Global seed dormancy patterns are driven by macroclimate but not fire regime

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Summary

- Seed dormancy maximizes plant recruitment in habitats with variation in environmental suitability for seedling establishment. Yet, we still lack a comprehensive synthesis of the macroecological drivers of nondormancy and the different classes of seed dormancy: physiological dormancy, morphophysiological dormancy and physical dormancy.
- We examined current geographic patterns and environmental correlates of global seed dormancy variation. Combining the most updated data set on seed dormancy classes for > 10 000 species with > 4 million georeferenced species occurrences covering all of the world's biomes, we test how this distribution is driven by climate and fire regime.
- Seed dormancy is prevalent in seasonally cold and dry climates. Physiological dormancy occurs in relatively dry climates with high temperature seasonality (e.g. temperate grasslands). Morphophysiological dormancy is more common in forest-dominated, cold biomes with comparatively high and evenly distributed precipitation. Physical dormancy is associated with dry climates with strong seasonal temperature and precipitation fluctuations (e.g. deserts and savannas). Nondormancy is associated with stable, warm and wetter climates (e.g. tropical rain forest). Pyroclimate had no significant effect on the distribution of seed dormancy.
- The environmental drivers considered in this study had a comparatively low predictive power, suggesting that macroclimate is just one of several global drivers of seed dormancy.

Introduction

Under continuously ideal conditions for plant growth and reproduction, ripe seeds should, in theory, germinate immediately after they are dispersed, since early germination increases fitness of the individual by extending its growth period and therefore allowing a larger size to be attained before its reproductive season begins (Ross & Harper, [1972](#); Kelly & Levin, [1997](#); Verdú & Traveset, [2005](#)). Furthermore, early germination decreases risks related to seed predation and pathogen attack (Long *et al.*, [2015](#)). Yet, many plant species exhibit seed dormancy, that is a mechanism preventing germination of intact, viable seeds under otherwise favourable conditions (Bewley, [1997](#)). The ecological function of seed dormancy is assumed to be the maximization of successful plant recruitment in sites subjected to seasonal or interannual variation in habitat suitability for seedling establishment. Three main strategies for plant reproduction from seeds have been proposed:

(**1**) spreading germination of a seed population over several seasons, thereby maximizing the chance that at least a small fraction of the population will germinate in a favourable season, that is 'bet-hedging' (Cohen, [1966](#); Venable, [2007](#); Pausas *et al.*, [2022](#));

(**2**) matching germination with the onset of the season during which risks for seedling death are lowest and conditions for growth are optimal, thus maximizing seedling establishment once seeds have germinated ('best-bet'; Donohue *et al.*, [2005](#); Baskin & Baskin, [2014](#); Pausas *et al.*, [2022](#)); and

(**3**) a combination of 'bet-hedging' and 'best-bet' in a single seed population. Traditionally, bet-hedging has been associated with species growing in environments with unpredictable favourable conditions for seedling recruitment, that is rain events in deserts (Venable, [2007](#)), whereas best-bet has been considered the main

strategy for environments with predictable, seasonal climatic fluctuations, for example alternating cold and warm seasons in temperate climates (Baskin & Baskin, 2014).

Importantly, these strategies delay germination and consequently form a soil seed bank (Saatkamp et al., 2014; Pausas et al., 2022; but see Gioria et al., 2020), which has a profound consequence on ecosystem services and ecosystem resilience in the face of global climate change. In addition, seed dormancy facilitates seed dispersal over long distances in space, for example hard (water-impermeable) seed coat in physically dormant seeds increases survival chances during endozoochoric dispersal (Baskin & Baskin, 2014; Soltani et al., 2018), and time, for example dormant seeds tend to persist longer in soil (Gioria et al., 2020), and thus it contributes to the maintenance of biodiverse landscapes and species-rich communities (Grubb, 1977). Seed dormancy is an evolutionary trait (Willis et al., 2014) subject to natural selection (Donohue et al., 2005, 2010), but nevertheless it is shaped by phylogenetic relatedness, exhibiting substantial phylogenetic clustering (Carta et al., 2022a).

Numerous studies conducted at different scales from microhabitats to biomes have demonstrated that temporal changes from unfavourable to favourable environments for germination can trigger dormancy loss by interacting with a complex of morphological and physiological seed traits (Baskin & Baskin, 2021). The biological mechanisms controlling dormancy induction and dormancy release (see Supporting Information Notes S1 for further details) are the foundation of the current seed dormancy classification by Baskin & Baskin (2021) that includes nondormancy (ND) and five classes of dormancy: physiological (PD), physical (PY), combinational (PY + PD), morphological (MD) and morphophysiological (MPD).

