

## RESEARCH ARTICLE

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# Phylogenetic relatedness mediates persistence and density of soil seed banks

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## Abstract

1. Soil seed banks can strongly affect survival and expansion of plant populations by spreading mortality risks and distributing genetic diversity through time. Knowledge of the main factors regulating the ability of seeds to persist in the soil beyond the first germination season is however limited. While morphological and physiological seed traits, and the degree of environmental uncertainty are considered important in shaping the seed banking strategies of plants, global assessments that explicitly account for phylogenetic relatedness are lacking.
2. Using a global seed bank database comprising data for 2,350 angiosperms, we examined the extent to which two seed bank properties, i.e. seed bank type (transient vs. persistent) and density of viable seed banks, are determined by phylogenetic relatedness. We then tested phylogenetic correlations between these properties with seed mass and seed dormancy (dormant vs. non-dormant), and the contribution of phylogenetic relatedness relative to that of climatic and habitat-related variables in shaping seed bank properties.
3. We found significant phylogenetic signal in seed bank type and density, providing evidence that the ability to form persistent seed banks is not randomly distributed across the phylogeny. While the ability to persist in the soil was phylogenetically correlated to the production of dormant and smaller seeds, seed mass and seed dormancy per se were poor predictors of seed persistence. Interestingly, habitat-related variables (mainly disturbance and canopy openness) but not climate significantly affect the ability of seed plants to form persistent seed banks.
4. *Synthesis.* Our study is the first to show that phylogenetic relatedness plays an important role in explaining seed bank properties in angiosperms and how these properties relate to early life-history traits, climate and habitat-related variables. These findings represent a starting point to assess the generality of persistent seed banks as a bet-hedging strategy in unpredictable environments and provide important insights into how seed plants might respond to global environmental changes.

## KEYWORDS

angiosperm, phylogenetic signal, reproductive ecology, seed dormancy, seed mass, seed persistence, viable seeds

## 1 | INTRODUCTION

Characterizing the mechanisms and processes regulating the ability of seeds to persist as latent propagules in the soil and spread mortality risks through time is critical in understanding how plants cope with environmental uncertainty (Long et al., 2015; Saatkamp et al., 2019; Venable, 2007; Venable & Brown, 1988). Soil seed banks, i.e. reserves of dormant and non-dormant seeds (Dekker, 1999) in or on the soil (Roberts, 1981), have long been recognized as playing a critical role in determining vegetation dynamics (Harper, 1977). In relation to their temporal dimension, an important distinction is made between persistent seed banks, which include seeds that remain viable in the soil for at least a year or beyond the start of the second germination season, as opposed to transient seed banks formed by seeds that germinate or perish before the beginning of the second germination season (Thompson, Bakker, & Bekker, 1997; Walck, Baskin, Baskin, & Hidayati, 2005). The ability of plant species to form persistent seed banks is a beneficial demographic adaptation for the maintenance and expansion of populations (Blossey, Nuzzo, & Dávalos, 2017; Cabin & Marshall, 2000; Donohue, Rubio de Casas, Burghardt, Kovach, & Willis, 2010; Harper, 1977; Poschlod & Rosbakh, 2018; Villa Martín, Muñoz, & Pigolotti, 2019) in their native as well as in their alien distribution range (Gioria, Le Roux, Hirsch, Moravcová, & Pyšek, 2019).

From an ecological point of view, the formation of persistent seed banks can be viewed as a bet-hedging strategy (Cohen, 1966) that facilitates the survival of species and mitigates the risks of reproductive failure under unfavourable conditions (Fenner & Thompson, 2005; Harper, 1977; Venable & Brown, 1988). Such a strategy is particularly important when the environmental and biotic conditions are highly unpredictable (Bossuyt & Honnay, 2008; Phartyal, Rosbakh, Ritz, & Poschlod, 2019; Poschlod & Rosbakh, 2018; Venable & Brown, 1988; Venable, Flores-Martinez, Müller-Landau, Barron-Gafford, & Becerra, 2008). As reserves of genetic variability (Levin, 1990) that store genotypes produced over many seasons (Cabin, 1996), persistent seed banks can influence the evolutionary responses of plants to variation in environmental conditions (Cabin, 1996; Donohue et al., 2010; Harper, 1977; Templeton & Levin, 1979) and buffer populations against changes in genetic composition that may occur following severe fluctuations in population size (Levin, 1990).

Persistence in the soil depends on the physical and physiological properties of seeds and how these are influenced by the characteristics of the environment (Baskin & Baskin, 2014; Long et al., 2015; Saatkamp et al., 2019). Observed correlations between seed traits, such as seed mass and seed dormancy (Baskin & Baskin, 2014; Moles et al., 2005; Moles, Hodson, & Webb, 2000; Thompson, Band, & Hodgson, 1993), while varying in strength and being mediated by environmental and biotic conditions (Baskin & Baskin, 2014; Long et al., 2015; Phartyal et al., 2019; Poschlod et al., 2013; Saatkamp et al., 2019; Venable & Brown, 1988), suggest that the ability of seed plants to form persistent seed banks is likely non-randomly distributed across phylogenies. Yet, examinations of the main drivers of

the seed banking strategies of seed plants that account explicitly for phylogenetic relationships are lacking.

Here, we addressed this gap in knowledge by using information on the historical relationships of lineages (phylogenies) to evaluate the contribution of phylogenetic relatedness in determining the seed bank properties of 2,350 angiosperm taxa in over 11,800 global records (site level), based on published information on seed bank type (transient vs. persistent) and density. Specifically, we measured the phylogenetic signal, i.e. the tendency for related species to share similar trait values than for species drawn at random from the same phylogenetic tree (Blomberg, Garland Jr., & Ives, 2003; Revell, Harmon, & Collar, 2008), in seed bank type and density. We then assessed the importance of phylogenetic relatedness relative to that of (a) three plant traits (seed mass, seed dormancy and life form) and (b) climatic and habitat-related variables in explaining patterns in these properties of the seed bank. The findings of this study provide important insights into the predictability of seed bank properties based on knowledge of phylogenetic relationships, species traits and characteristics of the environment.

## 2 | MATERIALS AND METHODS

### 2.1 | Soil seed bank database

To identify the most important factors affecting the properties of the seed bank on a global scale, we used the GloSSBank (Global Species Seed Banks) database, which contains soil seed bank data collected from the native and alien distribution range for 2,596 angiosperm taxa (for an earlier version of this database, see Gioria et al., 2019). From this dataset, we extracted 11,893 unique viable seed bank records from the native range only (81% of all records) for 2,350 taxa in 865 genera and 143 families, obtained from 195 studies (Table S1). Relevant literature was identified by searching the Web of Science (ISI) and Google Scholar, using the keyword 'seed' or 'diaspore' in combination with 'bank', 'below-ground', 'buried', 'community', 'flora', 'reservoir', 'soil' and 'stored'. Additional studies were searched by screening the reference lists provided in the resulting papers as well as papers citing the papers originally retrieved. For papers that contained potentially relevant data that could not be extracted directly, we contacted the authors for additional information. A full description of the methodology used to compile an earlier version of this dataset (updated until April 2018) is described in Gioria et al. (2019), including the criteria used to identify and select the sources from which seed bank data were extracted. The last search for relevant literature in this study was conducted in February 2020.

