suffer increased mortality risk due to usage rather than storage of resources that subsequently become limiting (Shefferson & Roach 2010).

Shorter-lived species were more likely to exhibit dormancy than longer-lived species, refuting the lifespan prediction, and also more likely to exhibit sprouting costs. This may be because they need to allocate resources to sprouting even in very unfavourable years in order to reproduce at all, or because they invest less in storage. If dormancy is indeed an adaptive response to stress (Shefferson *et al.* 2005), short-lived species have depleted resource pools more often than longer-lived species, due to previous sprouting and growth, increasing their probabilities of dormancy and mortality. This interpretation is supported by our finding that costs of large size are more common in shorter-lived species, implying a higher probability of exhausting resources on aboveground growth in order to reproduce.

Environmental stress

Support for the hypothesis that environmental stress results in greater dormancy was equivocal. Maximum dormancy duration was negatively correlated with annual precipitation (the common weather prediction), although the influence of this factor was weaker than those of sprouting costs and perennating structure. Other evidence supported an impact of biotic, rather than abiotic, stress. For example, most studies providing data on herbivory or defoliation demonstrated that both increase dormancy levels (e.g., Ehrlén 2003; Knight 2003; McEachern *et al.* 2009). Some previous studies have suggested that herbivory may be the primary driver of dormancy (Tamm 1972; Gregg 2011).

Contrary to our prediction that latitudinal gradients in abiotic environmental stress should result in greater dormancy at higher latitude, maximum dormancy duration decreased with increasing latitude. If longer dormancy indicates stress, this suggests that low-latitude environments are somehow more stressful. This could be explained by stronger biotic interactions nearer the equator (Schemske *et al.* 2009). For example, the negative impacts of higher conspecific density, including stronger competition and increased exposure to pathogens, are strongest in the tropics (LaManna *et al.* 2017), as is the impact of herbivory (Zhang *et al.* 2016). It is also possible that climate-dependent life history costs contribute to or create the latitudinal gradient that we observed (Sletvold & Ågren 2015). Such biotic impacts may explain why costs of sprouting and growth are also more common at lower latitudes, as these trade-offs may be stronger with greater competition or herbivory.

Future research and conclusions

Our search for drivers of dormancy was limited in ways that suggest a need for further research. Firstly, our interpretation of life history costs is based on a broad definition of trade-offs that includes any mechanisms yielding negative correlations, including physiological constraints and negative genetic correlations, linked gene expression, correlated selection, and indirect relationships driven by factors yielding opposite patterns in unrelated traits

(Bell & Kofopanou 1986; Reznick *et al.* 2000; Knops *et al.* 2007). Secondly, although we found evidence that weather and climate drive dormancy, we acknowledge that it may depend more strongly on annual variation in weather (Kéry *et al.* 2005; Smith *et al.* 2005), rather than mean weather variables. Finally, mixotrophy has only recently been subjected to rigorous study, and it is possible that some species we treated as autotrophs are actually mixotrophs (Selosse & Roy 2009).

We found widespread evidence for costs of sprouting promoting dormancy, and for environmental influences, and multiple evolutionary origins affecting patterns of dormancy in different clades. However, the mechanisms triggering dormancy, and producing sprouting and growth costs, are still not understood (Gregg 2011). We and others have reported different impacts of temperature, precipitation, and herbivory on dormancy in different species (Kéry & Gregg 2004; Miller *et al.* 2004; Light & MacConaill 2006; Hutchings 2010), and that closely-related dormancy-prone species can respond differently to the same climatic variables (Shefferson *et al.* 2017). The mean proportion of dormant plants in populations in different years is also known to vary spatially, even within species (Shefferson & Tali 2007), and the sprouting behaviour of plants within populations depends on their size, age, life stage, genetic background, and microclimate (Lacey 1986; Jäkäläniemi *et al.* 2011). The impacts of biotic factors such as herbivory on dormancy has been insufficiently explored. The hypothesis that herbivory creates strong costs of sprouting that favour dormancy requires direct testing. The possible role of biotic interactions in causing stronger manifestations of dormancy near the equator should also be examined.

This study has demonstrated the importance of life history costs and environmental factors as drivers of dormancy wherever it is found. Trade-offs were identified that drive the life history evolution of many herbaceous perennials, the most notable of which were costs of sprouting and growth, and their relationships with nutritional mode. We observed complex but common relationships with environmental factors, and also with latitude, that require further inquiry. We also demonstrated hitherto unidentified impacts of study length on life history metrics. We urge biologists to focus their efforts on unravelling the specific mechanisms yielding these patterns. These outcomes suggest productive avenues for further research, including detailed studies of life history evolution in herbaceous plant species, the ecology, genetics and physiology behind its expression, and the urgent need for longer-term demographic studies.

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RH: Drivers of dormancy

Figure Legend.

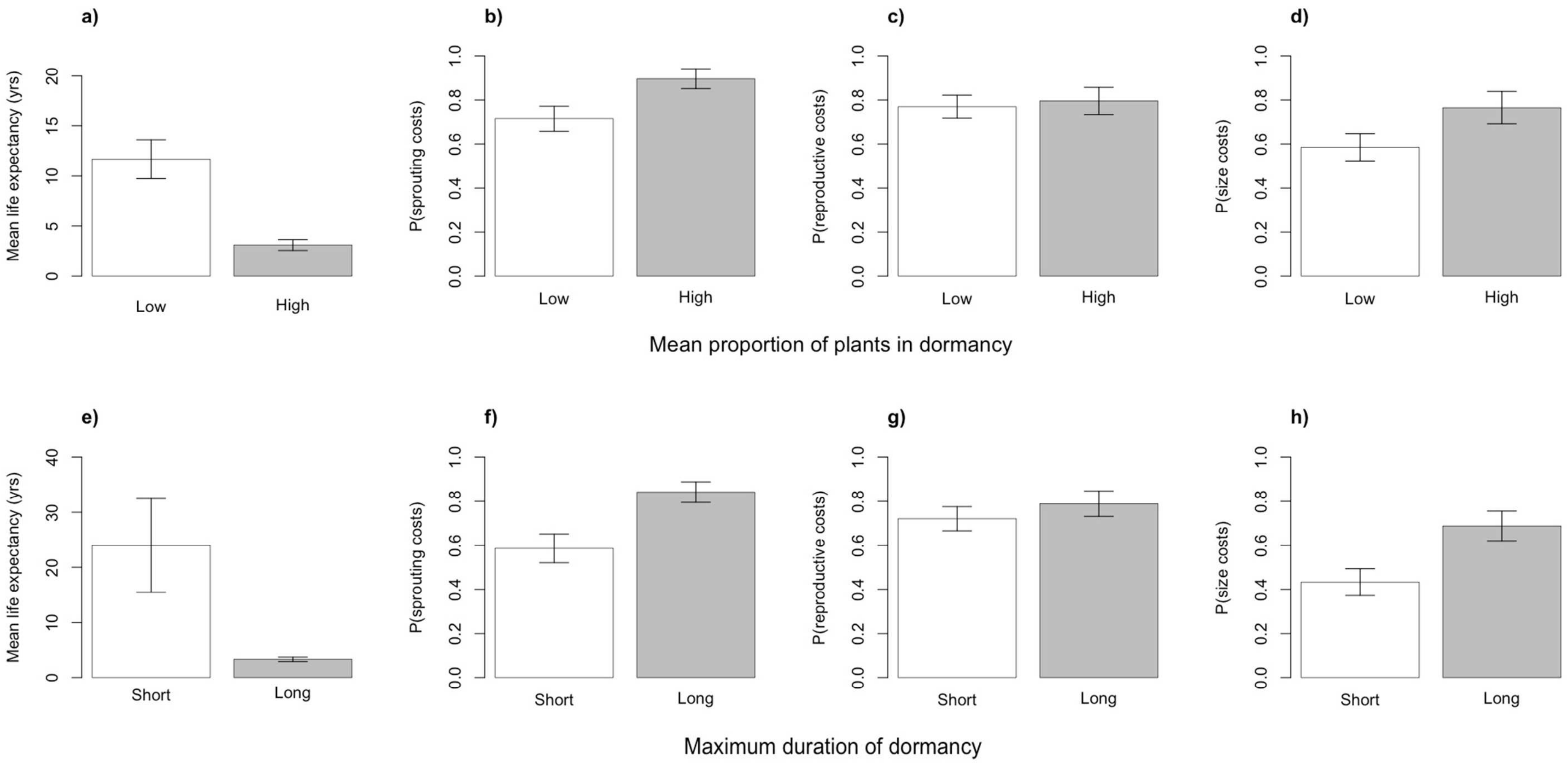
Figure 1. Life history characteristics of populations with high vs. low mean proportions of plants in dormancy (a-d), and short vs. long maximum dormancy lengths (e-h). Characteristics shown are mean life expectancy (a, e), probability of sprouting costs (b, f), probability of reproductive costs (c, g), and probability of size costs (d, h). Means ± 1 SE are shown.

Figure 2. Mean proportions of plants dormant per population as a function of nutritional mode (a) and perennating structure (b). In (b), corm refers to plants with corms, bulbs, or tubers. Means ± 1 SE are shown.

Figure 3. Maximum observed length of dormancy as a function of (a) mean total annual precipitation occurring at the study sites, (b) latitude at which studies were carried out, and (c) study length in years. No distinction is made between latitude in the Northern and Southern Hemispheres. Points represent actual values from individual populations, and lines represent the relationship given using the best-fit mixed model explaining maximum observed duration of dormancy. Solid line indicates trends in maximum dormancy duration with no sprouting costs, while the dashed line indicates maximum dormancy trends with sprouting costs.

RH: Drivers of dormancy

773 Figure 1.



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RH: Drivers of dormancy

776 Figure 2.

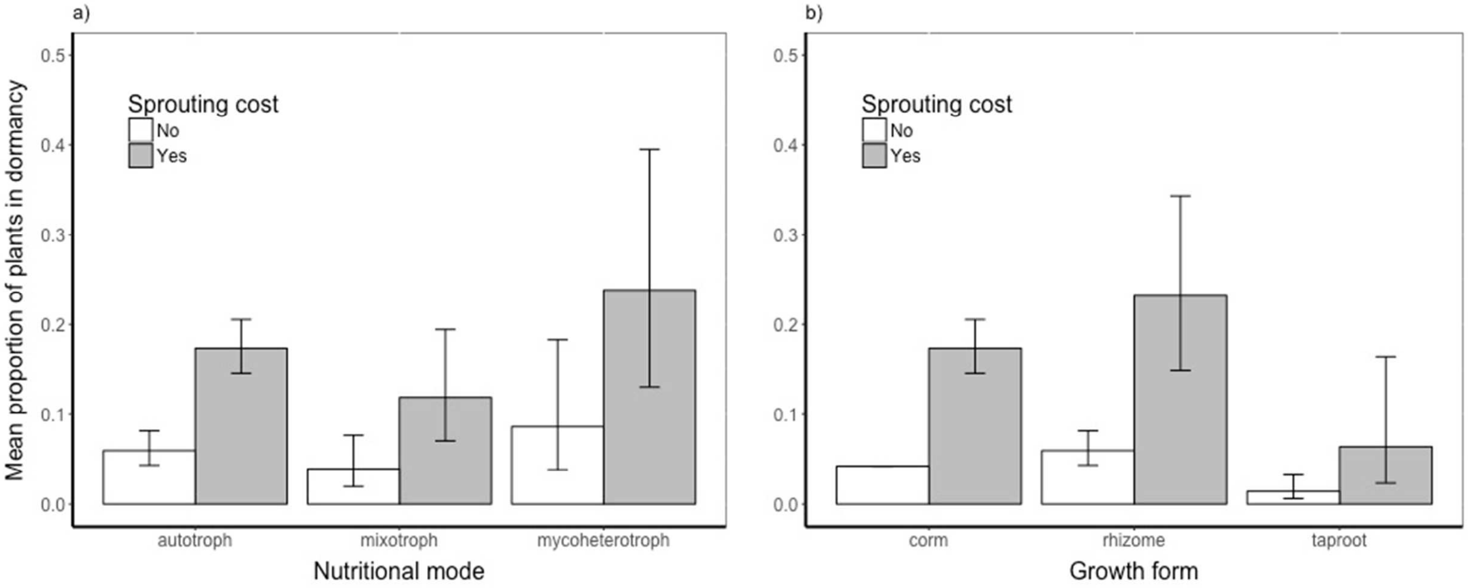

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Figure 3.