Observations of nonrandom distribution of seed dormancy classes across biomes have prompted research projects aiming to understand the drivers of dormancy–environment relationships. Many species with ND seeds occur in frost-, fire- and drought-free environments, such as tropical rainforests (Jurado & Flores, 2005; Rubio de Casas et al., 2017; Zhang et al., 2022); however, species with ND seeds also occur in all major vegetation zones on earth (fig. 12.1 in Baskin & Baskin, 2014). By contrast, species that occur in regions with seasonal climates or in those subject to strong stochastic disturbance such as fire (Collette & Ooi, 2021; Pausas & Lamont, 2022) usually have some kind of seed dormancy. A high proportion of species with dormant seeds often has been reported for temperate, arcto-alpine and arid environments (Baskin & Baskin, 2003; Rubio de Casas et al., 2017; Fernandez-Pascual et al., 2021). These patterns seem to be consistent across different spatial (from microhabitats to biomes) and temporal (past and present climate) scales, as well as among species of different life forms (Zhang et al., 2022). For example, decreasing mean annual temperature (MAT) increased the proportion of species with PD seeds in a montane flora (Rosbakh et al., 2022), whereas increasing rainfall seasonality led to an increasing proportion of PY species (Collette & Ooi, 2021).

Yet, most of this research has been either conducted at regional (Rosbakh et al., 2022) or intracontinental (Collette & Ooi, 2021) scales or limited to one lineage (e.g. Fabaceae; Wyse

& Dickie, 2018) or biome (e.g. alpine; Fernandez-Pascual et al., 2021). The two existing global-scale studies (Baskin & Baskin, 2003; Zhang et al., 2022) suggested a few climate–dormancy relationships, yet their strength has never been tested explicitly (i.e. no metrics of the corresponding models' performance were reported). Importantly, previous research tended to ignore differences between dormancy classes (i.e. in most studies, the focus was on nondormant vs dormant seeds) that might obscure details of the underlying selection pressures and evolutionary processes involved in the control of germination timing (Wyse & Dickie, 2018). Finally, the other selective pressures unrelated to global climate-driven dormancy patterns such as fire have not been recognized in these recent studies (Pausas et al., 2022). Taken together, we still lack a comprehensive global perspective on the evolutionary and environmental drivers of ND and the different seed dormancy classes along with their relative contribution in determining adaptive strategies of plant regeneration from seeds.

Here, we close this gap in knowledge by examining current geographic patterns and drivers of seed dormancy variation at a global scale. Using an extensive data set on seed dormancy for > 10 000 species with > 4 million georeferenced occurrences covering all of the world's biomes, we first explore the global biogeographic patterns of ND and seed dormancy classes by determining their proportions ('dormancy profile') in the world's main biomes. Furthermore, we used phylogenetically informed Bayesian statistics, to formally test whether macroscale variability in climate and fire regime drives variability of seed dormancy sensu lato (i.e. nondormant vs dormant seeds) and the five classes of seed dormancy. Specifically, we re-test and quantify the previously established link between macroclimatic temperature and precipitation variability and seed dormancy (i.e. climatically variable environments select for dormant species; Baskin & Baskin, 2003; Jurado & Flores, 2005; Pausas et al., 2022; Zhang et al., 2022). By reconducting this analysis separately for each of three most common dormancy classes (PD, M(P)D and PY/PY + PD), we capture the diversity of dormancy strategies developed by plants as an adaptation to unfavourable environments. Finally, in both analyses, we include fire regime, an alternative driver of seed dormancy unrelated to climate-associated bet-hedging (Pausas et al., 2022; Pausas & Lamont, 2022).

Materials and Methods

Seed dormancy data

We used two previously published large data sets on seed dormancy of c. 14 000 (Baskin & Baskin, 2014) and c. 3000 (Rosbakh et al., 2020) species, which were augmented by data on c. 1000 species published between 2014 and 2020 in peer-reviewed journals (Table S1). All species in the data set were first classified into nondormant (ND) and dormant (D). The species with dormant seeds were further classified into five dormancy classes following (Baskin & Baskin, 2021):
(1) physiological dormancy (germination prevented by the seed's internal balance of ABA/GA);
(2) morphological dormancy (germination prevented by a small or underdeveloped embryo at the time of dispersal);

(**3**) morphophysiological dormancy (germination prevented by both physiological and morphological dormancy);

(**4**) physical dormancy (germination prevented by a water-impermeable ('hard') seed or fruit coat); and

(**5**) combinational dormancy (PY + PD; germination prevented by both physical and physiological dormancy).

Because of their similarity in underlying dormancy mechanisms and the relative rareness in the data set, species with MD and MPD and those with PY and PY + PD dormancy were grouped and analysed together in combined 'M(P)D' and 'PY (PD)' groups, respectively. Six *Caragana* (Fabaceae) species with a mixture of dormant states (e.g. different studies reported either ND or PY; Table S1) were treated as dormant, with the reported dormancy class. All species names were standardized against 'The Plant List' (2010).

Environmental data/macroclimatic predictors

To characterize climatic requirements for each species, we used the geographic coordinates from the Global Biodiversity Information Facility (GBIF) as curated and provided by Carta *et al.* (2022b). All records from the GBIF underwent cleaning by discarding occurrence records without species identification, flagging records with missing or badly formatted global positioning system (GPS) coordinates and identifying records potentially associated with biodiversity institutions, country's capital, country's political centroid, having zero latitude and longitude, equal latitude and longitude or having coordinates falling in the open ocean (see Carta *et al.*, 2022b for a full description of the method).

