Letters

Bet-hedging and best-bet strategies shape seed dormancy

Seasonality and the bet-hedging strategy

Seed dormancy (i.e. delayed germination even when conditions are favourable) is a key plant characteristic that occurs among many species worldwide. But, what selective pressures led to seed dormancy? A recent study provides a major analysis of the factors driving this trait at the global scale (Zhang *et al*., 2022). Using *c*. 12 000 species and 10 million records across the globe, they conclude that dormancy is a strategy for plants living under 'seasonal/unpredictable' environments; and suggest that bet-hedging could be the major mechanism behind the pattern. To reach their conclusions the authors relate the proportion of species with dormant seeds in a grid-cell global map against climate variables related to annual precipitation, temperature and seasonality. Then they showed that the most significant variables were those related to climate seasonality that they equate with unpredictable climates (although seasonal climates usually are highly predictable in their seasonal cycles).

The mechanism by which an unpredictable environment selects for seed dormancy is via the bet-hedging strategy, that is, spreading germination over a number of years to reduce year-to-year variation in fitness but taking advantage of exceptionally good years for establishment (Cohen, 1966; Philippi, 1993). However, actual unpredictability (i.e. interannual variability; Cowling *et al*., 2005) was not tested by Zhang *et al*. (2022). Furthermore, it is difficult to think of a mechanism for the selection of dormancy as an adaptive response to seasonality as such (i.e. predictable intra-annual variation); here nondormancy would appear to be equally adaptive if the same seasonal conditions suitable for germination are repeated every year. There may be some correlation between seasonality and unpredictability but, from a biological point of view, they are quite different constraints and select for different plant strategies. Note that in all of these studies (and here as well, unless otherwise stated), seed dormancy refers to inherent (also called primary or organic) dormancy, which is dormancy driven by seed characteristics, and includes physical, physiological and morphological dormancy (Baskin & Baskin, 2014). Once this dormancy is broken (or if the seeds produced are nondormant), seeds still do not germinate until the hydrothermal conditions are suitable. Overcoming this additional, environmentally imposed dormancy is controlled by when the wet season actually starts or local temperatures reaching certain thresholds, but this imposed dormancy is not considered in current broad-scale studies.

The importance of climatic variables, including seasonality, as correlates of (inherent) dormancy aligns well with other recent global studies focused on Fabaceae (Rubio de Casas *et al*., 2017; Wyse & Dickie, 2018) and on germination responses at the European scale (Carta *et al*., 2022). Another recent analysis of seedbank data for 2000 species across the globe (Gioria *et al*., 2020) considered binary variables related to habitat type, habitat openness (yes/no) and disturbance (yes/no) in addition to climate, and came up with a different conclusion. They concluded that habitat-related variables (disturbance and canopy openness), but not climate, affected the ability of seed plants to form persistent seed banks, and concluded that dormancy, the prerequisite for seedbanks, is a bet-hedging strategy in unpredictable environments.

Overall, these studies suggest that the mechanism selecting for seed dormancy is the bet-hedging strategy for dealing with unpredictable environments. Although this is notable in some ecosystems (especially arid regions; Cohen, 1966, Philippi, 1993, Venable, 2007), here we draw attention to the fact that there are other selective pressures unrelated to climate-associated bet-hedging that have shaped seed dormancy in many species across the globe but are not recognized in these recent studies. Our own contributions have been centred on seed germination in fire-prone environments, and hence have an emphasis on fire vs climate.

The best-bet strategy

A large part of the world has a seasonal climate with a dry season during which the vegetation is highly flammable (mediterranean, savanna, warm temperate, and dry boreal ecosystems). In these ecosystems, wildfires are frequent. Fire intervals are usually shorter than lifespan of the dominant species; thus, they act as a selective force shaping survival and reproductive traits of plants (Keeley *et al*., 2012). Among the adaptive traits is fire-released seed dormancy (see reviews in Keeley, 1991, Pausas & Lamont, 2022). Fires provide both a mechanism for dormancy release (proximate cause) and conditions (postfire) optimal for germination and establishment (low competition, high resource availability, low predation, low pathogen load) that increase fitness and allow maintenance of the population (ultimate cause). Thus, fires create a unique window of opportunity for recruitment, especially among weakly competitive, shade-intolerant plants. That is, fire is worth waiting for!