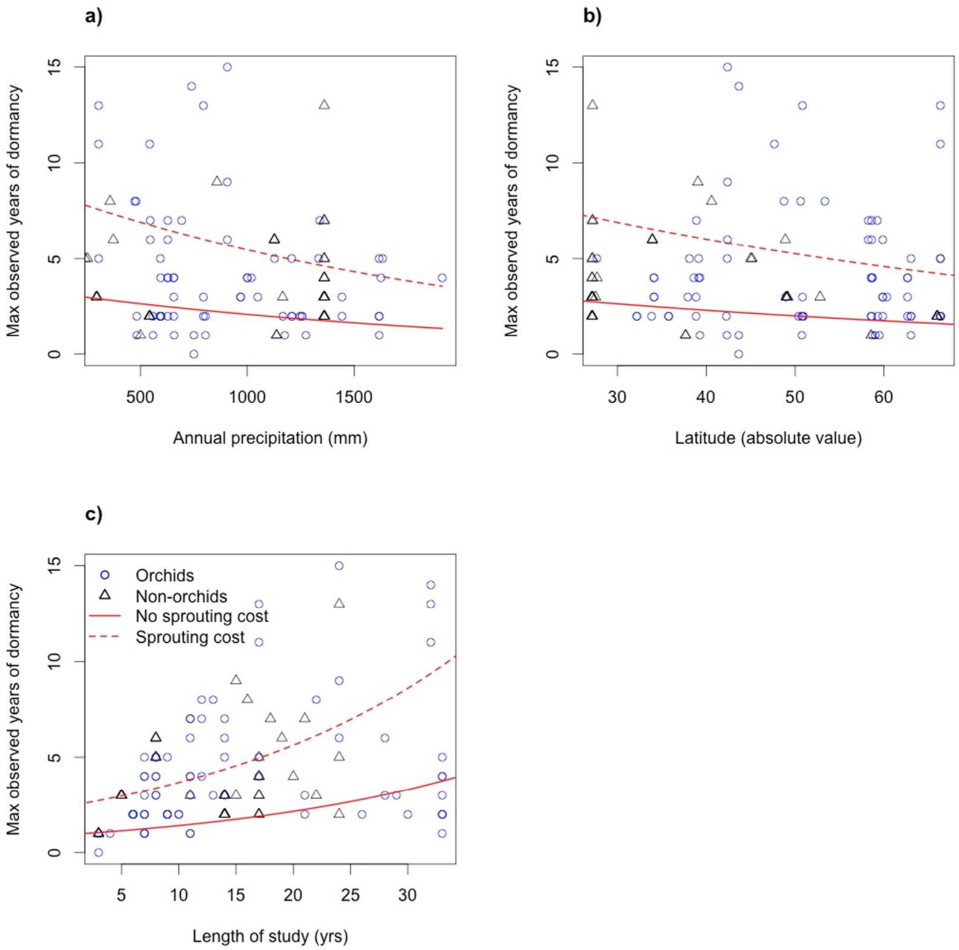
a)
Max observed years of dormancy
0
5
10
15
500
1000
1500
Annual precipitation (mm)
b)
Max observed years of dormancy
0
5
10
15
30
40
50
60
Latitude (absolute value)
c)
Max observed years of dormancy
0
5
10
15
5
10
15
20
25
30
Length of study (yrs)
○ Orchids
△ Non-orchids
No sprouting cost
Sprouting cost

Figure Legend

Figure S1. Quartiles of (a) mean proportion dormant per population and (b) maximum duration of dormancy per population in years across plant families. Numbers show the number of populations included in each distribution, which are not the same in (a) and (b) because of inconsistent availability of metrics across studies. Only families with estimated values for each of the dormancy metrics are shown.

Figure S2. The reconstructed evolutionary history of (a) maximum proportion dormant per population and (b) maximum duration of dormancy in years, shown on the Open Tree of Life. In both cases, green labels indicate species in which dormancy is thought not to occur, based on evidence from demographic monitoring. For mean proportion dormant, white, grey, and black refer to species with <10%, 10-20%, and ≥20% of the individuals dormant on average per population, respectively. For maximum duration of dormancy, white, grey, and black refer to species with <2, 2-4, and ≥4 years maximum duration of dormancy, respectively. Taxon labels are omitted, except for key families of interest.

Figure S3. The relationship between mean expected longevity and study length, both in years, as a function of nutritional mode. Lines indicate patterns in autotrophs (solid lines), mixotrophs (dashed lines), and mycoheterotrophs (dotted lines), in rhizomatous species with sprouting costs (a), species with taproots and sprouting costs (b), species with corms, bulbs, or tubers, and sprouting costs (c), and rhizomatous species without sprouting costs (d). Lines are derived from the best-fit mixed linear models of mean life expectancy across the entire dataset, and we indicate data points for the Orchidaceae (blue circles) and non-Orchidaceae (red triangles) as symbols in the background of each plot.

Figure S4. Locations of populations included in this study. 299 populations were included, approximately half of which were species in the Orchidaceae (blue circles). Non-Orchidaceae are shown by red circles. Many sites included sympatric populations. As a consequence, fewer than 299 points are displayed on the map. Latitudes of study sites ranged from 19.52° to 66.37° in the Northern Hemisphere, and 27.67° to 43.03° in the Southern Hemisphere.

Figure S5. The standard deviation of the proportion of individuals that were dormant per population per species as a function of the mean proportion of plants that were dormant per species. The black line indicates the linear regression between these two variables (slope = 0.344 ± 0.066; $F_{1,30} = 27.25$, $P = 1.25 \times 10^{-5}$).

Figure S1a.

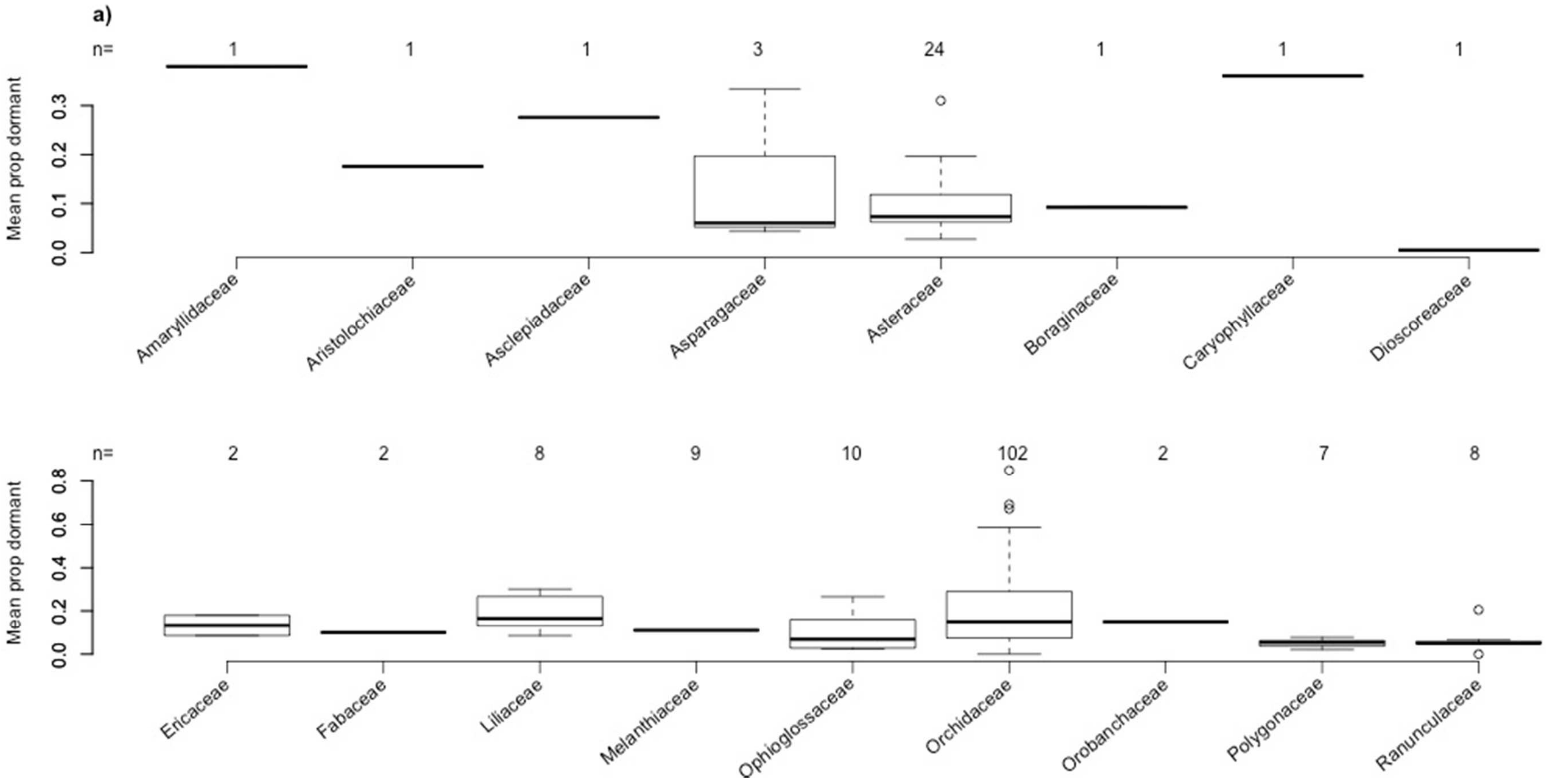
a)
n=
1
1
1
3
24
1
1
1
Mean prop dormant
0.0
0.1
0.2
0.3
Amaryllidaceae
Aristolochiaceae
Asclepiadaceae
Asparagaceae
Asteraceae
Boraginaceae
Caryophyllaceae
Dioscoreaceae
n=
2
2
8
9
10
102
2
7
8
Mean prop dormant
0.0
0.2
0.4
0.6
0.8
Ericaceae
Fabaceae
Liliaceae
Melanthiaceae
Ophioglossaceae
Orchidaceae
Orobanchaceae
Polygonaceae
Ranunculaceae

Figure S1b.

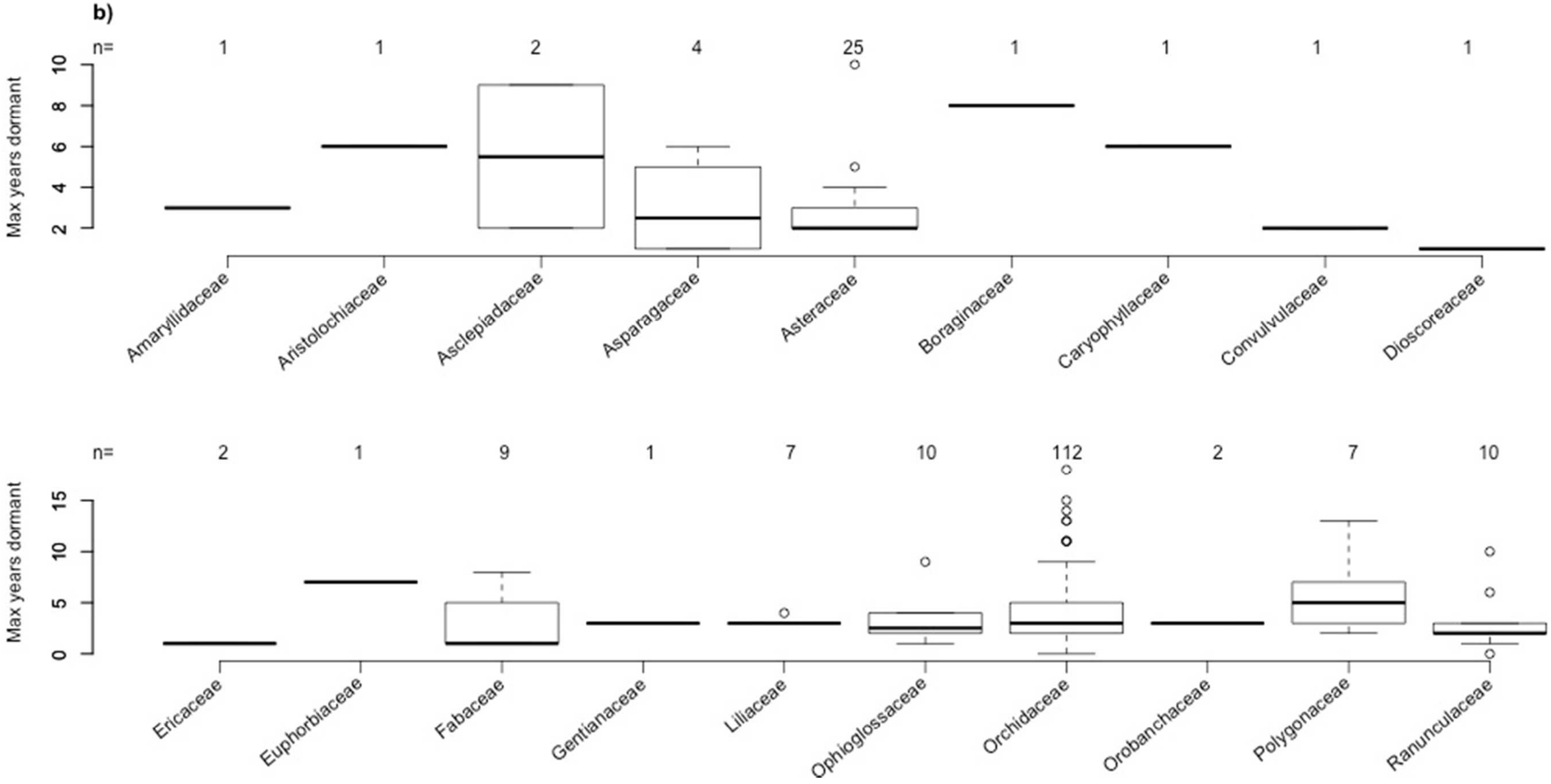
b)
n=
1
1
2
4
25
1
1
1
1
Max years dormant
2
4
6
8
10
Amaryllidaceae
Aristolochiaceae
Asclepiadaceae
Asparagaceae
Asteraceae
Boraginaceae
Caryophyllaceae
Convulvulaceae
Dioscoreaceae
n=
2
1
9
1
7
10
112
2
7
10
Max years dormant
0
5
10
15
Ericaceae
Euphorbiaceae
Fabaceae
Gentianaceae
Liliaceae
Ophioglossaceae
Orchidaceae
Orobanchaceae
Polygonaceae
Ranunculaceae

Figure S2a.