To exclude underrepresented species (i.e. limited geographical representation), we considered only species with > 10 recorded locations. Then, for each coordinate, we extracted data on bioclimate (mean annual temperature (MAT, 'BIO1') and total annual precipitation (TAP; 'BIO12')) and their seasonal variability (temperature annual range (TempR; 'BIO7') and precipitation seasonality (PrecipS; 'BIO15')) from the WORLDCLIM database (Fick & Hijmans, 2017). We selected these climatic variables because previous studies have shown that they have strong predictive power in explaining dormancy patterns across large scales (Rubio de Casas *et al.*, 2017; Collette & Ooi, 2021; Zhang *et al.*, 2022). To quantify the local wildland fire activity, we used present potential fire season length ('FSL') in months as described by Senande-Rivera *et al.* (2022).

Finally, using the extracted MAT and TAP data, we determined species affinity to one or more of the world's biomes (Whittaker, 1970) using the package PLOTBIOMES (https://github.com/valentinitnelav/plotbiomes).

Statistical analysis

Univariate modelling All statistical analyses were performed using the R software v.4.2.0 (R Core Development Team, 2022).

To estimate the effects of climatic variability on seed dormancy *per se* and on dormancy classes, we fitted Bayesian logistic phylogenetically informed generalized mixed models using the MCMCGLMM package (Hadfield, 2010). The main advantage of this approach is that it accounts for nonindependence among species by including the phylogenetic relationships as a random variable; the phylogenetic tree for all the study species was compiled using the R package V.PHYLOMAKER (Jin & Qian, 2019).

In all models, dormancy, the response variable, was a binary response variable (0 – ND or 1 – dormant; in the case of remaining regressions 1 refers to a particular dormancy class). One model was fitted on nondormant vs dormant seeds and one for each dormancy class (PD, M(P)D and PY(PD), i.e. we assessed each dormancy class against all other seed dormancy classes). The fixed effects of the models (i.e. the predictors) were the climatic variables and fire season length averaged per species (as a median), that is species macroclimate preferences were expressed as an average MAT, TAP, TempR and PrecipS and as a median over all species occurrences in our data set. Thus, a unit of observation in the analysis was a species occurrence with corresponding (pyro)climatic variables. All variables were centred and scaled to unit variance so their effects could be compared.

In all analyses, we used weakly informative Gelman priors (Gelman *et al.*, 2008; Hadfield, 2010) with parameter expanded priors for the random effects and residual variance fixed to 1 (Hadfield, 2010). Each model was run using four chains of 500 000 MCMC steps, with an initial burn-in phase of 50 000 and a thinning interval of 100 (de Villemereuil & Nakagawa, 2014). Parameter estimates were computed by combining the output of the four chains. From the resulting posterior distributions, we calculated mean parameter estimates and 95% credible intervals (CIs). Significance of model parameters was estimated by examining CIs. Parameters with CIs overlapping zero were considered to be nonsignificant. We also evaluated the explanatory power of our models by computing the conditional R^2 (i.e. the proportion of variance explained by both the fixed (the climatic variables and fire season length) and random factors (the phylogeny)) and the marginal (i.e. the proportion of variance explained by the fixed factors only) using the approach described by (Nakagawa *et al.*, 2013) with code available at https://github.com/itchyshin/R2. Multicollinearity was not a problem since the models' predictors were weakly correlated with each other (Fig. 1).

Multivariate ordination To visualize the relationships between kinds of seed dormancy and ND and species' climatic requirements, we used principal component analysis (PCA) implemented in the package FACTOMINER (Lê *et al.*, 2008). First, we predicted dormancy classes for each species by fitting phylogenetic binary generalized mixed models with the same sets and predictors as above for the univariate modelling. Next, predicted probabilities of ND or of dormancy class for each species and the climatic requirements and fire regime to which they are exposed were used in the multivariate ordination.