Soil seed bank data, at each study site (record) included two variables: *local seed bank type* (two levels: transient (<1 year) versus persistent (>1 year), sensu Thompson et al., 1997), and *local seed bank density*, expressed as the mean number of seeds recorded per square metre of surface area. Classification of seed banks into transient versus persistent was either provided by the authors of the source papers or derived from a combination of criteria, as recommended

by Thompson et al. (1997), including the presence versus absence of a species in the standing vegetation and the high proportion of seeds recorded in deep soil layers as opposed to seeds close to the surface only. Seed banks could only be classified reliably into two categories for seed bank type, since few studies provided information on seed bank persistence that could be used to distinguish further categories (e.g. classification into short-term persistent and long-term persistent, *sensu* Thompson et al., 1997) or those based on whether seeds retained their viability until the next germination season (Walck et al., 2005).

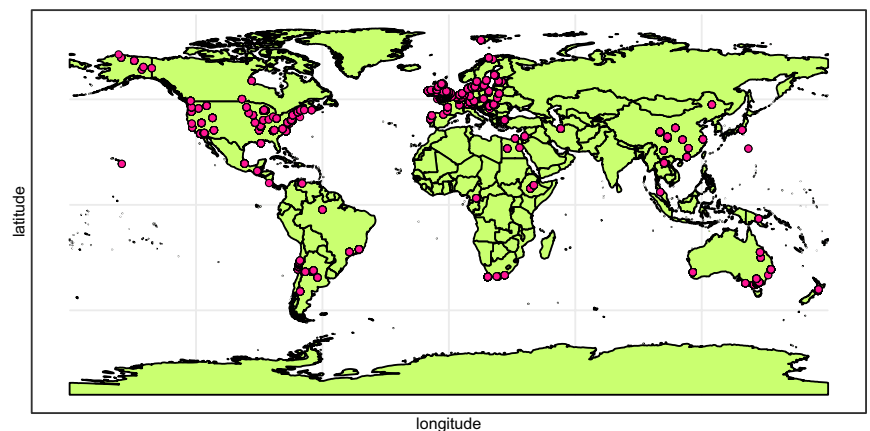
Information on seed bank type at the record level was used to create a second variable at the species level (*species seed bank type*), based on whether at least one persistent seed bank record for a species had been reported. For seed bank density, we also provided values at the species level (*species seed bank density*), calculated as the mean value of *local seed bank density* values, for species for which multiple records were available (1,604 species out of 2,350 species), while this value coincided with local seed bank density when only one record per species was available. Classification of seed banks into transient versus persistent *sensu* Thompson et al. (1997) has been challenged since seed longevity and persistence in the soil cannot be regarded as a species trait *per se* but vary with local environmental conditions (Abedi, Bartelheimer, & Poschlod, 2014; Long et al., 2015; Saatkamp, Affre, Dutoit, & Poschlod, 2009). However, by assigning a seed bank type category at the record level (*local seed bank type*) we accounted for the effects of environmental factors on seed persistence in the soil. In contrast, *species seed bank type* can be interpreted as the *ability* of a species to form persistent seed banks under certain environmental conditions rather than a fixed species trait, avoiding any potential issue associated with a rigid classification of the type of seed banks for each species.

Records only include seed bank data that were estimated using the seedling emergence approach (Thompson et al., 1997), since we were interested only in the viable component of the seed bank (Thompson & Grime, 1979). Also, in this study we only included seed bank data collected from the native distribution range of the taxa present in our database, to avoid introducing noise associated with potential differences in seed traits between the native and non-native distribution range. Recent evidence, in fact, indicates

that some seed traits, including the degree of seed dormancy and seed size, differ in the non-native range, with these differences being interpreted as adaptive changes to the novel conditions encountered abroad (Hierro et al., 2020; see Gioria & Pyšek, 2017 for a review of this topic). The native status of the species in each record was derived directly from the source papers, or from regional and local floras, in a range of databases (see Gioria et al., 2019 for details). The taxonomic status of each species was validated using The Plant List V.1.1 database (<http://www.theplantlist.org/>). The final dataset includes only those species whose taxonomic status is regarded as 'resolved'.

To assess the relationship between seed bank properties and species traits that are known to affect soil seed persistence (Abedi et al., 2014; Fenner & Thompson, 2005; Long et al., 2015; Saatkamp et al., 2019), we collected information on (a) life form (three levels: annuals, perennials and woody species), based on a combination of sources (see Gioria et al., 2019) or directly from the source papers; (b) seed mass (mg), obtained from the Royal Botanic Gardens Kew Seed Information Database (2020); and (c) seed dormancy (dormant vs. non-dormant; Table S2). The dormancy category of each species was based on the classification provided in the Baskin Dormancy Database (Baskin & Baskin, 2014; Willis et al., 2014), with species possessing one or more of five kinds of dormancy (physical, physiological, morphological dormancy or a combination thereof) being categorized as 'dormant'.

To assess the importance of climate on the characteristics of the seed bank (Ooi, 2012; Poschlod et al., 2013), for each record we derived the geographic coordinates and extracted 11 climatic variables (2.5 min) from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Table S2). Seed bank data were available from a broad latitudinal range. The final dataset includes records ranging from  $-62.16$  to  $78.08$  in latitude (Figure 1). The vast majority of records come from studies conducted in Europe (60% of records from 43% of studies) and North America (15% of records from 28% of studies). However, both the number of records and the proportion of records from regions other than Europe and North America has increased substantially since 2000 (Figure S1). Still, this geographical bias is inevitably reflected in a biome/ecosystem bias, with little information available from the tropics, while other systems such as temperate



**FIGURE 1** Distribution map showing 340 sites where data on soil seed bank type and density had been collected, for 2,350 species in 11,893 records from the native distribution range, based on 195 source papers (Table S1)

grasslands and forests were overrepresented in the database. A geographical bias might, in part, reflect a language bias. Here, we focused on literature published in English or providing English keywords. To minimize this gap in our search for global literature, we contacted experts from regions with a small proportion of records/studies.