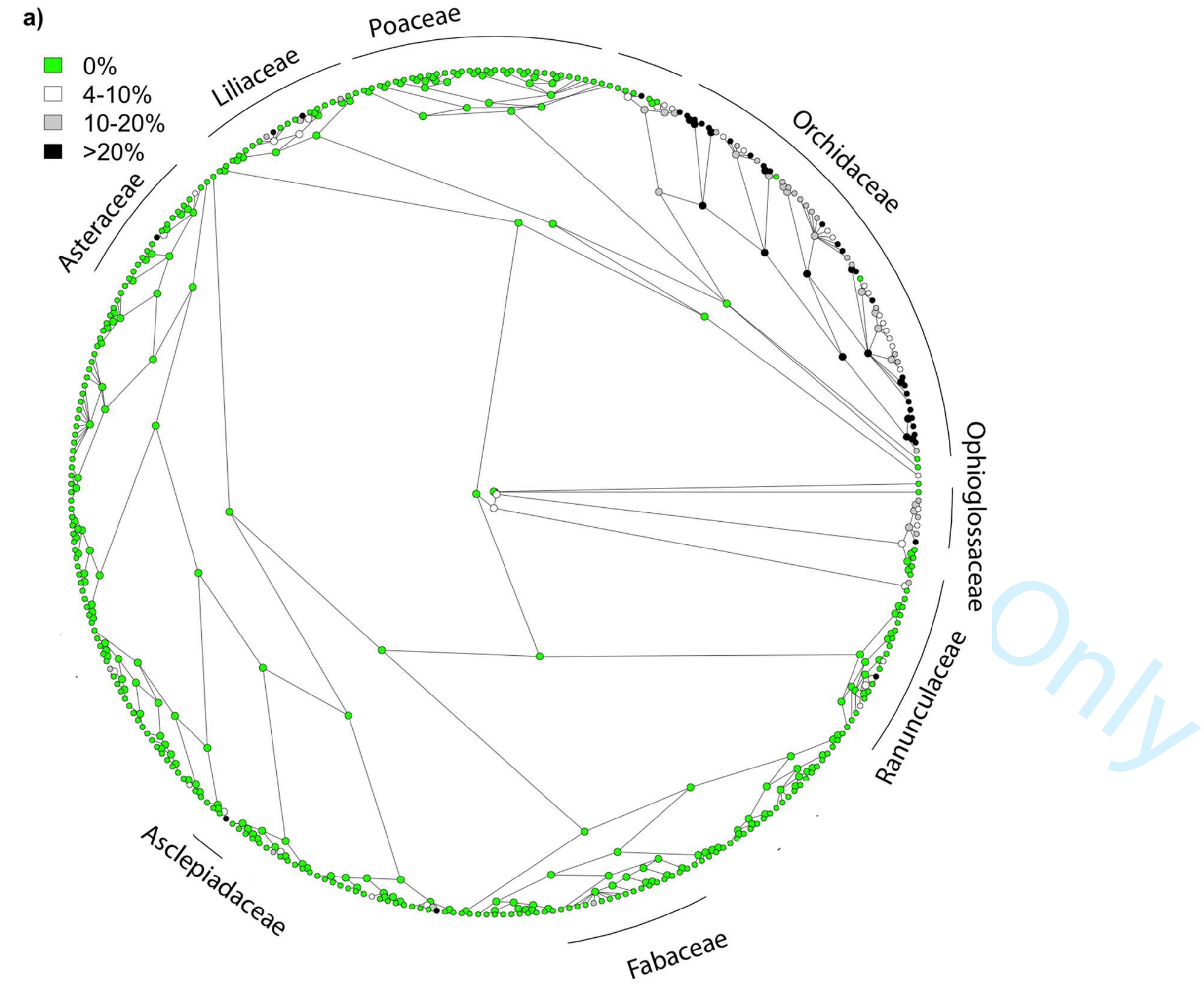
a)
0%
4-10%
10-20%
>20%
Poaceae
Liliaceae
Asteraceae
Orchidaceae
Ophioglossaceae
Ranunculaceae
Fabaceae
Asclepiadaceae

Figure S2b.

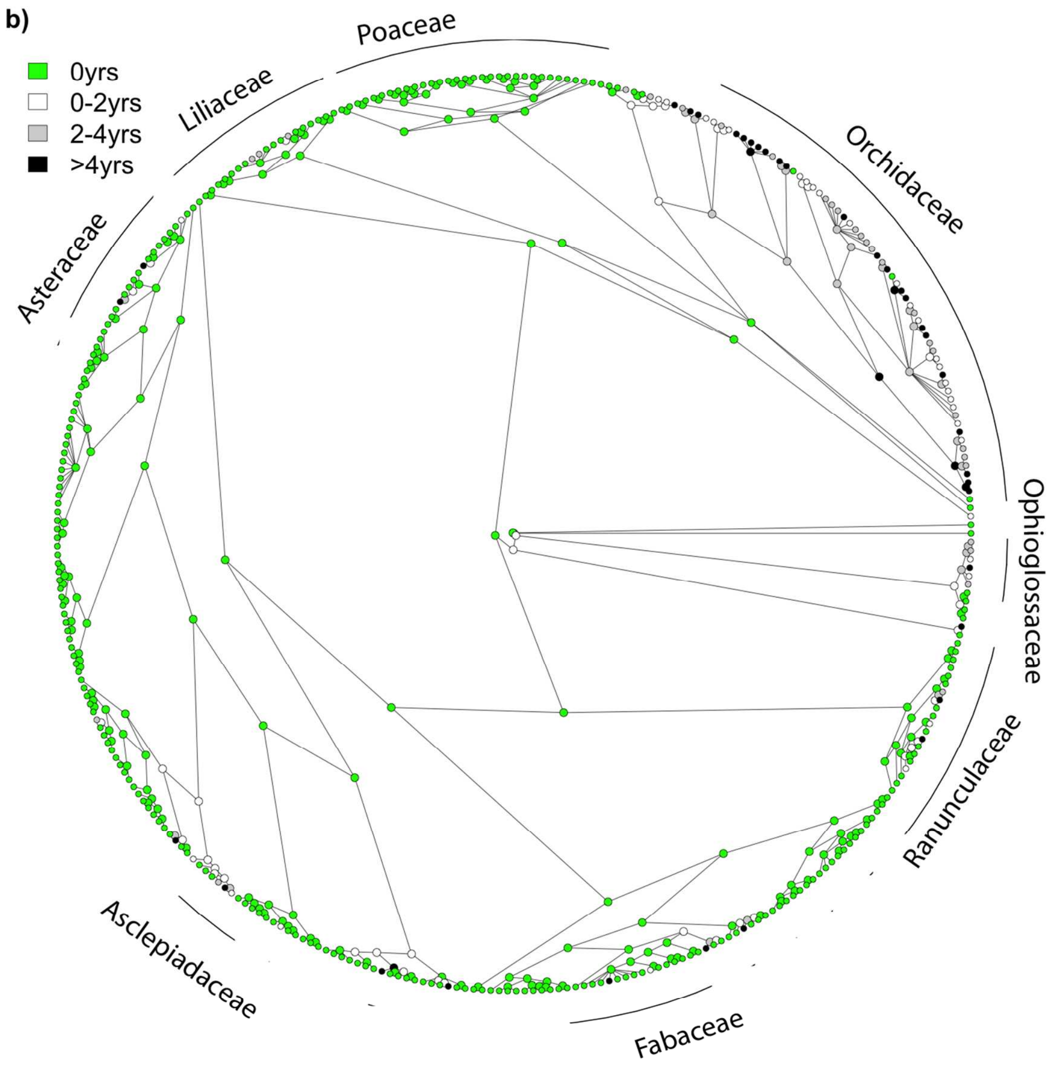
b)
🟩 0yrs
☐ 0-2yrs
▨ 2-4yrs
■ >4yrs
Poaceae
Liliaceae
Asteraceae
Orchidaceae
Ophioglossaceae
Ranunculaceae
Fabaceae
Asclepiadaceae

Figure S3.

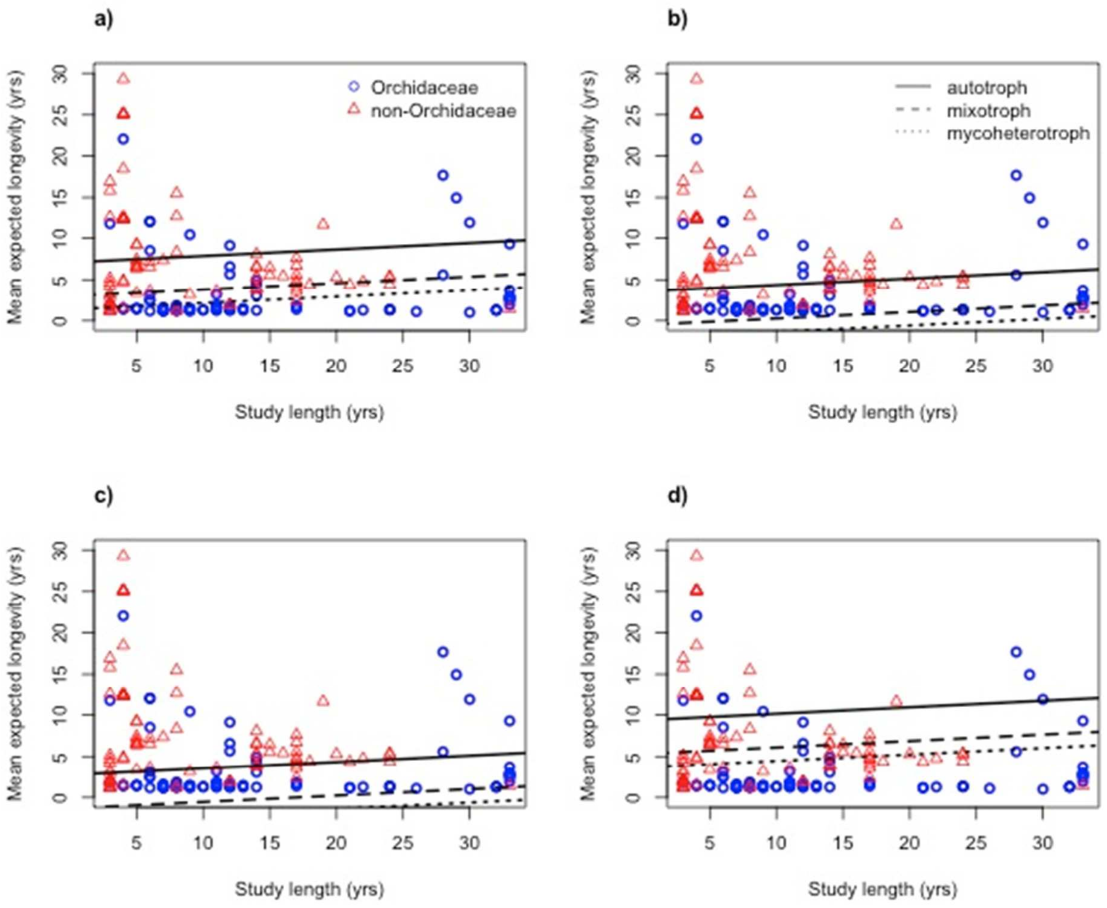
a)
b)
c)
d)
Orchidaceae
non-Orchidaceae
autotroph
mixotroph
mycoheterotroph
Mean expected longevity (yrs)
0
5
10
15
20
25
30
Study length (yrs)
5
10
15
20
25
30

Figure S4.

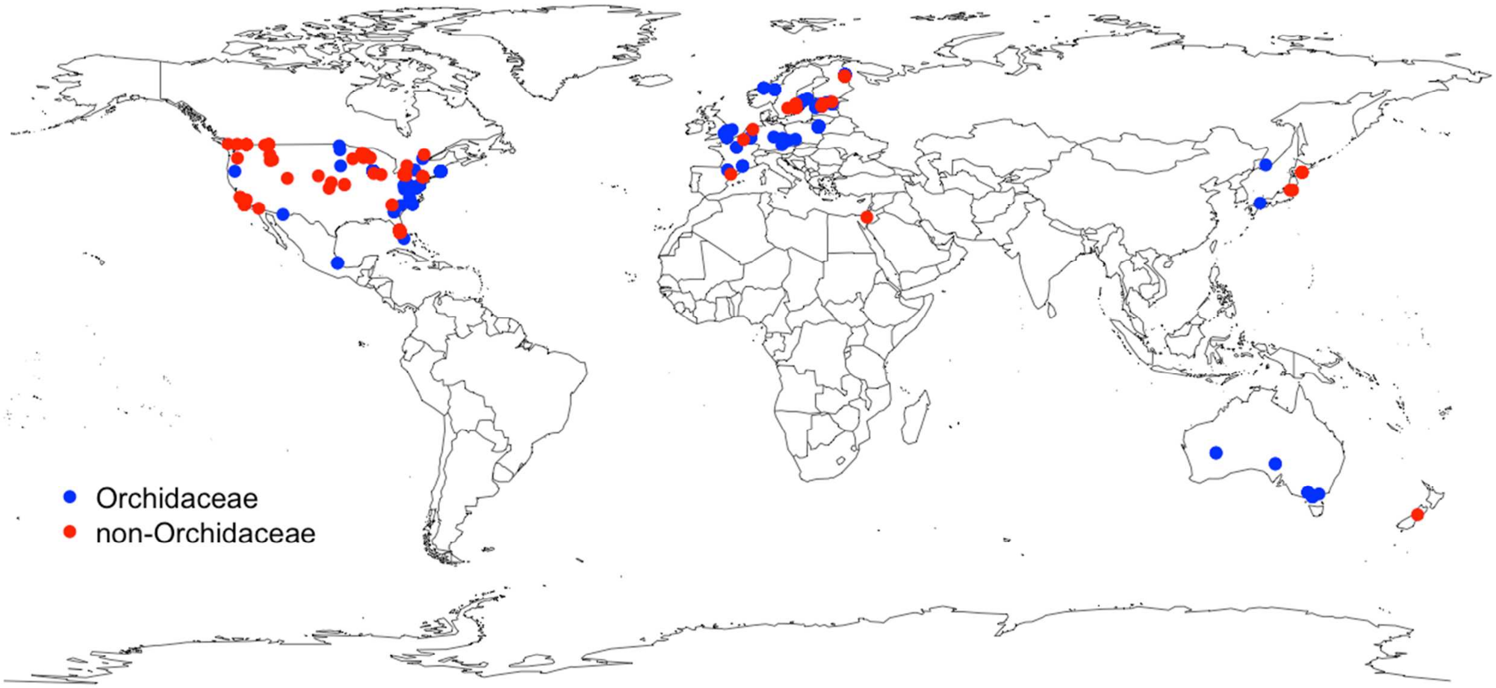

Figure S5.