Results

The final data set included 10 170 angiosperm plant species representing 305 families, for which we had 4033 119 occurrence data points covering all of the world's biomes (Figs 1, 2).
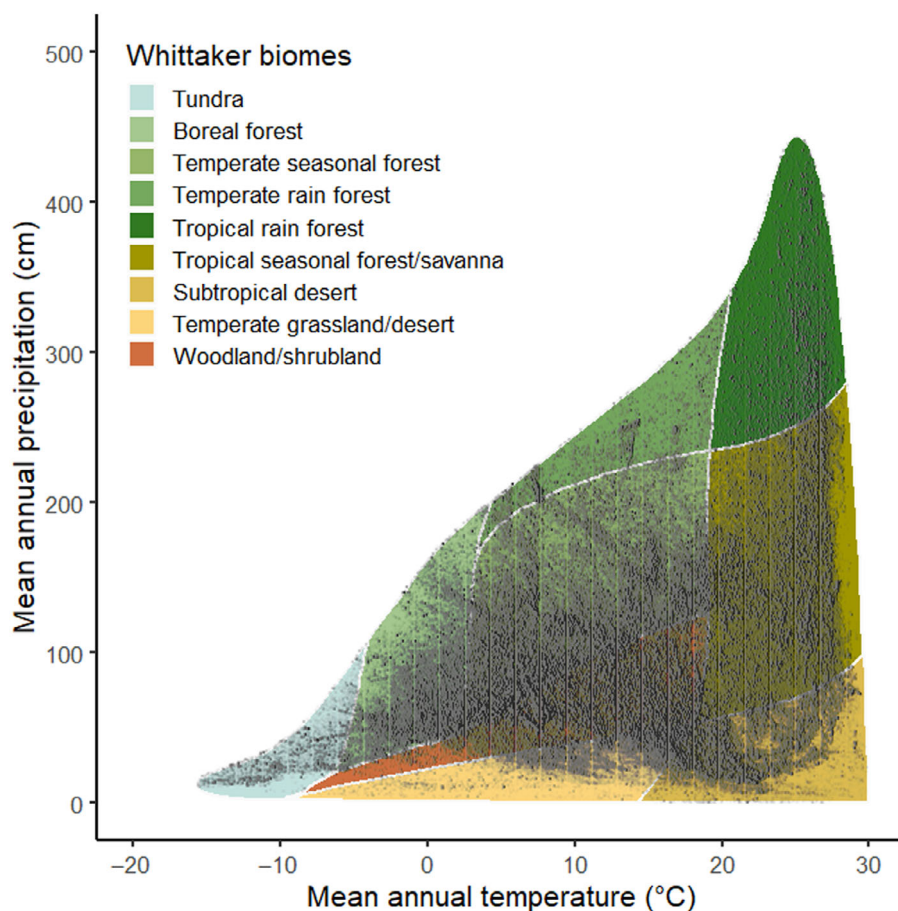
Fig. 1 Distribution of occurrence data for 10 170 study species (grey dots) within world's biomes (Whittaker, 1970). The species occurrence (one grey dot corresponds to one occurrence record) data were obtained from the Global Biodiversity Information Facility (www.gbif.org; Carta *et al.*, 2022b).

Most of the study species (8298 or 82%) had dormant seeds, among which PD (5486 species or 54%) was the most common class of dormancy (from 43% of all species in tropical rain forests to 68% in tundra or boreal forest; Fig. 2) followed by PY(PD) (1499 species or 15%) and M(P)D (1313 species or 13%). The relative proportion of ND seeds ranged from 7% in boreal forest to 31% in tropical rain forest.

The highest relative proportion of PY(PD) species (21%) was in subtropical deserts and lowest in the tundra biome (4%). The proportion of M(P)D species was highest in tundra and boreal forest (18% and 17%, respectively) and the lowest in subtropical desert (7%).

Univariate modelling

The model estimating distribution of ND vs D seeds revealed that all climatic variables had significant effects on seed dormancy patterns, while fire season length did not have any effect on the probability of species having dormant seeds (Table 1; Fig. 3). Specifically, increasing climate severity (both decreasing MAT and TAP) increased the proportion of species with dormant seeds; their effect sizes were quite similar (MAT: 0.40, TAP: 0.51; Table 1). Climatic seasonality significantly affected seed dormancy class (including ND) distribution, with the strongest effects detected for temperature annual range (effect size: −0.77) and precipitation seasonality (effect size: 0.17).

Physiological dormancy species also were affected only by the climatic variables, with a high proportion of species having PD in relatively drier climates (effect sizes for TAP: −0.50). Increasing annual range of temperature had a significant positive effect on proportion of PD species (0.42; Table 1; Fig. 3). Precipitation seasonality had a small negative, yet significant effect on PD (effect size: −0.18). Mean annual temperature had no significant effect on PD.

The model for M(P)D species revealed that increasing MAT negatively affected (effect size: −0.41), the proportion of species with M(P)D (Table 1; Fig. 3). Climates with high precipitation seasonality had a significantly smaller proportion of M(P)D species (−0.23), whereas temperature seasonality and total annual precipitation had no significant effects on distribution of species with M(P)D.

Temperature seasonality had the strongest effect on distribution of species with PY(PD), with a highly seasonal climate favouring this dormancy class (effect size: 0.65; Table 1; Fig. 3). Increasing TAP also had a strong significant negative effect on PY species (−0.57; Table 1). Neither mean annual temperature nor precipitation seasonality had a significant effect on PY species.

Fire season length had no significant effects on either distribution of species with dormant seeds or on distribution of specific classes of dormancy or ND (Fig. 3; Table 1).