In order to benefit from postfire conditions, seeds of many species have acquired the ability to survive the passage of fire and detect presence of the fire gap to initiate germination. Seeds possess two means of detecting a fire event in order to break dormancy and prime the seeds for germination: they are sensitive either to heat or chemicals produced during the combustion of organic matter (collectively called 'smoke', although it may include ash and charcoal). Species with these mechanisms exhibit two syndromes:

heat-released dormancy and smoke-released dormancy (Pausas & Lamont, 2022). The first is associated mainly with physical dormancy and the latter with physiological dormancy, although some seeds may respond to both fire cues (heat may increase permeability to by-products of combustion).

There are 100s of articles that provide experimental evidence among many species of the fitness benefits (enhanced germination and seedling establishment) when their seeds are subjected to smoke or heat intensities compatible with fire (reviewed in Pausas & Lamont, 2022). In most cases, these species accumulate seeds in the soil during their entire lifespan, and recruitment occurs in a single cohort after fire (postfire seeder species; Figs 1, 2, Supporting Information Fig. S1). That is, postfire recruitment occurs in a single pulse after fire. Here selection does not favour spreading the risk of recruitment failure over many years (*bet-hedging*) but, instead, maximizes germination in a single year when conditions are optimal, thus following the first substantial rains after fire. We call this strategy the *best-bet strategy* (Table 1) or *environmental matching* (*sensu* Pausas & Lamont, 2022). Although this strategy entails risks, it has adaptive advantages when fires are sufficiently frequent and predictable to occur within the interval between plant maturation and senescence (Pausas & Keeley, 2014). In these ecosystems, seed-dormancy release is not just a fail-safe response to unpredictable seasonal climates but also a routine response following a stochastic disturbance expected within the lifespan of most species in the plant community.

Fire-released dormancy is prominent in ecosystems that are seasonal and have dense, woody vegetation that limits recruitment of nondormant seeds. Under such conditions, fires are intense (crown-fire ecosystems) and create extensive gaps for recruitment. Prime examples include mediterranean, warm temperate and subtropical shrublands distributed all over the world (Menges & Kohfeldt, 1995; Bradstock *et al.*, 2012; Keeley *et al.*, 2012; Pausas *et al.*, 2021). Fire-released dormancy also is present, but less important, in grassy ecosystems with scattered woody shrubs and trees (surface-fire regimes) such as Brazilian savannas (Zirondi *et al.*, 2019). Fire-released dormancy is almost absent in deserts, extremely cold environments and rainforests; in some of these ecosystems, seed dormancy may be common but unlinked to fire (nonfire-released dormancy), and thus is more aligned to the bet-hedging strategy. For *Helianthemum*, a large genus in Cistaceae, loss of hard-seededness and heat-released dormancy are notable only among a few recently evolved species that now occupy fire-free habitats, such as gypsum outcrops, deserts and saline wetlands (Pausas & Lamont, 2022).

Serotiny (delayed seed release and dispersal) also is a strategy to accumulate seeds over the years, in this case held in closed cones or fruits stored in the plant crown (Lamont *et al.*, 2020). It occurs mainly among conifers (in the Northern Hemisphere), and in a range of families in the Southern Hemisphere (Proteaceae, Myrtaceae, Casuarinaceae, Bruniaceae, and more rarely among Asteraceae, Anacardiaceae and Ericaceae). Fire again is the mechanism for cone/fruit opening and for creating the appropriate environment for dispersal and for suitable recruitment conditions of the dispersed seeds. Consequently, serotinous species recruit

Fig. 1 Examples of massive postfire recruitment from a seed bank as a best-bet strategy: *Convolvulus lanuginosus* (Convolvulaceae) 1-month postfire (top), *Ulex parviflorus* (Fabaceae) 1-year postfire (the dead stem is the mother plant killed by fire) in eastern Spain (middle), and *Pinus attenuata* (Pinaceae) 2-years postfire in southern Oregon USA (bottom). The first two are recruitment from the soil seed bank, the third from a canopy seed bank (serotinous pine). Photos: J. G. Pausas (top and middle) and S. Greenler (bottom). For more examples see Supporting Information Fig. S1.