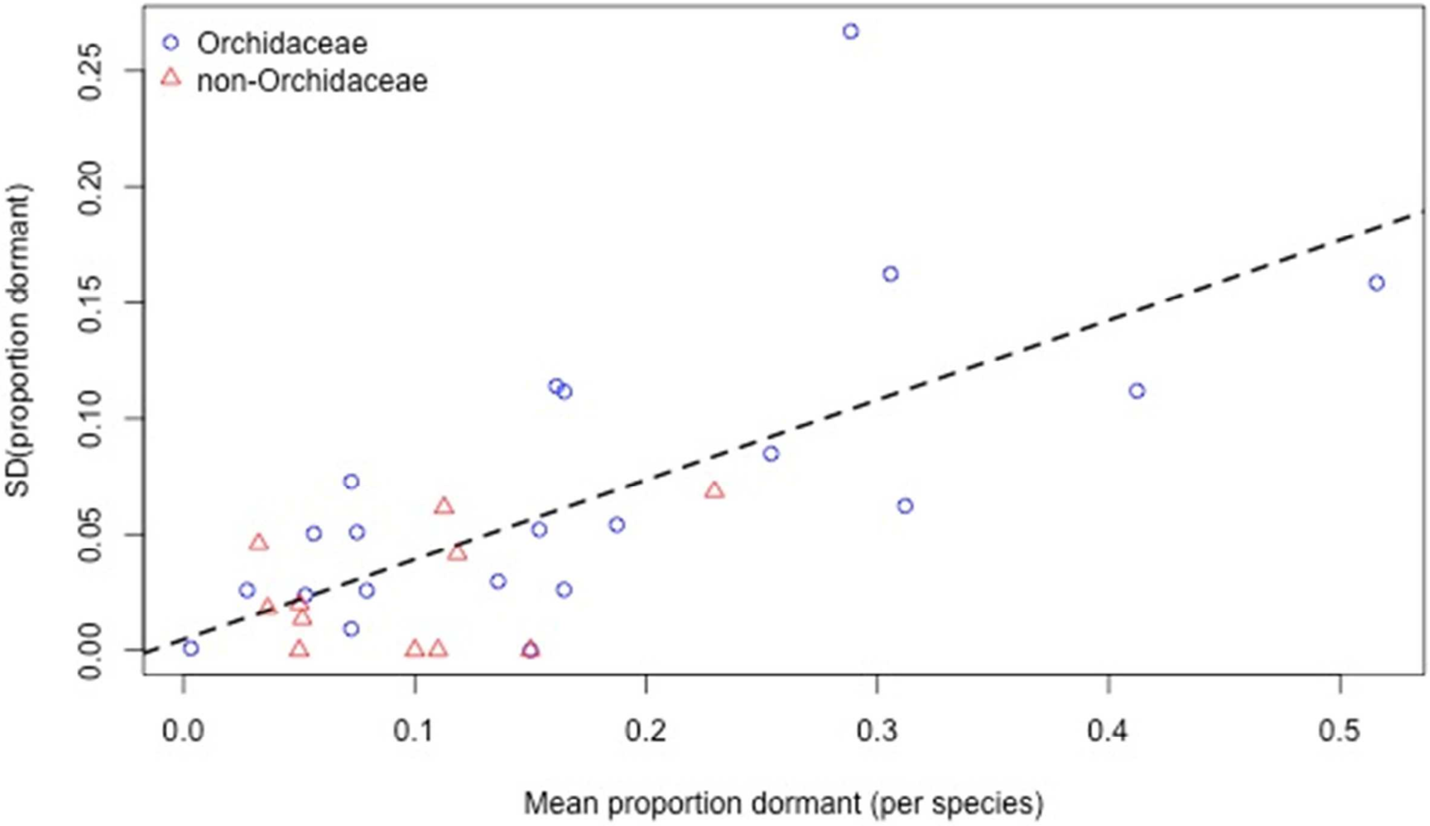
○ Orchidaceae
△ non-Orchidaceae
SD(proportion dormant)
0.00
0.05
0.10
0.15
0.20
0.25
0.0
0.1
0.2
0.3
0.4
0.5
Mean proportion dormant (per species)

Table S1. Summary of species and the 99 papers included in our demographic analysis of the characteristics of vegetative dormancy in herbaceous perennials. Synonyms used by the Open Tree of Life Project and hence used in our phylogenetic analyses are noted in parentheses. Asterisks in the populations column indicate the presence of albinos, which were treated demographically as distinct from green plants demographically. Missing locations, study periods, and sample sizes occur in cases where these descriptions were not provided. We entered "≥1" under Populations when insufficient information was provided to determine the number of populations studied, and ">x" when we felt certain that a number of individuals greater than x was sampled (generally due to incomplete reporting of sample size in a paper).

Family	Species	Populations	Regions	No. of years	Sample size	Citation
Amaryllidaceae	*Allium amplectens*	1	British Columbia, Canada	1995-2000	481	(Hawryzki *et al.* 2011)
Apiaceae	*Chaerophyllum*	≥1	Former Soviet			(Rabotnov 1969)

	prescotti		Union			
Araliaceae	*Panax quinquefolius*	4	Québec, Canada	1986-1988	345	(Charron & Gagnon 1991; Nantel *et al.* 1996)
Aristolochiaceae	*Hexastylis arifolia* (*Asarum arifolium*)	1	Georgia, USA	1999-2006	6235	R. Pulliam *unpublished data*
Asclepiadaceae	*Asclepias incarnata*	≥1				(Reintal *et al.* 2010)
	Asclepias meadii	1	Kansas, USA	1992-2006	252	(Alexander *et al.* 2009, 2012)
		2	Illinois, USA	1995-2000		(Bowles *et al.* 2001)

Asparagaceae	*Chlorogalum purpureum*	1	California, USA	1998-2004	375	(Guretzky *et al.* 2005)
	Polygonatum biflorum	1	Georgia, USA	1999-2006	4715	R. Pulliam *unpublished data*
	Polygonatum multiflorum	1	Estonia			(Reintal *et al.* 2010)
	Polygonatum odoratum	1	Estonia			(Reintal *et al.* 2010)
Asteraceae	*Arnica angustifolia*	6	Finland	1996-2009	600	(Jäkäläniemi 2011)
	Echinacea angustifolia	5	Kansas, USA	1996-1998		(Hurlburt 1999)
		1	Kansas, USA	1939-1971	417	(Dalgleish *et al.*

						2010)
	Liatris ohlingerae	19	Florida, USA	1997-2016	2995	(Tye *et al.* 2016); E. Menges *unpublished data*
	Liatris scariosa	1	Indiana, USA	1995-2000		(Ellis *et al.* 2012)
	Solidago missouriensis	1	Minnesota, USA	1984-2001	140	(Morrow & Olfelt 2003)
Boraginaceae	*Cryptantha flava*	1	Utah, USA	1997-2012	3835	(Salguero-Gómez *et al.* 2012)
Caryophyllaceae	*Silene spaldingii*	1	Montana, USA	1987-2005	179	(Lesica & Crone 2007)
Convulvulaceae	*Ipomoea*	2	Nebraska, USA	1979-1989	320	(Keeler 1991)

	leptophylla					
Dioscoreaceae	*Borderea chouardii* (*Dioscorea chouardii*)	1	Spain	1995-2002	545	(García 2003)
Dryopteridaceae	*Dryopteris carthusiana*	3	Estonia	2001-2003	510	(Rünk *et al.* 2006)
	Dryopteris dilatata	3	Estonia	2001-2003	277	(Rünk *et al.* 2006)
	Dryopteris expansa	3	Estonia	2001-2003	258	(Rünk *et al.* 2006)
Ericaceae	*Pyrola japonica*	1	Japan	2015-2017	127	R. Shefferson *unpublished data*
	Pyrola subaphylla	1	Japan	2015-2017	83	R. Shefferson *unpublished data*

Euphorbiaceae	*Euphorbia rosescens*	1	Florida, USA	2004-2008	1463	(Smith & Menges 2016)
Fabaceae	*Astragalus scaphoides*	2	Montana & Idaho, USA	1986-1993	>375	(Lesica 1995)
	Crotalaria avonensis	1	Florida, USA	1998-2014	803	(Menges *et al.* 2016)
	Lathyrus vernus	6	Sweden	1988-1991; 1988-1995	2599	(Ehrlén 1995; Ehrlén & Van Groenendael 2001; Ehrlén 2002)
Gentianaceae	*Gentiana pneumonanthe*	6	Netherlands	1987-1991		(Oostermeijer *et al.* 1994)

Liliaceae	*Calochortus lyallii*	3	British Columbia, Canada	1996-2000	2600	(Miller *et al.* 2004, 2007, 2012)
	Calochortus macrocarpus	3	British Columbia, Canada	1996-2000	1000	(Miller *et al.* 2004, 2007, 2012)
	Tulipa systola	2	Israel	1981-1985	500	(Boeken 1991)
Lythraceae	*Lythrum salicaria*	2	Québec, Canada	1995-1997		(Lacroix 2004)
Melanthiaceae	*Trillium grandiflorum*	9	Wisconsin, USA	1997-2000	2004	(Rooney & Gross 2003)
		12	Pennsylvania, USA	1998-2002; 1999-2002	547	(Knight 2003)

	Trillium ovatum	3	Montana, USA	2001-2009		COMPADRE Database
Ophioglossaceae	*Botrychium australe*	1	New Zealand	1987-1993	117	(Kelly 1994)
	Botrychium campestre	≥1	USA	1987-1993		(Reintal *et al.* 2010)
	Botrychium gallicomontanum	≥1	USA	1987-1993		(Reintal *et al.* 2010)
	Botrychium hesperium	1	Alberta, Canada	1989-1994	250	(Lesica & Ahlenslager 1996)
	Botrychium matricariifolium	1	Belgium	1986-1990	56	(MULLER 1993)
	Botrychium paradoxum	1	Alberta, Canada	1989-1994	100	(Lesica & Ahlenslager 1996)

	Botrychium simplex	≥1	USA	1987-1993		(Reintal *et al.* 2010)
	Botrychium watertonense	1	Alberta, Canada	1989-1994	25	(Lesica & Ahlenslager 1996)
	Sceptridium dissectum	5	Pennsylvania, USA	1977-1988	300	(Montgomery 1990)
Orchidaceae	*Caladenia amoena*	1	Victoria, Australia	1996-2007	80	(Tremblay *et al.* 2009)
	Caladenia argocalla	1	South Australia, Australia	2003-2007	429	(Tremblay *et al.* 2009)
	Caladenia clavigera	1	Victoria, Australia	1997-2007	6	(Tremblay *et al.* 2009)
	Caladenia elegans	1	Western Australia,	1998-2002	22	(Tremblay *et al.* 2009)

			Australia			
	Caladenia graniticola	1	Western Australia, Australia	2004-2007	18	(Tremblay *et al.* 2009)
	Caladenia macroclavia	1	South Australia, Australia	2001-2007	98	(Tremblay *et al.* 2009)
	Caladenia oenochila	1	Victoria, Australia	1997-2007	22	(Tremblay *et al.* 2009)
	Caladenia orientalis	2	Victoria, Australia	2000-2008; 2002-2008	186	(Coates & Duncan 2009)
	Caladenia rosella	1	Victoria, Australia	2003-2007	17	(Tremblay *et al.* 2009)
	Caladenia valida	1	Victoria, Australia	2000-2007	188	(Tremblay *et al.* 2009)
	Calypso bulbosa	5	Finland	2002-2010	307	(Jäkäläniemi &

						Tuomi 2017; Metsähallitus 2017)
	Cephalanthera damasonium	1*	France	2006-2008	657	(Shefferson *et al.* 2016)
	Cephalanthera longifolia	3	Estonia	2002-2008	142	(Shefferson *et al.* 2005, 2012)
		1*	Estonia	1992-2005	36	(Shefferson *et al.* 2016)
	Cephalanthera rubra	1	Estonia	1994-2007	31	T. Kull *unpublished data*
	Cleistesiopsis bifaria	2	W. Virginia and Florida, USA	1983-1996	695	(Gregg & Kéry 2006)
		2	North Carolina, USA	1985-1992; 1991-1998	118	(Gregg 1991); K. Gregg *unpublished*

						data
	Cleistesiopsis divaricata	2	North Carolina, USA	1985-1992; 1991-1998	136	(Gregg 1991); K. Gregg *unpublished data*
	Coeloglossum viride (*Dactylorhiza viridis*)	1	Netherlands	1989-1995	161	(Willems & Melser 1998)
	Corallorhiza odontorhiza	1	Maryland, USA	1998-2008	2042	(Shefferson *et al.* 2011)
	Corallorhiza trifida	1	Spain	2001-2006		(Salguero-Gómez *et al.* 2015)
	Cyclopogon cranichoides	1	Florida, USA	1986-1989	36	(Calvo 1990)
	Cyclopogon luteoalbus	2	Veracruz, Mexico	2006-2009	891	(Juárez *et al.* 2014)

	Cypripedium acaule	3	Massachusetts, USA	1984-1994; 1984-1991	627	(Primack & Stacy 1998)
	Cypripedium × andrewsii	1	Illinois, USA	1994-2017	16	R. Shefferson *unpublished data*
	Cypripedium calceolus	3	Poland	1989-2000	391	(Brzosko 2002; Nicolè *et al.* 2005)
		2	Estonia	2002-2008	106	(Shefferson *et al.* 2005, 2012)
		3	Finland	2000-2016	273	(Metsähallitus n.d.; Jäkäläniemi *et al.* 2017)
		1	Spain	1994-2002	567	(García *et al.* 2002)
	Cypripedium candidum	1	Illinois, USA	1994-2017	119	(Shefferson 2006; Shefferson & Simms 2007), R.