Interestingly, the predictive power of all models was relatively weak, as the marginal R^2s were relatively small in all the models.
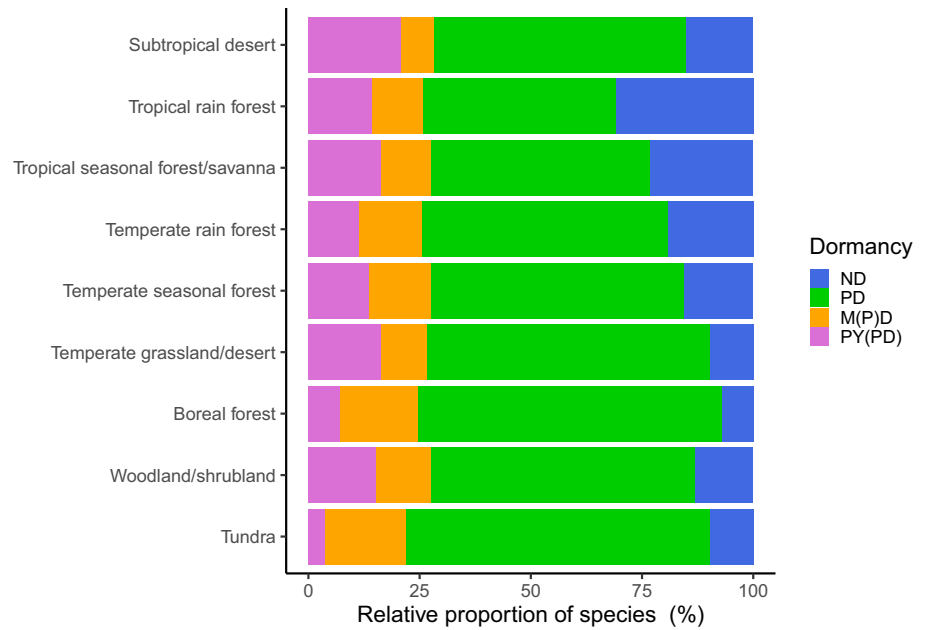
Fig. 2 Relative proportion of three dormancy classes and nondormancy across the world's biomes. ND, nondormant; PD, physiological dormancy; M(P)D, morphological and morphophysiological dormancy (combined); PY(PD), physical and physical-physiological dormancy (combined).

Table 1 Effects of macroclimate and fire season length on distribution of ND and three dormancy classes across the globe as determined from Bayesian logistic phylogenetically informed generalized mixed models.

| Dormancy kind | Mean parameter estimate | | | | | R^2 marginal | R^2 conditional |
	Mean annual temperature (BIO1)	Temperature annual range (BIO7)	Total annual precipitation (BIO12)	Precipitation seasonality (BIO15)	Potential fire season length (FSL)		
Nondormancy (ND)	**0.40**	**−0.77**	**0.51**	**0.17**	0.06	0.09	0.83
Morphological dormancy (M(P)D)	**−0.41**	0.11	0.34	**−0.22**	−0.06	0.02	0.83
Physiological dormancy (PD)	−0.19	**0.42**	**−0.50**	**−0.18**	−0.03	0.03	0.87
Physical dormancy (PY(PD))	0.15	**0.65**	**−0.57**	0.21	−0.11	0.05	0.81

Bold entries indicate parameter estimates significantly different from zero ($P < 0.05$).

The cumulative proportion of variance explained by a model was highest in the ND-D model ($R^2 = 0.09$) followed by the PY(PD) (0.05), PD (0.03) and M(P)D (0.02) models. By contrast, conditional R^2s were higher than 0.80 in all the models, showing the major contribution of phylogenetic relationships on variation of dormancy class or ND.

Multivariate ordination

Variation in seed dormancy and ND and their relationship with climate can be summarized by two principal components (PCs) that together accounted for 58% of the total variance (Fig. 4). PC1 explained 38% of the variance and loaded most heavily and positively on ND, MAT and TAP and negatively on PD and M(P)D. Thus, PC1 separates species with ND seeds occurring in stable, warmer and wetter climates from species with dormant seeds (with both M(P)D and PD) occurring in comparatively harsher climates with lower annual temperatures and precipitation and higher temperature seasonality.

PC2 explained 19.9% of the total variability. The main contributing variables along axis 2 were PY proportion, precipitation seasonality, fire season length (all positively loaded on the PC2) and TAP (negatively loaded on the PC2). That is, this vertical axis ordered the occurrence of species with PY seeds in drier climates with high seasonal variability in precipitation from the occurrence of species with ND seeds in wetter, stable climates with comparatively short fire seasons.

The intermediate loading of fire season length on axes 1 and 2 suggests that species occurring in regions with pronounced fire season tend to have either PY, PD or ND seeds.