To assess the importance of habitat-related features in determining seed bank properties, we included the original classification of the habitat at each site provided by the authors of the source papers. Since 133 habitat types had been defined, we created three variables that summarize the main characteristics of these habitats (Table S2): (a) disturbance (two levels: relatively nondisturbed vs. disturbed sites, depending on whether the sites were characterized by human-related activities or recurrent natural disturbances); (b) soil moisture (three levels: dry; moist and wet); (c) openness (two levels: open vs. close canopies). While the classes identified for each habitat variable were relatively broad, they allowed testing for the effects of site-specific environmental conditions. For instance, sites in similar habitats differed in their disturbance regime, especially grasslands and forest. Certain sites found in arid and semi-arid regions were characterized by relatively high soil moisture, while at certain sites found in humid regions with high precipitation values soil moisture was low. Also, some seed banks had been collected in woodlands/forests where breaks in the canopy result in high light availability.

Overall, our criteria for inclusion in the database were quite strict. We included only studies providing mean density values at the study sites, coming from multiple samples (and not values from single samples at each site), maximum densities per site, total numbers of seeds/seedlings per site or frequency values. This was done to minimize any potential confounding effect associated with the large spatial and temporal variation that characterizes soil seed banks (Fenner & Thompson, 2005).

## 2.2 | Phylogenetic analyses

The phylogenetic tree for 2,350 angiosperm taxa was reconstructed using the R package V.PHYLOMAKER (Jin & Qian, 2019). V.PHYLOMAKER contains a mega-tree named 'GBOTB.extended.tre', which is a combination of GBOTB for seed plants (Smith & Brown, 2018) and the clade in Zanne et al.'s (2014) phylogeny for pteridophytes, with updates, corrections and expansion (Jin & Qian, 2019). Taxa absent from the mega-tree were attached to their designated relatives using the *bind.relative* function.

To assess how variation in seed bank properties is correlated with phylogenetic relatedness for the species in the phylogeny (Blomberg et al., 2003; Revell et al., 2008), we determined the phylogenetic signal in seed bank type (*species seed bank type*, binary variable) by applying the *D* statistics (Fritz & Purvis, 2010), while the Pagel's  $\lambda$  statistics (Pagel, 1999) was used to calculate the signal in seed bank density. Since multiple *local seed bank density* values were

available for the majority of species in our database (68% of all species), we incorporated within-species variation into the calculation of the phylogenetic signal in *species seed bank density*, to account for what is considered statistically as a 'measurement error' (Ives, Midford, & Garland Jr., 2007). We also estimated the phylogenetic signal in seed mass (Pagel's  $\lambda$ ) and seed dormancy (*D* statistics), for comparative purposes. The value of *D* can be negative (indicative of highly conserved traits) or greater than 1 (indicative of overdispersion). Distributions of *D* from the simulations (1,000) were used to assess the significance of the observed scaled *D*. On the contrary, when  $\lambda$  equals zero, related taxa are no more similar than expected by chance, while significant phylogenetic signal occurs when  $\lambda > 0$ , meaning that taxa are more similar than expected by chance; significant departure from 0 was assessed using a likelihood ratio test. Phylogenetic signals of each seed bank property/seed trait were estimated for all the species in the phylogeny (2,350 taxa), as well as separately, for herbaceous versus woody species (1,907 vs. 443 species), monocots and eudicots (597 vs. 743 species) and for the most speciose clades (>100 species), based on the APG IV classification (APG IV, 2016), i.e. campanulids, commelinids, fabids, lamiids and malvids (432, 535, 433, 318 and 197 species respectively). Signals for these groups were estimated to provide an indication of the variability in seed bank properties within each group associated with phylogenetic relatedness, without making any inference on potential evolutionary processes underlying such patterns. We calculated signals for the most speciose clades only to mitigate potential effects of high variability in the data associated with the small number of species found in other clades. The R package CAPER (Orme et al., 2012) was used to calculate *D* values (*phylo.d* function), while the R package PHYTOOLS (Revell, 2012) was used to calculate the  $\lambda$  statistics (*phylosig* function).

Since natural selection rarely acts on single traits (Wilson et al., 2010), we examined phylogenetic correlations between *species seed bank type* with seed mass, seed dormancy and life form, and between seed bank density with these three traits. This was done by performing bivariate generalized mixed models with Bayesian estimation (bivariate Markov Chain Monte Carlo generalized linear mixed models [MCMCGLMM]; Wilson et al., 2010), which allow calculating the phylogenetic covariance (and correlation) between two traits and the phylogenetic variance for each trait, using the R package MCMCGLMM (Hadfield, 2010).

To evaluate the importance of environmental variables in shaping seed bank properties in angiosperms, we tested, in a phylogenetic framework, the effects of habitat-related variables and climatic variables on soil seed bank properties recorded at the site level. To model *local seed bank type*, we used binary generalized mixed models with Bayesian estimation (binary MCMCGLMM; Hadfield & Nakagawa, 2010). The reconstructed phylogeny was used as a random effect, together with species identity, species nested in source (with source being the source paper(s)) and study region, while fixed effects included three habitat-related variables (disturbance, soil moisture and openness) and 11 climatic variables. Latitude and its interaction with climatic variables also was

included among the fixed effects, given that important seed traits such as seed mass and seed dormancy are strongly related to latitude (Baskin & Baskin, 2014; Moles & Westoby, 2003; Rubio de Casas et al., 2017). A log-transformation was also applied to climatic variables and latitude, after they were all transformed into positive values by adding the minimum absolute value for each variable.

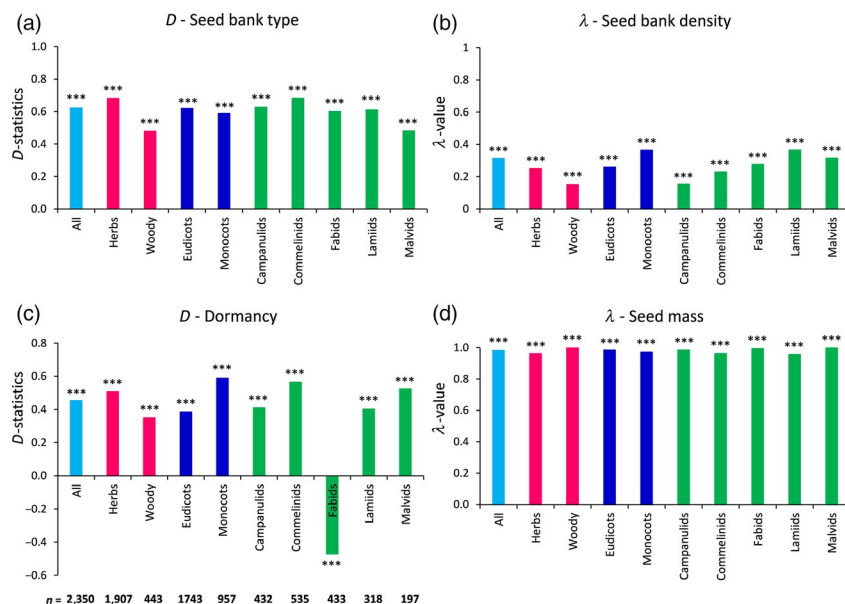
To model *local seed bank density* (log-transformed), we used Gaussian models, since diagnostic analyses showed that the response follows a Gaussian distribution and confirmed the suitability of this procedure to model this variable, while excluding the suitability of other distributions, including the Poisson distribution. In these models, we used the same fixed and random effects as in the binary models. Since preliminary analyses showed that persistent seed banks were significantly denser than transient ones locally, we also performed the models of *local seed bank density* using only persistent records (1,170 species in 6,192 records). This allowed us to exclude from the analyses potentially under- or over-estimated density values for transient seed banks, which strongly depend on time in relation to seed dispersal and germination when seed bank samples are collected (Baskin & Baskin, 2014; Gioria et al., 2019). We used weakly informative priors for our models, fixing the residual covariance matrix for binary traits while using parameter expanded priors for the random effects for continuous response variables. Each model was run for 1,000,000 MCMC steps, with an initial burn-in phase of 10,000 and a thinning interval of 100 (de Villemereuil & Nakagawa, 2014),