						Shefferson *unpublished data*
		1	New York, USA	1986-1990	970	(Falb & Leopold 1993)
	Cypripedium fasciculatum	29	Oregon, USA	1996-2007	892	(Thorpe *et al.* 2011)
	Cypripedium parviflorum	1	Illinois, USA	1994-2017	1472	(Shefferson *et al.* 2001, 2003; Shefferson & Simms 2007; Shefferson *et al.* 2014)
	Cypripedium reginae	2	W. Virginia, USA	1993-2003; 1989-1999	356	(Kéry & Gregg 2004)
	Dactylorhiza	1	Norway	1981-2013	296	Sletvold, Moen &

	cruenta					Øien *unpublished data*
	Dactylorhiza incarnata	1	Sweden	1944-1971	33	(Tamm 1972)
		1	Norway	1983-2013	472	Sletvold, Moen & Øien *unpublished data*
	Dactylorhiza lapponica	2	Norway	1981-2013	1407	(Sletvold *et al.* 2013), Sletvold, Moen & Øien *unpublished data*
		1	Norway	1999-2001	399	(Øien & Pedersen 2005)
	Dactylorhiza maculata	2	Norway	1981-2013	246	Sletvold, Moen & Øien *unpublished*

						data
	Dactylorhiza sambucina	2	Sweden	1942-1971; 1943-1971	128	(Tamm 1972)
		1	Czech Republic	1999-2012	439	J. Jersakova *unpublished data*
	Epipactis albensis	1	Czech Republic	1979-1993	833	(Rydlo 1995)
	Epipactis atrorubens	2	Finland	2000-2008	332	(Jäkäläniemi *et al.* 2011)
	Epipactis helleborine	1	Canada	1985-2004	1591	(Light & MacConaill 2006)
	Gymnadenia conopsea	2	England	1977-1997	8145	M. Hutchings *unpublished data*
		2	Norway	1981-2013	513	Sletvold, Moen & Øien *unpublished data*

	Herminium monorchis	1	England	1966-1995	?	(Wells *et al.* 1998)
	Himantoglossum hircinum	1	Germany	1976-2001	2900	(Pfeifer *et al.* 2006)
	Isotria medeoloides	5	SE. USA	1979-1984	300	(Mehrhoff 1989)
		2	Virginia, USA	2008-2015	359	M. McCormick *unpublished data*
	Liparis lilifolia	1	Maryland, USA	1986-1990	40	(Whigham & O'Neill 1991)
		1	West Virginia, USA	2008-2014	247	K. Gregg *unpublished data*
	Liparis loeselii	1	England	1983-1990	517	(Wheeler *et al.* 1998)
	Listera ovata (*Neottia ovata*)	1	Sweden	1944-1971	79	(Tamm 1972)

	Listera smallii	1	West Virginia, USA	2008-2014	397	K. Gregg *unpublished data*
	Malaxis monophyllos	1	Sweden			(Elveland 1993)
	Malaxis unifolia	1	West Virginia, USA	2008-2014	113	K. Gregg *unpublished data*
	Neotinea tridentata	1	Czech Republic	1997-2009	865	M. Dostalik *unpublished data*
	Neotinea ustulata	6	Estonia	1993-2004	1013	(Shefferson & Tali 2007)
	Neottia nidus-avis	1	Estonia	1984-1989	14	(Kull & Tuulik 1994)
	Ophrys apifera	1	England	1979-1989	468	(Wells & Cox 1991)
	Ophrys insectifera	1	Netherlands	1996-2005		(Dorland &

						Willems 2002)
	Ophrys sphegodes	1	England	1975-2006	3681	(Hutchings 1987a, b, 2010)
	Orchis mascula	1	Sweden	1943-1956	52	(Tamm 1972)
	Orchis militaris	1	England	1977-1995	100	(Hutchings *et al.* 1998)
	Orchis morio (*Anacamptis morio*)	1	England	1978-1995	103	(Wells *et al.* 1998)
	Orchis purpurea	2	Belgium	2003-2013	689	H. Jacquemyn *unpublished data*
		2	Belgium	2003-2009	592	(Jacquemyn *et al.* 2010)
	Orchis simia	1	Netherlands	1972-1981	57	(Willems 1982)
	Platanthera bifolia	2	Poland	1996-2001; 1996-2008	750	(Brzosko 2003); E. Brzosko

						unpublished data
		1	Czech Republic	2001-2006	52	J. Jersakova *unpublished data*
	Platanthera ciliaris	1	West Virginia, USA	1983-1986	62	(Gregg 1990)
	Platanthera praeclara	3	Minnesota, USA	1985-2015; 1995-2015	612	(Sather & Anderson 2010); MN Dept. of Natural Resources (*unpublished data*)
	Pogonia japonica	3	Japan	2001-2003		(Tatarenko & Kondo 2006)
		4	Primorskiy Kraj, Russia	1984-1986		(Tatarenko & Kondo 2006)
	Prasophyllum	1	Australia	1992-2003	124	(Coates *et al.*

	correctum					2006)
	Spiranthes delitescens	2	USA	1983-1989	196	(McClaran & Sundt 1992)
	Spiranthes spiralis	1	England	1962-1965	559	(Wells 1967)
Orobanchaceae	*Castilleja mollis*	2	California, USA	1995-2006	3500	(McEachern *et al.* 2009)
Polygonaceae	*Eriogonum longifolium* var. *gnaphalifolium*	7	Florida, USA	1990-2013	2067	(Satterthwaite *et al.* 2002)E. Menges *unpublished data*
Ranunculaceae	*Actaea elata*	2	British Columbia, Canada	2005-2007		(Mayberry & Elle 2010)

		3	Oregon, USA	1992-1997		(Kaye & Pyke 2003)
	Anemone americana	1	Georgia, USA	1999-2006	3873	(Shefferson *et al.* 2014)
	Callianthemum miyabeanum	5	Hokkaido, Japan	2001-2004	522	(Nishikawa *et al.* 2005)
	Delphinium gypsophilum	1	California, USA	1941-1952 (or longer)		(Epling & Lewis 1952)
	Delphinium parishii	1	California, USA			(Epling & Lewis 1952)

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Table S2. Strength of factors determining life history costs, mean life expectancy, mean proportion dormant, and maximum years of dormancy. Here, the strength of each factor (column) is given as the summed Akaike weight of models incorporating that factor in the model selection table resulting from general mixed modeling of the response term listed for each row. Bold indicates factors in the best-fit model for each response term, and asterisks indicate factors in the best-fit model that were lacking in equally parsimonious models (those with ΔAICc ≤ 2.0). Blanks indicate that the factor was not tested for that response term.

Response	**Absolute latitude**	**Annual precipitation**	**Annual temperature**	**Perennating structure**	**Nutrition**	**Mean life expectancy**	**Study duration**
Reproductive cost	**0.630***	**0.748***	0.345	0.198	0.136	0.250	0.347
Sprouting cost	**0.845**	**0.993**	0.451	0.083	**0.340***	0.367	**0.709***
Growth cost	**0.466***	0.315	**0.644***	**0.997**	0.218	0.341	0.349
Size cost	**0.827**	**0.628**	0.308	0.255	0.218	**0.634**	**0.605**
Dormancy cost	0.261	0.316	0.249	0.116	0.223	0.248	**0.605***
Mean life expectancy	0.362	< 0.001	< 0.001	**0.986**	**0.964**		**0.431***

Mean proportion dormant	0.028	< 0.001	0.056	**0.550***	**0.525***	0.008	0.060
Maximum years dormant	**0.370***	**0.603***	0.271	**0.713**	0.160	0.299	**0.999**

Response	**Study duration**	**Sample size**	**Reproductive costs**	**Sprouting costs**	**Continent**	**Longitude | continent**
Reproductive cost	0.347	**0.987**				
Sprouting cost	**0.709***	**0.999**				
Growth cost	0.349	**0.736**				
Size cost	**0.605**	0.589				
Dormancy cost	**0.605***	0.257				
Mean life expectancy	**0.431***	< 0.001	0.326	**0.960**	0.264	0.036
Mean proportion	0.060	0.003	0.143	**0.999**	0.239	0.023

dormant						
Maximum years dormant	**0.999**	0.501	0.246	**0.999**	0.255	0.164

Table S3. Model selection table showing the characteristics of the top ten mixed models describing the presence of reproductive costs. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of reproductive costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Mean life expectancy**
1	-0.469	0.059	-0.002			
2	2.902		-0.003			
3	2.393		-0.003			
4	-3.624	0.089				
5	-4.050	0.110	-0.002	0.133		
6	-0.009	0.044	-0.002			

7	-6.938	0.137		0.122		
8	-0.486	0.068	-0.002		+	
9	3.158		-0.002	-0.051		
10	-0.443	0.061	-0.002			-0.008

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	0.005		5	119.150	0	0.082
2	0.005		4	119.572	0.422	0.067
3	0.004		5	119.616	0.466	0.065
4	0.004		4	119.962	0.812	0.055
5	0.004	0.133	6	120.182	1.032	0.049
6	0.004		6	120.543	1.393	0.041
7	0.004	0.122	5	121.021	1.871	0.032

8	0.004		7	121.207	2.057	0.029
9	0.005	-0.051	5	121.213	2.063	0.029
10	0.005		6	121.303	2.153	0.028

Table S4. Model selection table showing the characteristics of the top ten mixed models describing the presence of sprouting costs. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of sprouting costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Nutritional mode**
1	100.735	-2.095	-0.044		+
2	119.682	-1.664	-0.024	-2.073	
3	132.618	-1.960	-0.027	-2.058	
4	86.511	-1.478	-0.045		+
5	59.690	-0.612	-0.028		
6	100.281	-1.327	-0.038		
7	173.911	-2.645	-0.058		

8	50.457		-0.072	3.589	
9	83.009	-1.060	-0.020	-1.049	
10	64.823	-0.765	-0.026		

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		0.282	1.468	8	44.970	0	0.162
2	-0.253	0.037	0.712	8	45.631	0.660	0.116
3		0.060	0.807	7	45.780	0.809	0.108
4	-0.275	0.206	1.198	9	46.692	1.722	0.068
5		0.233		5	46.826	1.856	0.064
6		0.124	0.561	6	47.064	2.093	0.057
7	-0.384	0.165	1.695	7	47.216	2.246	0.053
8		0.271		5	47.660	2.690	0.042

9		0.093		6	47.953	2.982	0.036
10	-0.048	0.120		6	48.910	3.939	0.023

Table S5. Model selection table showing the characteristics of the top ten mixed models describing the presence of growth costs. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of growth costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**
1	8.863	-0.118		-0.274	+	
2	7.448	-0.106	0.001	-0.282	+	
3	8.324	-0.121		-0.269	+	
4	1.236			-0.058	+	
5	0.472		0.001	-0.111	+	
6	0.502				+	

7	8.045	-0.103		-0.247	+	
8	1.551			-0.061	+	
9	-0.158				+	
10	9.038	-0.121		-0.280	+	+

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		0.001		7	98.057	0	0.076
2		0.001		8	99.361	1.304	0.040
3		0.001	0.037	8	99.444	1.387	0.038
4		0.001		6	99.513	1.456	0.037
5		0.001		7	99.567	1.510	0.036
6		0.001		5	99.842	1.785	0.031
7	-0.031	0.001		8	99.922	1.865	0.030

8	-0.053	0.001		7	100.062	2.005	0.028
9		0.001	0.043	6	100.343	2.286	0.024
10		0.001		9	100.548	2.491	0.022

Table S6. Model selection table showing the characteristics of the top ten mixed models describing the presence of size costs. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of size costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**
1	10.789	0.679	-0.014			
2	6.892	0.721	-0.014			
3	4.853	0.766	-0.013	0.197		
4	-2.002	0.061				
5	-1.594	0.065			+	+
6	-1.559	0.066			+	
7	-2.385	0.078				

8	10.048	0.679	-0.013			+
9	10.251	0.690	-0.014		+	
10	-4.190	0.999	-0.015	0.181		

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	-0.473		-0.654	6	112.110	0	0.203
2	-0.460	0.001	-0.639	7	113.590	1.480	0.097
3	-0.480		-0.660	7	114.114	2.004	0.074
4		0.001		4	115.644	3.535	0.035
5		0.001		8	116.181	4.072	0.026
6		0.001		6	116.509	4.400	0.022
7	-0.033	0.001		5	116.559	4.450	0.022
8	-0.466		-0.642	8	116.702	4.592	0.020

9	-0.480		-0.656	8	116.760	4.651	0.020
10	-0.535	0.002	-0.775	8	117.232	5.122	0.016

Table S7. Model selection table showing the characteristics of the top ten mixed models describing the presence of dormancy costs. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of dormancy costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Nutritional mode**	**Mean life expectancy**
1	5.009					
2	8.705					
3	4.294		0.001			
4	4.702					
5	5.132					-0.024
6	4.896			0.009		
7	5.003	0.0002				

8	6.857		0.003			
9	0.939				+	
10	6.617	0.049				

Model #	Sample size	Study duration	df	AICc	ΔAICc	AICc weight
1		0.266	3	49.742	0	0.095
2			2	51.025	1.283	0.050
3		0.244	4	51.842	2.100	0.033
4	0.0002	0.282	4	51.843	2.100	0.033
5		0.272	4	51.898	2.156	0.032
6		0.266	4	51.935	2.193	0.032
7		0.266	4	51.939	2.196	0.032
8			3	52.078	2.335	0.030

9		0.186	5	52.111	2.369	0.029
10			3	52.944	3.202	0.019

Table S8. Model selection table showing the characteristics of the top ten mixed models describing mean life expectancy from germination. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Mean life expectancy was treated as a continuous Gaussian variable under an identity link, and species was included as a random factor in all models.