Discussion

Climate drives global distribution of species with dormant seeds

Dormancy strongly dominated over nondormancy in all of the world's biomes, and a comparatively large proportion of species
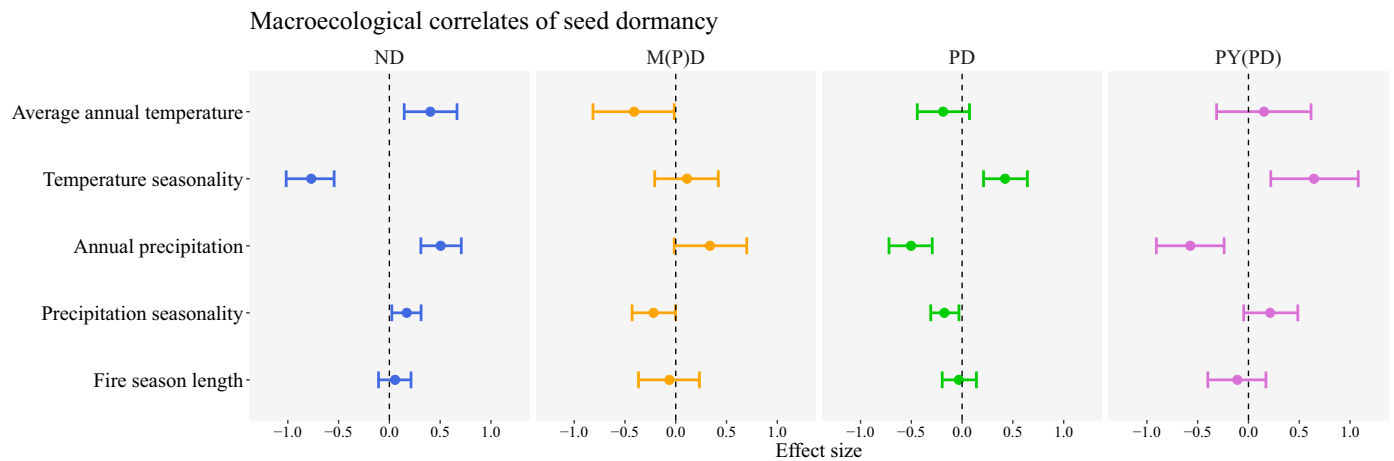
Fig. 3 Climatic and fire effects on proportion of nondormancy (ND) and of three seed dormancy classes according to the binomial phylogenetic mixed models with Bayesian estimation (MCMC$_{GLMMS}$). M(P)D, morphological and morphophysiological dormancy (combined); PD, physiological dormancy; PY (PD), physical and physical-physiological dormancy (combined). Closed circles indicate the posterior means of the interaction effect size. Horizontal bars represent the 95% credible intervals. Dashed vertical line indicates zero effect. When the credible intervals overlap with the zero-effect line, the interactive effect is not significant.
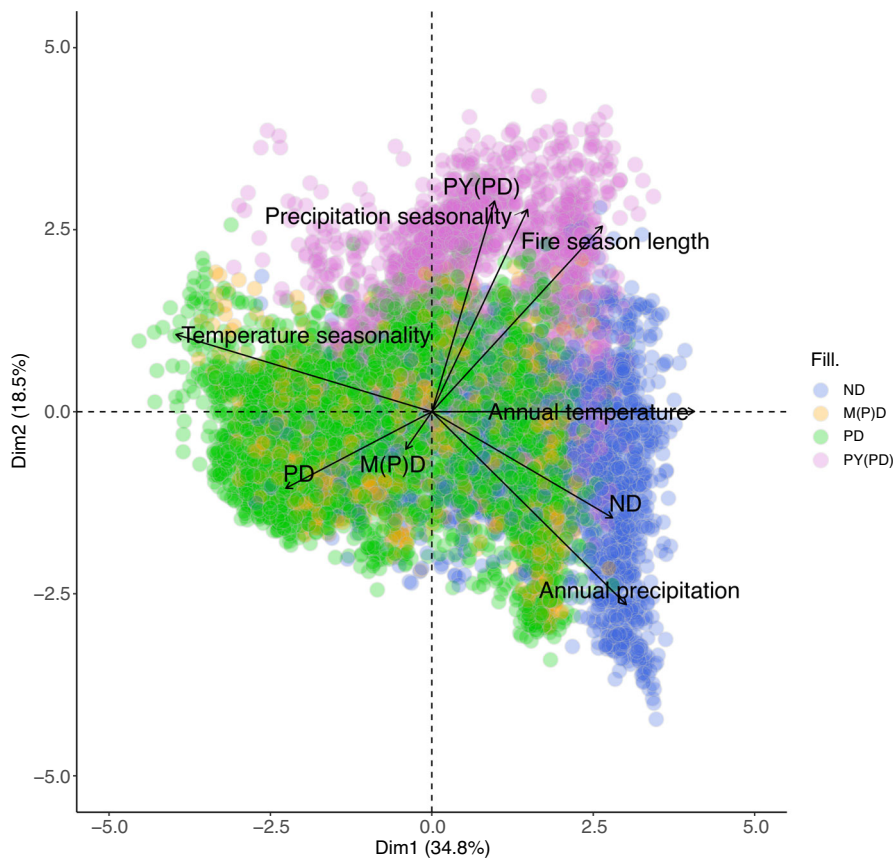

Fig. 4 Principal component analysis (PCA) ordination summarizing the relationships among three seed dormancy classes and nondormancy and macroclimate. Each closed circle corresponds to a species coloured by its dormancy class. M(P)D, morphological and morphophysiological dormancy (combined); ND, nondormant; PD, physiological dormancy; PY(PD), physical and physical-physiological dormancy (combined).

with ND seeds (> 25%) is found only in tropical rain forests, seasonal forests and savannas. This finding suggests that species evolved a strategy to maximize regeneration from seeds, which varies in function of a different combination of macroenvironmental variables.