resulting, on average, in 9,000 posterior distributions. From the resulting posterior distributions, we calculated mean parameter estimates and 95% highest posterior density and credible intervals (CI). Significance of model parameters was estimated by examining CIs where parameters with CIs overlapping with zero were considered not significant.

To visualize patterns in the seed bank associated with species traits, climatic variables and habitat-related factors, we performed multiple factor analysis (Lê & Pagès, 2010). This is a multivariate data analysis method for summarizing and visualizing complex data tables in which individuals (species in our study) are described by several sets of quantitative or qualitative variables structured into groups. This method allowed us to visualize the distance among the species in our dataset associated with selected groups of variables. All analyses were conducted in the R software environment (R Development Core Team, 2019). A description of the variables used in each type of model is provided in Table S2, while a list of the phylogenetic analyses performed in this study is presented in Table S3.

### 3 | RESULTS

We found a significant phylogenetic signal in seed bank type, considering all the taxa and within the most speciose clades (>100 species) in the phylogeny (Figure 2a). Significant signals were identified also for seed bank density, for the entire phylogeny and the

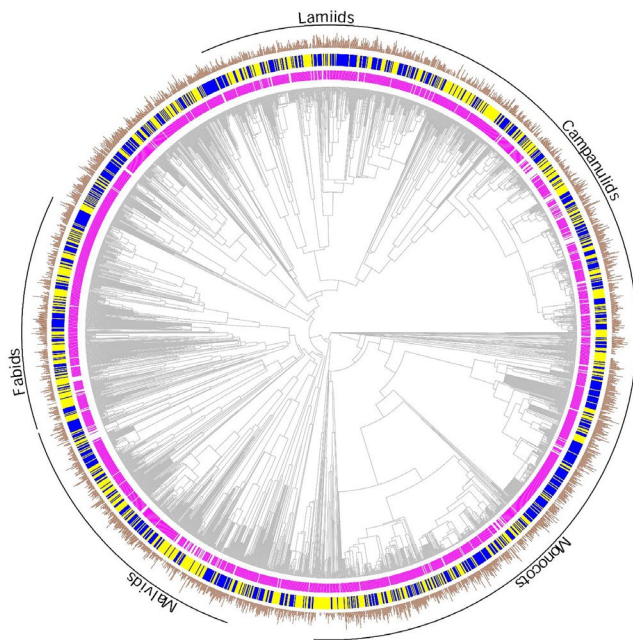


**FIGURE 2** Phylogenetic signal in seed bank type (a) and density (b), based on records collected from the native distribution range for 2,350 angiosperms, and of two seed traits, dormancy (c) and seed mass (d). *D* values were determined for seed bank type and dormancy (binary variables), while the Pagel's  $\lambda$  statistics were used to determine the signals in seed bank density and seed mass. For seed bank density, the phylogenetic signal was calculated by accounting for within-species variation. Phylogenetic signals were calculated for all the species in the phylogeny (2,350), and, separately, for herbaceous versus woody species, monocots versus eudicots and for the most speciose clades. The letter *n* indicates the number of species for which separated signals were calculated (\*\*\*, level of significance at the clade level,  $p < 0.001$ )

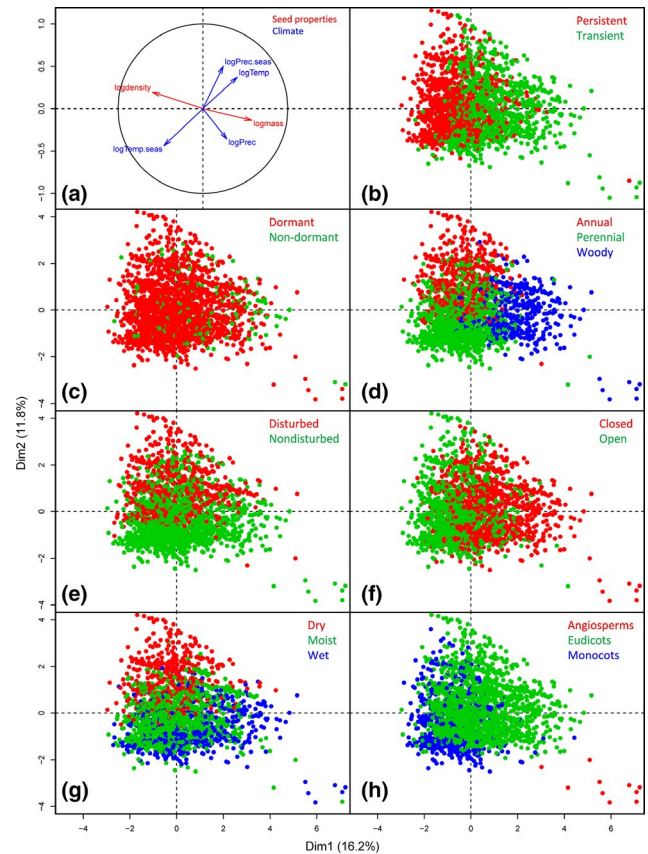


most speciose clades, despite the high variation in this property (Figure 2b). Woody species showed a weaker phylogenetic signal in seed bank density than herbs but relatively stronger in seed bank type. Significant signals, both positive and negative, were found for seed dormancy (vs. non-dormancy) throughout the phylogeny and for all examined clades. A considerably strong signal in dormancy was identified for fabids (Figure 2c), as indicated by negative values for this clade (for the  $D$  statistics, in fact, the lower the values the stronger the phylogenetic signal, including negative ones). A strong, significant signal was found for seed mass, for the entire phylogeny and the considered clades (Figure 2d).