Model #	**Intercept**	**Abs latitude**	**Perennating structure**	**Nutritional mode**	**Sprouting cost**	**Reproductive cost**
1	4.072		+	+	-2.349	
2	-2.535	0.186	+	+	-2.277	
3	6.721		+	+	-2.010	
4	4.169		+	+	-2.298	-0.166
5	-2.474	0.187	+	+	-2.206	-0.243
6	4.021		+	+	-2.308	

7	6.330		+	+	-1.952	
8	6.825		+	+	-1.948	-0.208
9	-2.535	0.186	+	+	-2.277	
10	4.119		+	+	-2.251	-0.179

Model #	**Study duration**	**Continent**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	0.160		9	709.974	0	0.172
2			9	710.362	0.387	0.142
3			8	711.226	1.252	0.092
4	0.159		10	711.547	1.572	0.079
5			10	711.767	1.793	0.070
6	0.153	+	10	712.089	2.115	0.060
7		+	9	712.416	2.441	0.051

8			9	712.635	2.661	0.046
9		+	10	712.702	2.727	0.044
10	0.152	+	11	713.685	3.711	0.027

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Table S9. Model selection table showing the characteristics of the top ten mixed models describing the mean proportion of individuals dormant in a population (logit-transformed). Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	**Intercept**	**Perennating structure**	**Nutritional mode**	**Sprouting cost**	**Reprod. cost**	**Continent**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	-3.242	+	+	1.666			8	306.981	0	0.161
2	-3.402	+		1.685			6	307.259	0.278	0.140
3	-3.078		+	1.641			6	307.538	0.558	0.122
4	-3.186			1.666			4	307.667	0.687	0.114
5	-3.242	+	+	1.666		+	9	309.304	2.324	0.050
6	-3.402	+		1.685		+	7	309.504	2.523	0.046
7	-3.078		+	1.641		+	7	309.784	2.803	0.040

8	-3.186			1.666		+	5	309.838	2.857	0.039
9	-3.177	+	+	1.689	-0.106		9	310.727	3.747	0.025
10	-3.333	+		1.710	-0.119		7	310.811	3.830	0.024

Table S10. Model selection table showing the characteristics of the top ten mixed models describing the maximum observed duration of dormancy in a population. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Sprouting cost**	**Sample size**
1	0.728	-0.014	-0.001		+	0.957	
2	-0.396				+	1.087	
3	-0.157		-0.0002		+	1.066	
4	-0.145		-0.0003		+	1.023	0.00007
5	0.636	-0.012	-0.0005		+	0.931	0.00006

6	-0.393				+	1.044	0.00007
7	-0.215		-0.0004	0.019	+	1.019	
8	-0.044		-0.0004		+	0.969	
9	-0.027		-0.0004		+	0.925	0.0001
10	-0.767				+	0.999	0.0001

Model #	**Study duration**	**Continent**	**Longitude | Continent**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	0.043			8	482.369	0	0.031
2	0.038			6	483.010	0.642	0.023
3	0.038			7	483.106	0.737	0.022
4	0.037			8	483.206	0.838	0.021
5	0.042			9	483.253	0.884	0.020

6	0.038			7	483.298	0.929	0.020
7	0.042			8	483.686	1.318	0.016
8	0.040	+		8	483.803	1.435	0.015
9	0.040	+		9	483.901	1.532	0.014
10	0.046		+	10	484.406	2.037	0.011

Table S11. Model selection table showing the characteristics of the top ten mixed models describing the presence of reproductive costs in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of reproductive costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Mean life expectancy**
1	-1.146	0.064	-0.002			
2	-4.309	0.094				
3	2.208		-0.003			
4	2.913		-0.003			
5	-0.732	0.063	-0.002			-0.045

6	3.334		-0.002	-0.112		
7	-0.544	0.048	-0.002			
8	-1.681	0.068	-0.002		+	
9	-4.070	0.094				-0.035
10	3.322		-0.003			-0.048

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	0.004		5	70.571	0.000	0.068
2	0.003		4	71.333	0.762	0.046
3	0.004	0.073	5	71.388	0.818	0.045
4	0.005		4	71.752	1.181	0.037
5	0.005		6	71.760	1.189	0.037
6	0.005		5	72.024	1.454	0.033

7	0.004	0.038	6	72.377	1.807	0.027
8	0.005		6	72.663	2.093	0.024
9	0.004		5	72.672	2.101	0.024
10	0.005		5	72.838	2.267	0.022

Table S12. Model selection table showing the characteristics of the top ten mixed models describing the presence of reproductive costs in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of reproductive costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutrition**
1	-37.962	1.424			+	
2	-47.461	1.805	0.023	-1.540	+	
3	-31.720	1.376			+	
4	-55.529	1.616	0.009		+	
5	-34.562	1.737		-0.580	+	

6	-49.123	1.597	0.008		+	
7	-61.357	2.282	0.025	-1.437	+	
8	-33.247	1.887		-0.597	+	
9	-37.632	1.409			+	
10	-37.920	1.423			+	+

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		0.005		6	43.930	0.000	0.081
2		0.006		8	44.385	0.455	0.065
3		0.005	-0.319	7	44.437	0.507	0.063
4		0.004		7	44.525	0.595	0.060
5		0.008		7	45.945	2.015	0.030
6		0.004	-0.271	8	46.010	2.080	0.029

7		0.007	-0.262	9	46.213	2.283	0.026
8		0.008	-0.330	8	46.447	2.517	0.023
9	0.016	0.005		7	46.508	2.578	0.022
10		0.005		7	46.510	2.580	0.022

Table S13. Model selection table showing the characteristics of the top ten mixed models describing the presence of sprouting costs in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of sprouting costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**
1	48.979	-0.605	-0.008	-1.319		
2	52.135	-0.669	-0.007	-1.547		+
3	62.090	-0.807	-0.012	-1.517		
4	75.052	-1.016	-0.013	-1.963		+
5	48.593	-0.590	-0.008	-1.341		
6	48.373	-0.605	-0.008	-1.366	+	

7	50.274	-0.657	-0.007	-1.569	+	+
8	53.817	-0.674	-0.007	-1.611		+
9	60.007	-0.770	-0.011	-1.508		
10	60.048	-0.787	-0.012	-1.526	+	

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		0.024		6	34.710	0.000	0.181
2		0.024		8	35.342	0.632	0.132
3		0.023	0.214	7	36.095	1.385	0.090
4		0.022	0.333	9	36.563	1.852	0.072
5	-0.053	0.023		7	36.643	1.933	0.069
6		0.028		7	36.879	2.169	0.061
7		0.027		9	37.725	3.015	0.040

8	-0.053	0.024		9	37.770	3.059	0.039
9	-0.045	0.022	0.192	8	38.286	3.576	0.030
10		0.027	0.205	8	38.452	3.742	0.028

315 **Table S14.** Model selection table showing the characteristics of the top ten mixed models describing the presence of sprouting costs in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of sprouting costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Nutritional mode**
1	250.668	-4.642			
2	420.385				
3	409.697	-6.572		-6.198	
4	216.754	-3.687			
5	252.330	-4.662	-0.001		
6	231.741	-4.330			

7	251.143	-4.654			
8	250.969	-4.648			+
9	98.388				
10	41.369				

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1				2	4.214	0.000	0.086
2	-25.953			2	4.214	0.000	0.086
3				3	6.436	2.222	0.028
4	-1.325			3	6.436	2.222	0.028
5				3	6.436	2.222	0.028
6		0.010		3	6.436	2.222	0.028
7			-0.001	3	6.436	2.222	0.028

8				3	6.436	2.222	0.028
9	-8.140		6.168	3	6.436	2.222	0.028
10	-4.282	0.175		3	6.436	2.222	0.028

Table S15. Model selection table showing the characteristics of the top ten mixed models describing the presence of growth costs in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of growth costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Mean life expectancy**
1	1.492					
2	1.256					
3	1.701					-0.028
4	1.095					
5	1.705				+	

6	2.193	-0.013				
7	1.201		0.000			
8	1.476			0.002		
9	1.440					-0.024
10	1.402				+	

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1			2	50.999	0.000	0.090
2	0.001		3	51.821	0.822	0.060
3			3	52.784	1.786	0.037
4		0.026	3	52.810	1.812	0.036
5			3	52.943	1.944	0.034
6			3	53.102	2.103	0.031

7			3	53.155	2.156	0.031
8			3	53.270	2.271	0.029
9	0.001		4	53.863	2.864	0.022
10	0.001		4	54.074	3.075	0.019

Table S16. Model selection table showing the characteristics of the top ten mixed models describing the presence of growth costs in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of growth costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**
1	2.981				+	
2	2.977				+	
3	2.904				+	+
4	2.627				+	
5	3.055	-0.004			+	

6	2.791			0.008	+	
7	2.849		0.000		+	
8	4.129		-0.001		+	
9	4.164			-0.044	+	
10	2.747	0.016			+	

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	-0.599	0.002		5	42.598	0.000	0.130
2	-0.503			4	43.327	0.730	0.090
3	-0.586	0.002		6	45.379	2.781	0.032
4	-0.580	0.002	0.017	6	45.382	2.784	0.032
5	-0.592	0.002		6	45.401	2.803	0.032
6	-0.593	0.002		6	45.401	2.803	0.032

7	-0.593	0.002		6	45.401	2.803	0.032
8	-0.590			5	45.633	3.036	0.029
9	-0.568			5	45.777	3.179	0.027
10	-0.552			5	45.858	3.260	0.026

Table S17. Model selection table showing the characteristics of the top ten mixed models describing the presence of size costs within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of size costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**
1	79.837	6.322	-0.122			
2	167.930	4.795	-0.130	-3.170		
3	88.855	4.738	-0.096		+	
4	97.156	5.326	-0.107			+
5	7.043		-0.004	-0.181		
6	9.673		-0.004	-0.355		
7	49.720		-0.025			

8	5.903		-0.005			
9	6.877		-0.005		+	
10	38.155		-0.017	-0.374		

Model #	**Mean life expectancy**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	-4.619		-7.629	6	41.391	0.000	0.636
2	-4.654		-6.588	7	45.390	3.998	0.086
3	-4.822		-6.127	7	46.211	4.819	0.057
4	-4.799		-6.895	8	47.370	5.979	0.032
5	-0.123	0.006		6	48.515	7.124	0.018
6	-0.158	0.009	-0.119	7	48.669	7.277	0.017
7	-0.565			4	49.632	8.240	0.010
8	-0.121	0.006		5	49.802	8.411	0.009

9	-0.098	0.004			6	50.397	9.005	0.007
10	-0.491				5	50.587	9.195	0.006

Table S18. Model selection table showing the characteristics of the top ten mixed models describing the presence of size costs outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of size costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutritional mode**	**Mean life expectancy**
1	-5.436			0.449			0.250
2	-21.524	0.379	0.012			+	
3	-58.779	0.896	0.012	1.088			
4	-59.609	1.077	0.031		+		
5	-12.304	0.111		0.614			0.230
6	-39.411	0.611	0.007	0.647			
7	-47.081	0.877	0.022			+	-0.267

8	-40.825	0.649	0.012	0.561		+	
9	-5.299		0.001	0.408			0.244
10	-5.477			0.450		+	0.251

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	0.002	-0.292	6	54.853	0.000	0.104
2	0.003	-0.318	7	55.379	0.527	0.080
3	0.004	-0.245	7	55.556	0.703	0.073
4	0.004	-0.703	8	56.052	1.199	0.057
5	0.002	-0.266	7	57.171	2.319	0.033
6	0.002		6	57.246	2.393	0.031
7	0.003	-0.326	8	57.260	2.407	0.031
8	0.003	-0.308	8	57.354	2.501	0.030

9	0.002	-0.294	7	57.569	2.716	0.027
10	0.002	-0.291	7	57.623	2.771	0.026

Table S19. Model selection table showing the characteristics of the top ten mixed models describing the presence of dormancy costs in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of dormancy costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Mean life expectancy**
1	0.316		0.008	-0.468		
2	-0.971		0.007	-0.422		
3	-2.158		0.007	-0.391		
4	-18.935	0.209	0.011			
5	-5.213	0.074	0.010	-0.440		
6	-0.176		0.008	-0.502		0.021

7	0.595		0.007	-0.466	+	
8	0.313		0.008	-0.467		
9	0.847					
10	-1.838		0.008	-0.474		0.036

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1			4	35.225	0.000	0.087
2		0.105	5	35.931	0.707	0.061
3	-0.001	0.206	6	36.934	1.709	0.037
4	-0.001	0.267	6	36.997	1.772	0.036
5			5	37.286	2.062	0.031
6			5	37.523	2.299	0.028
7			5	37.656	2.431	0.026

8	< 0.001		5	37.704	2.479	0.025
9		0.136	3	37.938	2.713	0.023
10		0.115	6	38.044	2.819	0.021

Table S20. Model selection table showing the characteristics of the top ten mixed models describing the presence of dormancy costs in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. The presence of dormancy costs was a binomial variable under a logit link, and species was included as the sole random factor.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Nutritional mode**	**Mean life expectancy**	**Sample size**
1	-86.262						
2	753.989	-11.674	-0.297				
3	-60.362		-0.267	22.852			
4	252.235	-4.678			+		
5	-57.402		-0.035				
6	-66.457						0.094

7	-86.264					0.002	
8	-83.730				+		
9	-80.778			-0.788			
10	-92.081	0.118					

Model #	Study duration	df	AICc	ΔAICc	AICc weight
1	21.597	2	4.333	0.000	0.098
2		3	6.686	2.352	0.030
3		3	6.686	2.352	0.030
4		3	6.686	2.352	0.030
5	18.046	3	6.686	2.352	0.030
6	11.304	3	6.686	2.352	0.030
7	21.595	3	6.686	2.352	0.030

8	21.067	3	6.686	2.352	0.030
9	22.131	3	6.686	2.352	0.030
10	21.576	3	6.686	2.352	0.030

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Table S21. Model selection table showing the characteristics of the top ten mixed models describing mean life expectancy from germination in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Mean life expectancy was treated as a continuous Gaussian variable under an identity link, and species was included as a random factor in all models.