Our findings support, on a global scale and in an explicitly phylogenetic framework, the results of previous studies that dormancy is prevalent in climatically unfavourable regions for

seedling recruitment (Jurado & Flores, 2005; Collette & Ooi, 2021; Zhang *et al.*, 2022). A comparison of effect sizes of the corresponding model indicates that climate seasonality in terms of both temperature and precipitation is a much stronger driver of global dormancy patterns than general climatic favourability (in terms of mean annual temperature and precipitation). Thus, seed dormancy promotes the timing of germination to periods of the year with the lowest probability of frost

(e.g. temperate climates) or drought (e.g. Mediterranean climates); that is, seed dormancy is a general adaptation for regeneration of plant species from seeds in climates that are seasonally unfavourable for plant growth (Venable, 2007; Rubio de Casas *et al.*, 2017; Wyse & Dickie, 2018; Collette & Ooi, 2021).

Different kinds of dormancy as specific solutions to climatic unfavorability

The proportion of species with PD, M(P)D and PY(PD) seeds followed nonrandom patterns along the macroenvironmental gradients. Physiological dormancy was positively associated with general climate unfavourability, and the proportion of species with PD seeds increased with decreasing total annual precipitation and with an increasing range of seasonal temperature variation. This result suggests that PD is the main adaptive mechanism to avoid seed germination in dry climates with limited water availability for seedling establishment such as hot (semi)deserts (Venable, 2007) or any climate with seasonal cycles of temperature and humidity (Van Assche *et al.*, 2003; Collette & Ooi, 2021). According to our model, one important characteristic of PD-dominated regions is the relatively uniform distribution of precipitation over the year (or pulse precipitation events in deserts at any time of the year), and PD was significantly, negatively correlated with precipitation seasonality. This finding correlates well with the biological mechanisms controlling PD. That is, many seeds with PD require a long enough supply of moisture to complete seasonal temperature stratification that is required to increase low embryo growth potential ('cold and warm stratification' *sensu* Baskin & Baskin (2021)). However, some seeds with nondeep PD can afterripen at warm dry conditions.

Morphological dormancy was more common in forest-dominated biomes with precipitation evenly distributed over the year, with a tendency to be more common in colder climates (i.e. temperate and boreal forests). From the ecological point of view, M(P)D seems to be an adaptive solution to coordinate seed germination with conditions suitable for seedling establishment regeneration windows in woodlands. For example, many herbaceous species with M(P)D occurring in the temperate deciduous forests of the Northern Hemisphere complete their life cycle and disperse seeds in spring before canopy closure, thereby avoiding competition for light. In some species, the embryo continues growth and develop throughout the summer months until it reaches a size at which germination could proceed in autumn, when light conditions again become suitable for growth of small seedlings and juveniles (Ali *et al.*, 2007; Newton *et al.*, 2015). However, depending on the level of M(P)D embryo growth may occur only during cold stratification (supported by the significant negative association of this dormancy kind with mean annual temperature), and embryo growth in some species does not occur until after seeds have received a period of warm stratification (Baskin & Baskin, 2014). In this context, the steady supply of moisture (as supported by the significant negative correlation

between M(P)D and precipitation seasonality) supports the water demand for the continuous embryo growth.

Physical dormancy was significantly associated with dry climates characterized by strong seasonal temperature fluctuations (e.g. deserts, savanna, temperate grasslands and Mediterranean woodlands and forests). These results support previous observations that the water impermeable (hard) seed coat protects PY seeds from desiccation during the dry seasons (Baskin & Baskin, 2000) and helps to maintain a low seed moisture content, thereby preventing germination (Pausas & Lamont, 2022). However, unlike PD that is broken during the unfavourable season for seedling establishment, opening of the water gap, that is breaking of PY, occurs at the beginning for the favourable season for plant growth. The dormancy breaking factors (i.e. factors that ease the water gap to open) in the PY seeds include, for example, high temperatures or fluctuating temperatures (McKeon & Mott, 1982; Vazquez-Yanes & Orozco-Segovia, 1982) or heat from fire, (Ooi *et al.*, 2014; see Notes S1). Traditionally, PY has been considered as an effective mechanism evolved in fire-prone ecosystems for timing seedlings to emerge into the postfire environment (Keeley, 1991; Collette & Ooi, 2021), operating via dormancy break by exposure to high temperatures during fire events ('heat-released dormancy'; Pausas & Lamont, 2022). Although the PCA showed the tendency for some PY species to occur in dry seasonal climates with a long potential fire season, the results of the Bayesian generalized mixed models showed that fire did not have any significant effects on the occurrence of PY. Additionally, we detected no significant fire effects on PD. In fire-prone ecosystems, products of combustion, such as smoke, are suggested to trigger postfire seedling establishment by dormancy break in species with PD seeds, that is 'smoke-released PD' (Pausas & Lamont, 2022). Furthermore, in fire-prone ecosystems, it is suggested that a large proportion of species with ND seeds exhibit rapid germination in short windows of opportunity following a fire, that is the 'non-dormancy syndrome' of Pausas & Lamont (2022). Cumulatively, our results contradict the assumption that fire events are the main dormancy-breaking factor in highly flammable ecosystems (Pausas & Lamont, 2022).