Bivariate MCMCGLMMs showed that *species seed bank type* significantly correlates with seed mass (posterior mean =  $-0.33$ ; CI =  $-0.46$  to  $-0.23$ ), with persistent seed banks being composed of seeds with low mass. A significant correlation was found between seed bank type and dormancy (posterior mean =  $0.22$ ; CI =  $0.04$  –  $0.37$ ), with the majority of species forming persistent seed banks possessing dormant seeds (Figure 3). A significant correlation was found between seed bank type and life form, showing that the probability of forming a persistent seed bank is higher for herbaceous than woody species (posterior mean =  $0.50$ ; CI =  $0.37$  –  $0.64$ ), and for annual than perennial herbs (posterior mean =  $0.28$ ; CI =  $0.12$  –  $0.46$ ). Seed bank density was significantly correlated with seed bank type, with persistent seed banks being denser than transient seed banks (posterior mean =  $0.88$ ; CI =  $0.79$  –  $0.94$ ) but not with seed dormancy (posterior mean =  $0.20$ ; CI =  $-0.02$  –  $0.42$ ).



**FIGURE 3** Phylogram showing the phylogeny of 2,350 angiosperm taxa, including information on seed bank type (persistent seed banks in blue, transient seed banks in yellow), seed dormancy (dormancy in magenta, non-dormancy in white) and mean seed bank density (brown lines), at the species level, on a log-scale. Only the most speciose clades are named



**FIGURE 4** Multiple factor analysis plots visualizing species-level data based on (a) seed bank density and seed mass (log-transformed), and significant climatic variables (log-transformed), (b) seed bank type, (c) seed dormancy, (d) life form, (e) disturbance (habitat), (f) openness (habitat), (g) soil moisture (habitat) and (h) clade, for 2,350 angiosperm taxa

Phylogenetic analyses based on local seed bank records showed that habitat disturbance has a significant effect on seed bank properties (Figure 4; Table S4). Persistent seed banks were more likely to be found in habitats characterized by either a natural or human-related disturbance regime compared to relatively nondisturbed habitats. Disturbed sites also supported higher seed bank densities than nondisturbed ones, regardless of whether the records of transient seed banks were included or not. The probability of forming persistent seed banks was higher in closed than open habitats, while the opposite was true for density, especially when only persistent seed bank records were analysed. Soil moisture did not have a significant effect on seed bank type, although significantly denser seed banks were observed in drier habitats and in wetlands compared to those found in habitats characterized by intermediate levels of moisture. Climatic variables, encompassing patterns in temperature and precipitation and their seasonality, did not significantly affect the type of seed bank. However, some temperature variables, especially the minimum temperature of coldest month (BIO6, WorldClim; Hijmans et al., 2005) and the mean temperature of driest quarter (BIO9, WorldClim; Hijmans et al., 2005), had marginally significant positive effects on seed

bank density (Table S4). In contrast, variables summarizing patterns in precipitation did not significantly affect the type and density of the seed bank nor did latitude. Multiple Factor Analysis plots (Figure 4) summarize the main patterns identified in our models.

## 4 | DISCUSSION

Examining the role of phylogenetic relatedness in determining soil seed bank properties and its contribution relative to that of species traits, climate and habitat-related variables can provide important insights into how plants respond to environmental uncertainty and the risks of reproductive failure. We found a significant phylogenetic signal in seed bank type, thereby providing evidence that the ability to form persistent seed banks is dependent on species relatedness and not randomly distributed across phylogeny. Significant, though weaker, signal was identified also for seed bank density, despite the high spatio-temporal variation characterizing this seed bank property (Fenner & Thompson, 2005). Overall, the ability to form persistent and dense seed banks was widely distributed across the major clades in our phylogeny. A weaker phylogenetic signal in seed bank density found for woody species compared to herbaceous species possibly reflects differences in reproductive traits between shrubs, vines, and trees, including large variation in seed dormancy mechanisms (Baskin & Baskin, 2014; Carta, Skourti, Mattana, Vandeloos, & Thanos, 2017; Fenner & Thompson, 2005; Long et al., 2015; Walck et al., 2005).

Phylogenetic correlations at the species level showed that the relationship between seed bank type and seed mass is phylogenetically mediated. A strong phylogenetic signal found for seed mass in our phylogeny supports previous evidence collected at different spatial scales that seed mass is a highly conserved species trait (Jiménez-Alfaro, Silveira, Fidelis, Poschlod, & Commander, 2016; Moles et al., 2005; Zheng, Guo, & Wang, 2017). A negative relationship between seed mass and the ability to form persistent seed banks, accord, on a global scale, with evidence available from regional floras (Moles et al., 2000, 2005; Thompson et al., 1993; Zheng et al., 2017). Although significant, this correlation was only moderate. This, combined with the high conservatism of seed mass indicated by the strength of the phylogenetic signal in this variable for the species in our phylogeny compared to that in seed bank type, provides evidence, but in a phylogenetic framework, that seed mass alone provides an insufficient basis for predicting seed persistence in the soil (see Moles et al., 2000, 2005).

Formation of a persistent seed bank was phylogenetically related to production of dormant seeds, since the majority of species forming persistent seed banks possessed seeds characterized by some kind of dormancy, being either morphological, physiological, physical or a combination thereof. However, dormancy was more widely distributed throughout our phylogeny than persistence in the soil, with many species producing dormant seeds forming

transient seed banks only. Moreover, seed dormancy was not significantly related to seed bank density, with non-dormant species also being able to form dense seed banks. These findings support previous evidence, but on a global scale and in an explicitly phylogenetic framework, that seed dormancy is an important mechanism promoting seed persistence in the soil but, overall, is a poor predictor of seed bank persistence (see Thompson, Ceriani, Bakker, & Bekker, 2003). The phylogenetic signal for seed dormancy was comparable, though slightly stronger, than that for seed bank type. The ability to produce dormant seeds was also widely distributed throughout the phylogeny, and very strong for fabids, since physical dormancy due to a water-impermeable seed coat characterizes many species in this clade (Baskin & Baskin, 2014; Rubio de Casas et al., 2017; Willis et al., 2014).

Positive and significant phylogenetic correlations showed that the probability of forming a persistent seed bank was higher for herbaceous than woody species and for annual than perennial herbs. This adds a phylogenetic perspective to the notion of the importance of a persistent seed bank as a bet-hedging strategy for species that complete their life cycle over 1 year (Gremer & Venable, 2014) and that seed persistence is greater in annual than in related perennial species (Thompson, Bakker, Bekker, & Hodgson, 1998).