Model #	**Intercept**	**Perennating structure**	**Nutritional mode**	**Sprouting cost**	**Reproductive cost**	**Study duration**
1	1.952	+	+	-1.526	-1.095	0.156
2	1.926	+		-1.550	-1.108	0.157
3	1.669	+	+	-1.838		0.147
4	4.495	+	+	-1.430		
5	4.809		+	-1.451		
6	4.807	+	+	-1.199	-0.765	

7	5.108		+	-1.209	-0.797	
8	1.537	+		-1.870		0.151
9	2.965		+	-1.506	-1.117	0.136
10	1.043	+	+		-1.406	0.144

Model #	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	9	388.005	0.000	0.080
2	7	388.344	0.339	0.067
3	8	388.615	0.610	0.059
4	7	388.853	0.848	0.052
5	6	389.009	1.004	0.048
6	8	389.040	1.035	0.047
7	7	389.054	1.049	0.047
8	6	389.158	1.153	0.045

9	8	389.447	1.442	0.039
10	8	389.607	1.602	0.036

Table S22. Model selection table showing the characteristics of the top ten mixed models describing mean life expectancy from germination in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Mean life expectancy was treated as a continuous Gaussian variable under an identity link, and species was included as a random factor in all models.

Model #	**Intercept**	**Abs latitude**	**Perennating structure**	**Nutritional mode**	**Sprouting cost**	**Reproductive cost**
1	33.198		+	+	-26.070	
2	33.429		+	+	-26.115	-0.197
3	11.285	0.334	+	+	-18.693	
4	11.340	0.337	+	+	-18.676	-0.209
5	34.809		+		-27.681	
6	32.824		+	+	-26.162	

7	34.528			+	-27.024	
8	10.816	0.362	+		-19.471	
9	35.020		+		-27.744	-0.157
10	9.945	0.348	+	+	-18.488	

Model #	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		7	246.587	0.000	0.410
2		8	248.510	1.923	0.157
3		8	248.566	1.979	0.152
4		9	250.577	3.990	0.056
5		6	250.823	4.236	0.049
6	0.061	8	251.899	5.312	0.029
7		5	252.293	5.706	0.024

8		7	252.433	5.846	0.022
9		7	252.691	6.104	0.019
10	0.068	9	253.854	7.267	0.011

Table S23. Model selection table showing the characteristics of the top ten mixed models describing the mean proportion of individuals dormant in a population (logit-transformed) in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	Intercept	Perennating structure	Nutritional mode	Sprouting cost	Reproductive cost
1	-3.132			1.681	
2	-3.457	+		1.684	
3	-2.943		+	1.656	
4	-3.225	+	+	1.662	
5	-2.003		+	1.772	
6	-3.082			1.706	-0.105
7	-2.178	+	+	1.769	

8	-3.408	+		1.708	-0.097
9	-2.543			1.771	
10	-2.917		+	1.670	-0.057

Model #	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		4	198.805	0.000	0.171
2		5	199.024	0.219	0.153
3		6	199.252	0.447	0.137
4		7	199.760	0.955	0.106
5	-0.055	7	200.464	1.659	0.075
6		5	201.945	3.140	0.036
7	-0.053	8	202.128	3.323	0.033
8		6	202.269	3.464	0.030

9	-0.043	5	202.507	3.702	0.027
10		7	202.659	3.854	0.025

Table S24. Model selection table showing the characteristics of the top ten mixed models describing the mean proportion of individuals dormant in a population (logit-transformed) in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	**Intercept**	**Perennating structure**	**Nutritional mode**	**Sprouting cost**	**Reproductive cost**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	-3.065	+		1.488		6	101.167	0.000	0.275
2	-3.018			1.325		4	102.154	0.987	0.168
3	-3.173	+	+	1.600		7	102.197	1.030	0.164
4	-3.018		+	1.363		5	103.536	2.369	0.084
5	-2.915	+		1.449	-0.114	7	104.932	3.765	0.042
6	-2.863			1.289	-0.155	5	105.397	4.230	0.033
7	-2.976	+	+	1.566	-0.172	8	105.561	4.394	0.031

8	-1.842					3	105.888	4.721	0.026
9	-2.825		+	1.337	-0.194	6	106.475	5.308	0.019
10	-1.544	+				5	106.570	5.403	0.018

Table S25. Model selection table showing the characteristics of the top ten mixed models describing the maximum observed duration of dormancy in a population in species within the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Sprouting cost**	**Reproductive cost**
1	-0.443				+	1.087	
2	-0.159					1.085	
3	-0.006	-0.010			+	1.097	
4	-0.645			0.018	+	1.119	
5	-0.253		0.001		+	1.043	

6	0.385	-0.013				1.099	
7	0.777	-0.017	< 0.001		+	1.009	
8	-0.460				+	1.062	0.077
9	-0.418			0.022		1.123	
10	-0.443				+	1.080	

Model #	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1		0.039	5	296.665	0.000	0.075
2		0.033	4	297.791	1.126	0.043
3		0.042	6	298.147	1.482	0.036
4		0.042	6	298.285	1.620	0.033
5		0.039	6	298.626	1.961	0.028

6		0.038	5	298.642	1.977	0.028
7		0.043	7	298.796	2.131	0.026
8		0.038	6	298.924	2.259	0.024
9		0.036	5	299.028	2.363	0.023
10	0.001	0.039	6	299.028	2.363	0.023

425 **Table S26.** Model selection table showing the characteristics of the top ten mixed models describing the maximum observed duration of dormancy in a population in species outside of the Orchidaceae. Models are arranged in decreasing explanatory power, beginning with the best-fit model (model 1). Numbers under factors indicate slope coefficients. The + sign indicates that the model included the categorical variable indicated (perennating structure or nutritional mode). Blanks indicate that the term was not included in that model. Species was included as a random factor in all models.

Model #	**Intercept**	**Abs latitude**	**Annual precipitation**	**Mean annual temperature**	**Perennating structure**	**Nutrition**	**Mean life expectancy**
1	-0.125				+	+	
2	-0.343				+	+	
3	-0.901				+	+	0.018
4	0.058				+	+	
5	-0.076				+	+	
6	-0.318	0.003			+	+	
7	-0.088			-0.005	+	+	

8	-0.087		0.001		+	+	
9	-0.205			-0.044			
10	-2.350	0.031					

Model #	**Sprouting cost**	**Reproductive cost**	**Sample size**	**Study duration**	**df**	**AICc**	**ΔAICc**	**AICc weight**
1	1.196				6	184.094	0.000	0.095
2	1.223			0.015	7	186.028	1.933	0.036
3	1.867				7	186.070	1.975	0.035
4	1.147	-0.161			7	186.165	2.071	0.034
5	1.140		0.001		7	186.613	2.518	0.027
6	1.279				7	186.720	2.625	0.025
7	1.242				7	186.739	2.645	0.025
8	1.204				7	186.778	2.684	0.025

9	1.277		0.001	0.065	6	187.966	3.872	0.014
10	1.538		0.001	0.072	6	188.031	3.937	0.013

SUPPLEMENTAL METHODS

Data table development: Literature search

We used Google Scholar (scholar.google.com) to search the literature for all papers documenting vegetative dormancy in any herbaceous perennial plant species. We searched for the following terms: "prolonged dormancy", "vegetative dormancy", "herbaceous perennial", and "geophyte". We then narrowed the scope of the search to include only studies that involved demographic monitoring, and finally searched manually for all papers documenting dormancy. We also included reviews of dormancy, most notably Lesica and Steele (1994), Shefferson (2009), and Reintal et al. (2010), and papers cited therein. From the final list of papers, we gathered descriptive (non-numerical) information about the species studied, as well as statistics on the studies themselves, information about the populations studied, and relationships between life history variables for each species (provided in the paragraphs below).

The empirical studies we used are highly diverse, but all share a common approach: they were all demographic studies in which the behaviour of individual plants was recorded over time by carrying out repeated censuses. We define dormancy as situations in which a plant was observed aboveground in one year, not observed in one or more subsequent years, and present aboveground in some later year. True dormancy could be confused with observer error (i.e. the plant had aboveground parts in a particular year, but the researcher did not see them or conducted the census prior to the individual's sprouting), within-year herbivory (i.e. the plant did produce aboveground parts in a particular year, but these were completely removed prior to census), or mortality followed by the recruitment of a new plant in the same location as the plant that previously died. To explore the significance of these possible causes of the absence of aboveground parts, some researchers have conducted multiple censuses within each year (Shefferson *et al.* 2001; Alexander *et al.* 2009). They have found the frequency of such sources to vary from case to case, although they are typically low. Although most studies of dormancy do not include explorations of detection error, the natural history and ease of observation of many of the species in our dataset makes it unlikely that such errors or within-year herbivory are major issues.

Species description variables. Species description variables included the species and subspecies name, subfamily and family, the dominant nutritional mode (i.e. autotrophic, mycoheterotrophic, or mixotrophic), the perennating structure (i.e. rhizome, taproot, corm, bulb, or tuber), and the presence or absence of a juvenile period prior to the seedling stage, potentially lasting longer than one year following germination (e.g. the protocorm stage in orchids).

Study description variables. Study description metrics included all of the following: the total number of plants for which there were records of behaviour in multiple years, the years in which data were collected, the study duration, the geographic coordinates (latitude and longitude) of each studied population, the country and continent in which the study took place, whether the study was experimental or observational, and the details of treatments applied if the study was experimental.

Population and individual plant variables. Population metrics were: the mean population growth rate (deterministic λ, estimated from population projection matrices), the mean life expectancy of individuals from seed germination and from the seedling stage (in some species, most notably terrestrial orchids, germination typically leads to an underground stage that can last for several years prior to the emergence of a true seedling), the observed mean (± 1 SE) percentage of the population that was dormant during the years of the study, the maximum duration (years) that the study species was observed to spend in dormancy, and various percentile lengths of dormancy (median, 75%, 90%, 95%, and 99%) observed both at the individual level and for the whole recorded population, and whether the authors assumed *a priori* a maximum dormancy duration.

Some of the population variables that we included were derived from demographic datasets and population projection matrices. Where possible, we also gathered demographic datasets or population projection matrices, including some datasets derived from published papers included in our literature review. We used these datasets in methodologically standardized demographic analyses to produce comparable data across datasets. When sufficient demographic data were not available, particularly when deterministic population growth rate and mean life expectancy were not available, we supplemented our data with matrix statistics derived from the COMPADRE database (Salguero-Gómez *et al.* 2015). We also supplemented our data with climatic data, either by recording the mean annual temperature and mean annual accumulated precipitation noted within a study, or by obtaining such data from the nearest weather station with publicly available historical climate data covering the period of the study.

Global dataset development: Analyses of individual monitoring datasets

Where data were available, we explored common influences on the probabilities of survival, sprouting, growth, flowering, and fruiting, and on the number of flowers and number of fruits produced, all of which were response terms in separate mixed models. Predictor terms included plant size (the metrics available for this differed between studies, but commonly included number of leaves, number of sprouts, or height of tallest sprout), sprouting status (emergent vs. dormant), and reproductive status (flowering vs. vegetative). Because of evidence that these characteristics can have different long- and short-term effects, we assessed the impacts of plant size, sprouting status, and reproductive status in both years *t*-1 and *t* (Shefferson *et al.* 2014). Survival was assessed as a response term from year *t* to year *t*+1, while all other response terms were assessed within year *t*+1. These seven response terms were dependent variables in general linear mixed models in which each response was tested against plant size in years *t*-1 and *t* (fixed), flowering status in years *t*-1 and *t* (fixed), and all two-way interactions between these terms. Year was included as a random factor in each global mixed model. We then conducted exhaustive model selection, reducing all independent factors down to models in which only a *y*-intercept and year were left. We developed our inferences from the best-fit model, which was the model with the lowest AICc or an equally parsimonious model (ΔAICc < 2.0) with the fewest parameters. We repeated this process twice, to test for impacts of both sprouting and growth. In the first instance, we substituted sprouting status (whether the plant sprouted in year *t*-1 and/or year *t*) for plant size, to enable us to test for the effects of sprouting status on all previously mentioned vital rates (sprouting status was correlated with plant size in many populations because we treated plants in dormancy as having a size of 0). In the second instance, we substituted growth between years *t*-1 and *t* for plant size in year *t* (where growth was the absolute difference in size between those two years per individual).