Alternatively, the lack of significant results may be due to the natural potential length of the fire season we used to characterize global pyroclimate, which does not include either fire severity or frequency. Furthermore, the binary character of dormancy variables used in the analysis (0 – absent, 1 – present) could mask a large variation in dormancy-breaking temperature thresholds, which serve as sensitive and effective mechanisms for germination timing in postfire environments (Collette & Ooi, 2021; Pausas & Lamont, 2022). Finally, fire season length and water availability in an ecosystem are highly correlated, which makes it difficult to test the separate effects of fire and climate on distribution of PD and PY species. Below, we discuss potential caveats of our approach that might explain the deviation of results obtained from the assumptions. Therefore, further work based on extensive characteristics of fire regimes is needed to quantify the link between dormancy and fire.

Climate is a weak predictor of dormancy patterns at global scale

While climate has been extensively linked to predicting dormancy patterns (Rubio de Casas *et al.*, 2017; Wyse & Dickie, 2018; Zhang *et al.*, 2022), we found that all climatic variables used in this study had low predictive power (the largest conditional R^2 was 0.1 in the dormancy vs nondormancy model). Surprisingly, most previous studies on global seed dormancy patterns have not quantified the dormancy–macroclimate relationship, especially for various kinds of dormancy. To the best of our knowledge, this has been considered only by Rubio de Casas *et al.* (2017) in their study on global dormancy patterns in Fabaceae. Yet, the R^2 values reported in the study included seed size and phylogeny effects. Our unexpected findings suggest that macroclimate is not the main driver of dormancy and support the view that multidimensional (spatially and temporally) selective pressures shaped variability in dormancy at the global scale.

In fact, dormancy provides multiple benefits to seeds (Pausas *et al.*, 2022), including adaptation to disturbance (Fenner & Thompson, 2005), endozoochorous dispersal (Jaganathan *et al.*, 2016), increased microbial activities and defence against predators in soil (Paulsen *et al.*, 2014; Dalling *et al.*, 2020). Alternatively, timing seed germination to the most favourable time/season could be achieved by (highly specific) requirements for temperature and water that can be much more sensitive to environmental fluctuations as compared with dormancy. Furthermore, dormancy patterns may not coincide with environmental variability due to biogeographic and phylogenetic constraints but see Zhang *et al.* (2022) who found no significant effects of paleoclimate on dormancy patterns. As for the former, limited dispersal can confine certain kinds of dormancy to regions where speciation events took place in the past or large-scale dispersal events (e.g. post- and periglacial recolonization) could transport dormancy far from where it evolved (Jurado & Flores, 2005; Coelho *et al.*, 2019). Finally, the low predictive power of our dormancy models could be rooted in the binary nature of the dormancy variables used that do not account either for evolvability or intraspecific variability of dormancy. Another reason for the relatively low model performance could be well-known biases in the species distribution data (e.g. fewer records in lower latitudes and overrepresentation of common species). Thus, future studies should consider the fact that a given species may have variation in the degree of dormancy within a given dormancy class, particularly for PD (Fernandez-Pascual *et al.*, 2019). Also, although this work is to date the largest study of global seed patterns, it must be considered that it only represents 3% (10K out of 300K) of angiosperm diversity. Thus, more work is needed to study and measure seed traits, including dormancy, in the world's flora, especially in the understudied regions, such as the tropics and the Arctic (e.g. Visscher *et al.*, 2022).

Competing interests

None declared.

Author contributions

SR, AC and EF-P conceived the study. SR and SSP collated the data and AC conducted the analyses. All authors contributed to the writing process, which was led by SR. All authors proofed and corrected the manuscript. SR and AC contributed equally to this work.

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Data availability

Data used in the analysis are publicly available in Willis *et al.* (2014), Rosbakh *et al.* (2020) and in the Table S1.

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Supporting Information

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

Fig. S1 Correlation matrix for (pyro)climatic predictors used to model seed dormancy global pattern (Pearson's correlation coefficient, r).

Fig. S2 Distribution of the species occurrence data used in the study.

Notes S1 Main kinds of seed dormancy and their environmental drivers.

Table S1 Seed dormancy data for $c.$ 1000 species between 2014 and 2020 in peer-reviewed journals.

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