Phylogenetic relatedness explained a large component of the variation in seed bank properties recorded at the site level and allowed proper characterization of the role of the main species traits and environmental conditions that are known to affect seed persistence and germination (Fenner & Thompson, 2005; Long et al., 2015; Thompson et al., 1993). Interestingly, climatic variables did not have significant effects on seed bank type, while complex, though relatively weak, effects of these variables were found on seed bank density. Precipitation patterns, including seasonality in precipitation, did not affect significantly either the type or the density of the seed bank nor did latitude. In contrast, habitat disturbance was a significant factor affecting seed bank properties, with persistent seed banks being more likely to be found in disturbed than in relatively nondisturbed habitats. Disturbed sites also supported higher seed bank densities than nondisturbed sites, regardless of whether the records of transient seed banks were included or not, indicating that the accumulation of persistent seeds is an important strategy in disturbed sites. These findings support evidence in a broad range of habitats and climatic conditions across different latitudes that the risks of reproductive failure associated with natural or human-related disturbances promote the formation of persistent seed banks (Bossuyt & Honnay, 2008; Fenner & Thompson, 2005; Harper, 1977; Leck, 1989; Thompson & Grime, 1979; Venable & Brown, 1988).

A higher probability of forming persistent seed banks was found in closed than open habitats. This could be due to a range of factors, including the importance of forming persistent seed banks in ephemeral habitats such as forest gaps (Hanski, 1987). Moreover, closed habitats in our study include those characterized by natural or

human-related disturbances, such as forested wetlands and managed forests. Open habitats also varied substantially in the degree of disturbance, ranging from nondisturbed grasslands to cropland. A large proportion of our seed bank records were collected from semi-natural grasslands, which are known to support a high proportion of species with transient seed banks, as opposed to highly degraded grasslands or cropland (Fenner & Thompson, 2005; Hopfensperger, 2007). In contrast, lower densities found in closed than open habitats are possibly associated with differences in seed inputs that reflect, in turn, differences in seed mass, with this trait being generally higher in woodlands than grasslands or arable weed communities (Thompson et al., 1998) and for woody than herbaceous species (Leishman, Wright, Moles, & Westoby, 2000).

The probability of forming a persistent seed bank did not differ significantly in dry, moist and wet habitats. However, denser seed banks were reported in dry and wet than in moist habitats. The effect of soil moisture on seed bank persistence depends on the sensitivity of a species to environmental factors (Abedi et al., 2014; Carta, Bottega, & Spanò, 2018) and their degree of adaptation to specific habitats. Thus, different species may have different ecological strategies to cope with the prevailing environmental conditions and their predictability (Phartyal et al., 2019). The fact that models based on persistent records only showed significantly denser seed banks in dry and wet habitats provides further evidence of the importance of persistent seed banks for survival and expansion in stressful habitats such as arid and semi-arid habitats (Gremer & Venable, 2014; Ooi, Auld, & Denham, 2009; Venable, 2007) and in wetlands subject to recurrent natural disturbances (Baskin, Baskin, & Chester, 2019; Leck, 1989; Nielsen, Podnar, Watts, & Wilson, 2013; Phartyal et al., 2019; Poschlod & Rosbakh, 2018; van der Valk & Davis, 1978). An interesting example is provided by mudflats, i.e. ephemeral habitats characterized by unpredictable flooding and drought events, with recent evidence showing that the ability to form persistent seed banks is critical for survival in these habitats, with mudflat species possessing very or extremely long-term persistent seed banks (Baskin et al., 2019; Poschlod & Rosbakh, 2018).

To conclude, we showed, on a global scale, that the ability of angiosperms' seeds to persist in the soil is mainly explained by phylogenetic relatedness. Moreover, we found that not accounting for phylogeny tend to overestimate the importance of species traits, habitat and climate in determining seed bank properties, while violating the assumption of independence among data points (Garamszegi, 2014). Interestingly, we found that habitat disturbance but not climate is important in differentiating the seed bank strategies that hedge against the risks of reproductive failure of plant species. Our findings also support evidence, but for a large number of species globally, that persistent seed banks are mainly found in species producing seeds characterized by dormancy mechanisms and/or small seeds, but that seed traits are, in general, poor predictors of the ability to form persistent seed banks (Grime, 2001; Thompson et al., 2003).

These findings represent a starting point to assess the generality of persistent seed banks as a bet-hedging strategy (Cohen, 1966; Venable, 2007). In the future, improved estimates of seed bank

persistence via standardized experimental protocols might reveal an even stronger contribution of phylogenetic relationships to determining seed bank properties in angiosperms. An improved understanding of the factors affecting the ability of species to form persistent (and dense) seed banks is critical to predicting how seed plants might respond to global environmental changes (Cabin & Marshall, 2000; Harper, 1977; Ooi, 2012; Ooi et al., 2009; Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). Predicting which species may form persistent seed banks based on phylogenetic relationships is also important for conservation or restoration purposes (Barak, Lichtenberger, Wellman-Houde, Kramer, & Larkin, 2018; Faist, Ferrenberg, & Collinge, 2013; Phartyal et al., 2019). This is also important to develop measures aimed at preventing the introduction and control potentially invasive alien plant species, whose ability to become naturalized and invasive has been recently shown to be associated with the ability to form persistent seed banks (Gioria et al., 2019; Pyšek et al., 2015).

Clearly, the representativeness of our findings might reflect the fact that the majority of seed bank records come from temperate grasslands and forests, more or less disturbed, while information from other biomes in our database is limited. However, analyses at the species level reduced this bias, given that a single seed bank type category and seed bank density value was assigned for individual species, so that the same weight was assigned to common and widespread species as well as species only found in less-examined ecosystems, such as those found in tropical and subtropical regions, arid and semi-arid regions or from the extremes of latitudinal range of our records, including Svalbard. We hope that our study will prompt new research across the globe aimed at assessing changes in the vegetation not only above-ground but also in the soil seed bank, which is both a memory of past vegetation but also a key determinant of future vegetation dynamics and species distribution.

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## AUTHORS' CONTRIBUTIONS

M.G. and A.C. conceived the idea; M.G. and P.P. compiled the Global Species Seed Banks database; M.G. wrote the manuscript; A.C. performed the phylogenetic analyses; P.P. and C.C.B. contributed to the interpretation of the results. All authors contributed to the writing and revision of the manuscript.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.8sf7m0cjh> (Gioria, Pyšek, Baskin, & Carta, 2020).