The results of general linear mixed modeling were used to infer various life history trade-offs. These trade-offs were: the costs of reproduction, costs of sprouting, costs of growth, costs of size, and costs of dormancy. In each population, qualitative relationships (positive, negative, non-significant) between each demographic variable and its predictors were determined from the sign of the effect in the best-fit model. We inferred costs of reproduction and sprouting, from observation of significant negative effects of flowering (binomial) or sprouting (binomial), respectively, in the best-fit model. For example, a cost to reproduction incurred by sprouting was indicated by a significant negative effect of sprouting (binomial) in year *t*-1 or year *t* in the best-fit model describing the probability of flowering or fruiting in year *t*+1, or in the model describing the number of flowers or fruits produced in year t+1. A cost to sprouting incurred by reproduction was indicated by a significant negative effect of flowering (binomial) in year t-1 or year t in the mixed model of the probability of sprouting in year t+1. A cost of dormancy was inferred from a significant positive effect associated with sprouting. Costs of size were inferred from significant negative effects associated with size in any vital rate, and from significant negative interactions between size in year t-1 and t in any vital rate. Finally, a cost of growth was inferred from a significant negative effect associated with growth between years t-1 and t. All analyses were performed in *R* 3.4.1 (R Core Team 2017), with mixed modelling performed using the *lme4* package (Bates, Maechler & Bolker 2012), and model selection using the *MuMIn* package in *R* (Bartoń 2014).

Where possible, we also used these mixed models to create high-resolution historical (i.e. 3yr, covering years t-1, t, and t+1) population projection matrices for each population in each year (Ehrlén 2000; Shefferson *et al.* 2014). In cases where the data were insufficient for the construction of historical matrices, or where mixed modeling suggested that historical matrices were not necessary, we created standard ahistorical matrices, in which state in year t+1 is solely a function of state in year t, using methods described by Caswell (2001). Transitions to and from dormancy were estimated *via* GLMMs, as were all other transitions, leading to the potential for biased transitions in studies with shorter durations (i.e. this bias would suggest shorter dormancy and higher mortality than is actually the case), but allowing statistical power to remain as high as possible (Shefferson *et al.* 2001, 2014). Population projection matrices were used to derive the mean deterministic population growth rate (λ), given as the dominant eigenvalue of the mean population projection matrix (Caswell 2001), and the mean life expectancy of individuals from either germination or the beginning of the seedling stage of plants in the population (Keyfitz & Caswell 2005; Steiner *et al.* 2012).

Next, we used mark-recapture methodology to estimate the mean proportion of each population that was dormant, and the lengths of all recorded instances of dormancy in each study. We estimated the mean proportion of the plants in each recorded population that were dormant over time using Cormack-Jolly-Seber (CJS) modeling in program MARK (White & Burnham 1999), in which the mean proportion that was dormant is the complement of the resighting rate, estimated in a model in which survival varied by year and the probability of resighting was constant ($\{\phi_t \, p_c\}$ in mark-recapture model notation, where ϕ refers to survival probability, p refers to resighting rate, t refers to time, and c is a constant) (Shefferson *et al.* 2001). We did not develop other models, or conduct model selection, to standardize model comparison across studies. This metric was not assumed to represent a transition probability, due to known bias in transition probability estimation *via* CJS modeling (Kéry *et al.* 2005).

Finally, we also documented every identifiable dormancy episode within each dataset. Identifiable dormancy episodes are defined as years in which an individual did not sprout occurring between years in which it was observed aboveground (i.e. the year before dormancy started and the year after it ended were both included in the period of observation). The length of each dormancy episode was recorded, and the frequency distribution of dormancy episodes was assessed both per population and per individual.

Historical matrix modelling of populations

We developed and parameterized historical matrices for the individual monitoring datasets using methods described in Ehrlén (2000) and Shefferson et al. (2014). Matrix transitions were the probabilities of transition, or rates of transition, from all possible pairs of stages in years t-1 and t, to all possible pairs of stages in years t and t+1, respectively. Transition probability values between life stages were given as:

$$a_{D,ji} = S_{ji} \times (1 - P_{ji}) \qquad (1)$$

$$a_{k(V),ji} = S_{ji} \times P_{ji} \times g_{k,ji} \times (1 - F_{k,ji}) \quad (2)$$

$$a_{k(F),ji} = S_{ji} \times P_{ji} \times g_{k,ji} \times F_{k,ji} \quad (3)$$

where $a_{k,ji}$ is the probability of transitioning to stage k in year t+1 (in individuals that became flowering or vegetative in year t+1, k refers to the size of the plant in that year), given state j in year t and state i in year t-1; S_{ji} is the probability of surviving from year t to year t+1, given state j in year t and state i in year t-1; P_{ji} is the probability of sprouting in year t+1, given survival from year t and state j in year t and state i in year t-1; $g_{k,ji}$ is the probability of growth to state k in year t+1, conditional upon survival to that time and given state j in year t and state i in year t-1; and $F_{k,ji}$ is the probability of flowering in year t+1, conditional upon survival to that point and sprouting in that year, and given state j in year t and state i in year t-1. D, V and F refer to dormancy, vegetative (i.e. non-flowering) sprouting, and flowering, respectively. When historical matrices could not be assembled, we created ahistorical matrices in which state in year t+1 was solely a function of state in year t, using methods described by Caswell (2001).

Phylogenetic analyses

First, we developed a phylogenetic tree of the 114 species in our dataset in which dormancy has been recorded, based on the Open Tree of Life (Hinchliff *et al.* 2015), using package *rotl* (Michonneau *et al.* 2016) for *R* (R Core Team 2017). To this tree we added species which, having been subject to detailed demographic study, have not revealed the capacity for dormancy. These species were obtained by filtering entries in the COMPADRE database for herbaceous perennial species monitored for ≥3 years in which adult dormancy has not been reported (Salguero-Gómez *et al.* 2015). Filtering for absence of dormancy identified 261 species. The original studies were checked for all these species to confirm that dormancy had not been recorded. Onto this tree, which included a total of 375 species, we plotted maximum recorded value for mean annual proportion dormant per population, and maximum observed duration of dormancy. Taxa with missing values for either maximum duration dormant or maximum proportion dormant were removed (this occurred only in a few cases in which published papers only reported one of these). We reconstructed ancestral character states of maximum dormancy duration and maximum proportion dormant *via* maximum likelihood with the *fastAnc* function in package *phytools* (Revell 2012) for *R* 3.3.2 (R Core Team 2017). Because both dormancy metrics were treated as continuous, we considered all proportional dormancy values below 0.04 (the minimum value observed in the literature) as zero, and rounded all predicted maximum dormancy durations down to the nearest integer. In cases where there was more than one study of a species in the dataset, we used the highest value for mean proportion of dormant plants recorded in any study of that species. We consider this value to be more representative of the species' capacity for dormancy than the mean value calculated across all studies of the species. The results were then used as a test of the common background hypothesis. Support for the hypothesis would be provided if the reconstructions indicated that dormancy had a single origin.

Finally, we investigated the possibility of phylogenetic signal in dormancy. We hypothesized that the maximum proportion of plants in dormancy and the maximum duration of dormancy would yield significant phylogenetic signal if dormancy in different species is driven by common ecological drivers, suggesting a common genetical background to its evolution. We analyzed phylogenetic signal in these two dormancy metrics using Blomberg's *K* with function *Kcalc* in package *picante* (Kembel *et al.* 2010) for *R* (R Core Team 2017). To determine significance, we ranked each value against the ordered vector of associated *K*s from 1000 random permutations of trait values on the phylogeny. Significant phylogenetic signal was inferred if the estimated *K* ranked within the highest 5% of bootstrapped *K*s. Demographic data are very sparsely distributed across the Plant Kingdom, and so we assumed that all missing species between those analyzed were capable of dormancy, rather than treating each instance of dormancy as having a unique evolutionary origin.

Mixed linear modeling of dormancy proportion and duration across taxonomy

The dataset developed was used to assess the impacts of a variety of factors on (i) the mean proportion of the plants in a population that were dormant, and (ii) the maximum length of dormancy in years. Because of the high proportion of orchid species in the dataset (55.3% of 114 species; 50.5% of 299 populations), we repeated the GLMM analysis described in the main paper (see *Statistical analyses* under **Materials and Methods**) on subsets of the dataset consisting of (a) only species in the Orchidaceae, and (b) only species from other families. As before, mixed model building and selection was performed with AICc as our criterion using packages *lme4* and *MuMIn* in R (Bartoń 2014; Bates *et al.* 2015; R Core Team 2017). The results were compared against each other, as well as against the results using the whole dataset, for inference.

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SUPPLEMENTAL RESULTS

General characteristics

We identified records of dormancy in 114 species from 24 plant families, plus a hybrid (Figure S4; Table S1). Of these, 63 species (55%) were in the family Orchidaceae, 9 species (8%) in the Ophioglossaceae, and 5 species (4%) each in the Asteraceae and Ranunculaceae. The 301 populations included in our database were monitored for a median of 8 years (range: 3-33yrs), and included a median of 148 monitored individuals per population (range: 2-6235). Population projection matrices taken from associated published studies, or constructed from original demographic datasets, incorporated a median of 7 life stages (range: 2-6335, where high dimensionality reflected the development of historical matrix models). The mean life expectancy (MLE) of monitored individuals of dormancy-prone species from germination, as estimated from available or estimated matrix models, was 11.6 ± 3.0 years across all populations (range: 1-522 years).

The proportion of plants in populations that were dormant in any year varied considerably. A mean of 16.5 ± 14.7% (± 1 SE) of the individuals in the populations were dormant per annum, with a range from 0.5% in *Orchis purpurea* (Orchidaceae) and *Borderea chouardii* (Dioscoreaceae) to 84.9% in *Corallorhiza odontorhiza* (Orchidaceae). The maximum duration of dormancy across all populations averaged 3.67 ± 0.21 years, and varied both between species and between populations within species. In 13 species (*Actaea elata*, *Anacamptis morio*, *Botrychium watertonense*, *Cephalanthera damasonium*, *Dactylorhiza viridis*, *Dioscorea chouardii*, *Lathyrus vernus*, *Platanthera ciliaris*, *Polygonatum multiflorum*, *P. odoratum*, *Pyrola japonica*, *P. subaphylla*, and *Ophrys insectifera*) from 7 families, the maximum recorded duration of dormancy was one year. *Dactylorhiza lapponica* was the only species in which some populations in the database exhibited no vegetative dormancy at all. The longest observed duration of dormancy was 18 years in *Epipactis helleborine*, followed by 15yrs in *Cypripedium parviflorum*, and 14 yrs in *Platanthera praeclara* (all Orchidaceae). In non-orchid species, the maximum proportion of plants dormant was 38% in *Allium amplectens*, and the maximum recorded duration of dormancy was 13 years in *Eriogonum longifolium*. Across all species, the standard deviation in the proportion of individuals that was dormant covaried positively with the mean proportion dormant ($F_{1,30} = 27.87$, $P < 0.0001$; Figure S5), suggesting that species with greater ability to display dormancy also show more variation in the extent of dormancy between different populations.

Comparison of Orchidaceae vs. non-Orchidaceae

Modeling the Orchidaceae and non-Orchidaceae separately in analyses of the factors determining the costs of reproduction, sprouting, growth, size, and dormancy yielded patterns that were largely consistent with those obtained from using the original models produced from using the whole dataset. The following minor differences were observed between the Orchidaceae and the non-Orchidaceae. Non-Orchidaceae exhibited differences in the presence of reproductive costs dependent on the type of perennating structure whereas members of the Orchidaceae did not. Dormancy in the Orchidaceae was sensitive to annual precipitation while in the non-Orchidaceae it was not (Tables S11 and S12). Sprouting costs were determined by precipitation and temperature in the Orchidaceae, but not in species outside this family (Tables S13 and S14). The presence of growth costs was dependent on perennating structure in the non-Orchidaceae whereas this was not the case in the Orchidaceae. Growth costs were negatively correlated with mean life expectancy in the non-Orchidaceae but there was no relationship in the Orchidaceae (Tables S15 and S16). The presence of size costs was negatively correlated with mean life expectancy and precipitation in the Orchidaceae, but positively correlated with mean life expectancy, annual temperature, and sample size in the non-Orchidaceae (Tables S17 and S18). Finally, costs of dormancy varied with both annual temperature and precipitation in the Orchidaceae, but showed no relationship with climate variables in the non-Orchidaceae (Tables S19 and S20).

Mean life expectancy, mean proportion dormant, and maximum length of dormancy were determined by similar factors between orchids and non-orchids. However, mean life expectancy was negatively correlated with the presence of reproductive costs in the Orchidaceae, but not in the non-Orchidaceae (Table S21 and S22). Whereas mean proportion of plants that were dormant was dependent on perennating structure in the non-Orchidaceae, this was not the case in the Orchidaceae (Tables S23 and S24). Finally, maximum duration of dormancy was dependent on nutritional mode in the non-Orchidaceae, but not in the Orchidaceae (Tables S25 and S26).