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## REFERENCES

- Abedi, M., Bartelheimer, M., & Poschlod, P. (2014). Effects of substrate type, moisture and its interactions on soil seed survival of three *Rumex* species. *Plant and Soil*, 374, 485–495. <https://doi.org/10.1007/s11104-013-1903-x>
- APG IV. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181, 1–20.
- Barak, R. S., Lichtenberger, T. M., Wellman-Houde, A., Kramer, A. T., & Larkin, D. J. (2018). Cracking the case: Seed traits and phylogeny predict time to germination in prairie restoration species. *Ecology and Evolution*, 8, 5551–5562. <https://doi.org/10.1002/ece3.4083>
- Baskin, C. C., & Baskin, J. M. (2014). *Seeds: Ecology, biogeography, and evolution of dormancy and germination* (2nd ed.). San Diego, CA: Academic/Elsevier.
- Baskin, C. C., Baskin, J. M., & Chester, E. W. (2019). Long-term persistence of summer annuals in soil seed banks of seasonally dewatered mudflats. *Plant Ecology*, 220, 731–740. <https://doi.org/10.1007/s11258-019-00948-7>
- Blomberg, S. P., Garland Jr., T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>
- Blossey, B., Nuzzo, V., & Dávalos, A. (2017). Climate and rapid local adaptation as drivers of germination and seed bank dynamics of *Alliaria petiolata* (garlic mustard) in North America. *Journal of Ecology*, 105, 1485–1495.
- Bossuyt, B., & Honnay, O. (2008). Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, 19, 875–884. <https://doi.org/10.3170/2008-8-18462>
- Cabin, R. J. (1996). Genetic comparisons of seed bank and seedling populations of the desert mustard *Lesquerella fendleri*. *Evolution*, 50, 1830–1841.
- Cabin, R. J., & Marshall, D. L. (2000). The demographic role of soil seed banks. I. Spatial and temporal comparisons of below- and above-ground populations of the desert mustard *Lesquerella fendleri*. *Journal of Ecology*, 88, 283–292. <https://doi.org/10.1046/j.1365-2745.2000.00443.x>
- Carta, A., Bottega, S., & Spanò, C. (2018). Aerobic environment ensures viability and anti-oxidant capacity when seeds are wet with negative effect when moist: Implications for persistence in the soil. *Seed Science Research*, 28, 16–23. <https://doi.org/10.1017/S0960258517000307>
- Carta, A., Skourti, E., Mattana, E., Vandelook, F., & Thanos, C. A. (2017). Photoinhibition of seed germination: Occurrence, ecology and phylogeny. *Seed Science Research*, 27, 131–153. <https://doi.org/10.1017/S0960258517000137>
- Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, 16, 267–282. [https://doi.org/10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3)
- de Villemereuil, P., & Nakagawa, S. (2014). General quantitative genetic methods for comparative biology. In L. Z. Garamszegi (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology* (pp. 287–303). Berlin, Germany: Springer-Verlag.
- Dekker, J. (1999). Soil weed seed banks and weed management. *Journal of Crop Production*, 2, 139–166. [https://doi.org/10.1300/J144v02n01\\_08](https://doi.org/10.1300/J144v02n01_08)
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K., & Willis, C. G. (2010). Germination post-germination adaptation and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, 41, 293–319. <https://doi.org/10.1146/annurev-ecolsys-102209-144715>
- Faist, A. M., Ferrenberg, S., & Collinge, S. K. (2013). Banking on the past: Seed banks as a reservoir for rare and native species in restored vernal pools. *AoB PLANTS*, 5, plt043. <https://doi.org/10.1093/aobpla/plt043>
- Fenner, M., & Thompson, K. (2005). *The ecology of seeds* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, 24, 1042–1051. <https://doi.org/10.1111/j.1523-1739.2010.01455.x>
- Garamszegi, L. Z. (2014). Uncertainties due to within-species variation in comparative studies: Measurement errors and statistical weights. In L. Z. Garamszegi (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology* (pp. 157–199). Berlin, Germany: Springer-Verlag.
- Gioria, M., Le Roux, J. J., Hirsch, H., Moravcová, L., & Pyšek, P. (2019). Characteristics of the soil seed bank of invasive and non-invasive plants in their native and alien distribution range. *Biological Invasions*, 21, 2313–2332. <https://doi.org/10.1007/s10530-019-01978-y>
- Gioria, M., & Pyšek, P. (2017). Early bird catches the worm: Germination as a critical step in plant invasion. *Biological Invasions*, 19, 1055–1080. <https://doi.org/10.1007/s10530-016-1349-1>
- Gioria, M., Pyšek, P., Baskin, C. C., & Carta, A. (2020). Data from: Phylogenetic relatedness mediates persistence and density of soil seed banks. *Dryad Data Repository*, <https://doi.org/10.5061/dryad.8sf7m0cjh>
- Gremer, J. R., & Venable, D. L. (2014). Bet hedging in desert winter annual plants: Optimal germination strategies in a variable environment. *Ecology Letters*, 17, 380–387. <https://doi.org/10.1111/ele.12241>
- Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed.). Oxford, UK: John Wiley and Sons Ltd.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22.
- Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23, 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>
- Hanski, I. (1987). Colonization of ephemeral habitats. In A. J. Gray, M. J. Crawley, & P. Edwards (Eds.), *Colonization, succession and stability* (pp. 155–185). Oxford, UK: Blackwell.
- Harper, J. (1977). *The population biology of plants*. London, UK: Academic Press.
- Hierro, J. L., Eren, Ö., Montesinos, D., Andonian, K., Kethsuriani, L., Özcan, R., ... French, K. (2020). Increments in weed seed size track global range expansion and contribute to colonization in a non-native region. *Biological Invasions*, 22, 969–982. <https://doi.org/10.1007/s10530-019-02137-z>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hopfensperger, K. N. (2007). A Review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, 16, 1438–1448. <https://doi.org/10.1111/j.0030-1299.2007.15818.x>
- Ives, A. R., Midford, P. E., & Garland Jr., T. (2007). Within-species variation and measurement error in phylogenetic comparative biology. *Systematic Biology*, 56, 252–270.
- Jiménez-Alfaro, B., Silveira, F. A. O., Fidelis, A., Poschlod, P., & Commander, L. E. (2016). Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science*, 27, 637–645.

- Jin, Y., & Qian, H. (2019). VPhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, 42, 1353–1359. <https://doi.org/10.1111/ecog.04434>
- Lê, S., & Pagès, J. (2010). DMFA: Dual hierarchical multiple factor analysis. *Communications in Statistics: Theory and Methods*, 39, 483–492.
- Leck, M. (1989). Wetland seed banks. In M. Leck, V. Parker, & R. Simpson (Eds.), *Ecology of soil seed banks* (pp. 283–305). San Diego, CA: Academic Press.
- Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In M. Fenner (Ed.), *Seeds: The Ecology of regeneration in plant communities* (pp. 31–57). Wallingford, UK: CAB International.
- Levin, D. (1990). The seed bank as a source of genetic novelty in plants. *The American Naturalist*, 135, 563–572. <https://doi.org/10.1086/285062>
- Long, R. L., Gorecki, M. J., Renton, M., Scott, J. K., Colville, L., Goggin, D. E., ... Finch-Savage, W. E. (2015). The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biological Reviews of the Cambridge Philosophical Society*, 90, 31–59. <https://doi.org/10.1111/brv.12095>
- Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., & Westoby, M. (2005). A brief history of seed size. *Science*, 307, 576–580. <https://doi.org/10.1126/science.1104863>
- Moles, A. T., Hodson, D. W., & Webb, C. J. (2000). Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos*, 89, 541–545. <https://doi.org/10.1034/j.1600-0706.2000.890313.x>
- Moles, A. T., & Westoby, M. (2003). Latitude, seed predation and seed mass. *Journal of Biogeography*, 30, 105–128. <https://doi.org/10.1046/j.1365-2699.2003.00781.x>
- Nielsen, D. L., Podnar, K., Watts, R. J., & Wilson, A. L. (2013). Empirical evidence linking increased hydrologic stability with decreased biotic diversity within wetlands. *Hydrobiologia*, 708, 81–96. <https://doi.org/10.1007/s10750-011-0989-5>
- Ooi, M. K. J. (2012). Seed bank persistence and climate change. *Seed Science Research*, 22(S1), S53–S60. <https://doi.org/10.1017/S0960258511000407>
- Ooi, M. K. J., Auld, T. D., & Denham, A. J. (2009). Climate change and bet-hedging: Interactions between increased soil temperatures and seed bank persistence. *Global Change Biology*, 15, 2375–2386. <https://doi.org/10.1111/j.1365-2486.2009.01887.x>
- Orme, C. D. L., Freckleton, R. P., Thomas, G. H., Petzoldt, T., Fritz, S. A., Isaac, N. J. B., & Pearse, W. (2012). caper: Comparative analyses of phylogenetics and evolution in R. *Methods in Ecology and Evolution*, 3, 145–151.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Phartyal, S. S., Rosbakh, S., Ritz, C., & Poschlod, P. (2019). Ready for change: Seed traits contribute to the high adaptability of mudflat species to their unpredictable habitat. *Journal of Vegetation Science*, 31(2), 331–342. <https://doi.org/10.1111/jvs.12841>
- Poschlod, P., Abedi, M., Bartelheimer, M., Drobnik, J., Rosbakh, S., & Saatkamp, A. (2013). Seed ecology and assembly rules in plant communities. In E. van der Maarel & J. Franklin (Eds.), *Vegetation ecology* (2nd ed., pp. 164–202). Oxford, UK: John Wiley & Sons Ltd.
- Poschlod, P., & Rosbakh, S. (2018). Mudflat species: Threatened or hidden? An extensive seed bank survey of 108 fish ponds in Southern Germany. *Biological Conservation*, 225, 154–163. <https://doi.org/10.1016/j.biocon.2018.06.024>
- Pyšek, P., Manceur, A. M., Alba, C., McGregor, K., Pergl, J., Stájerová, K., ... Kühn, I. (2015). Naturalization of central European plant species in North America: Species traits habitats propagule pressure residence time. *Ecology*, 96, 145–157.
- R Development Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Revell, L. J., Harmon, L. J., & Collar, D. C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, 57, 591–601. <https://doi.org/10.1080/10635150802302427>
- Roberts, H. (1981). Seed banks in soils. *Advances in Applied Biology*, 6, 1–54.
- Royal Botanic Gardens Kew. (2020). *Seed Information Database (SID)*. Version 7.1. Retrieved from <http://data.kew.org/sid/>
- Rubio de Casas, R., Willis, C. G., Pearse, W. D., Baskin, C. C., Baskin, J. M., & Cavender-Bares, J. (2017). Global biogeography of seed dormancy is determined by seasonality and seed size: A case study in the legumes. *New Phytologist*, 214, 1527–1536. <https://doi.org/10.1111/nph.14498>
- Saatkamp, A., Affre, L., Dutoit, T., & Poschlod, P. (2009). The seed bank longevity index revisited: Limited reliability evident from a burial experiment and database analyses. *Annals of Botany*, 104, 715–724. <https://doi.org/10.1093/aob/mcp148>
- Saatkamp, A., Cochrane, A., Commander, L., Guja, L. K., Jimenez-Alfaro, B., Larson, J., ... Walck, J. L. (2019). A research agenda for seed-trait functional ecology. *New Phytologist*, 221, 1764–1775. <https://doi.org/10.1111/nph.15502>
- Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105, 302–314. <https://doi.org/10.1002/ajb.2.1019>
- Templeton, A., & Levin, D. (1979). Evolutionary consequences of seed pools. *The American Naturalist*, 114, 232–249. <https://doi.org/10.1086/283471>
- Thompson, K., Bakker, J. P., & Bekker, R. M. (1997). *Soil seed banks of NW Europe: Methodology, density and longevity*. Cambridge, UK: Cambridge University Press.
- Thompson, K., Bakker, J. P., Bekker, R. M., & Hodgson, J. (1998). Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology*, 86, 163–169. <https://doi.org/10.1046/j.1365-2745.1998.00240.x>
- Thompson, K., Band, S., & Hodgson, J. (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, 7, 236–241.
- Thompson, K., Ceriani, R. M., Bakker, J. P., & Bekker, R. M. (2003). Are seed dormancy and persistence in soil related? *Seed Science Research*, 13, 97–100. <https://doi.org/10.1079/SSR2003128>
- Thompson, K., & Grime, P. J. (1979). Seasonal variation in seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, 67, 893–921.
- van der Valk, A., & Davis, C. (1978). The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*, 59, 322–335. <https://doi.org/10.2307/1936377>
- Venable, D. L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090. <https://doi.org/10.1890/06-1495>
- Venable, D. L., & Brown, J. S. (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, 131, 360–384. <https://doi.org/10.1086/284795>
- Venable, D. L., Flores-Martinez, A., Müller-Landau, H. C., Barron-Gafford, G., & Becerra, J. X. (2008). Seed dispersal of desert annuals. *Ecology*, 89, 2218–2227. <https://doi.org/10.1890/07-0386.1>
- Villa Martín, P., Muñoz, M. A., & Pigolotti, S. (2019). Bet-hedging strategies in expanding populations. *PLoS Computational Biology*, 15, e1006529.
- Walck, J. L., Baskin, J. M., Baskin, C. C., & Hidayati, S. N. (2005). Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. *Seed Science Research*, 15, 189–196. <https://doi.org/10.1079/SSR2005209>
- Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, 17, 2145–2216. <https://doi.org/10.1111/j.1365-2486.2010.02368.x>
- Willis, C. G., Baskin, C. C., Baskin, J. M., Auld, J. R., Venable, D. L., Cavender-Bares, J., ... The NESCent Germination Working Group. (2014). The evolution of seed dormancy: Environmental cues,

- evolutionary hubs, and diversification of the seed plants. *New Phytologist*, 203, 300–309. <https://doi.org/10.1111/nph.12782>
- Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., ... Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, 79, 13–26. <https://doi.org/10.1111/j.1365-2656.2009.01639.x>
- Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., ... Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92. <https://doi.org/10.1038/nature12872>
- Zheng, J., Guo, Z., & Wang, X. (2017). Seed mass of angiosperm woody plants better explained by life history traits than climate across China. *Scientific Reports*, 7, 2741. <https://doi.org/10.1038/s41598-017-03076-2>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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