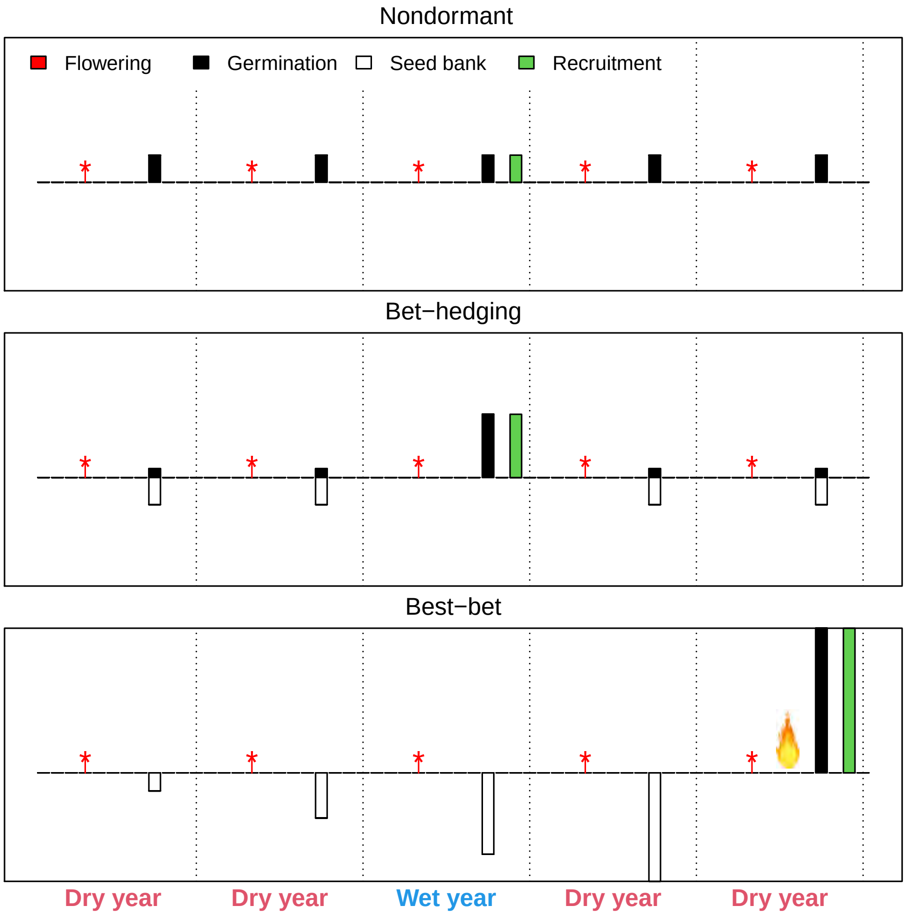

Fig. 2 Schematic representation of the dynamics of seed recruitment for plants lacking seed dormancy (nondormant; top panel), and for plants with dormant seeds following the bet-hedging strategy (middle panel) and the best-bet strategy (bottom panel). The figure shows the moment of flowering (red asterisk; spring), the germination (black bars; autumn), the seed bank in autumn (empty bars), the recruitment 2 months later (green bars) and the fire (flame; summer). As an example, the seasons are considered as in the Northern Hemisphere, and vertical dotted lines are the end of the year. Under the bet-hedging strategy plants germinate every year, but only produce a significant recruitment in the years with the appropriated conditions (here indicated as wet year). Plants under the best-bet strategy do not germinate until a fire (the heat or the smoke) release their dormancy and then most of the seedbank germinates – thus, they maximize the germination in a single (optimal) year.

Table 1 Main characteristics of the evolutionary strategies that select for seed dormancy and seed banks (bet-hedging, best-bet) and a strategy that selects for seed dormancy unrelated to seed bank (spatial bet-hedging), together with the nondormant strategy.

		Strategies that shape dormancy		
	Nondormant	(Temporal) bet-hedging	Best-bet	Spatial bet-hedging
Seed bank	None	Soil	Soil or canopy	None
Germination event*	Annual	Annual	Postfire only	Annual
Level of germination*	High (all of annual crop)	Low (small fraction of interannual crops)	Very high (most of interannual crops)	Med-high (most of annual crop)
Interannual fitness variation*	Low	Low	High	Low
Predictability of germination	High	Low	High	High
Recruitment and establishment	Continuous	Continuous	Single year cohort	Continuous
Fruit type	Variable	Dry	Dry (sometimes fleshy elaiosome)	Fleshy
Disturbance-prone	None	Small/light, unpredictable	Large/intense, predictable	None
Benefits	Low granivory	Spread mortality risk	Optimal establishment conditions	Transport to novel microsites
Climate (where dominant)	Ever-wet, tropical, cold temperate	Arid, alpine	Mediterranean, warm temperate	Tropical forests

*Given the appropriate hydrothermal conditions.

mostly after fire and not during the interfire period. Thus, serotiny (via pyriscence, fire-induced seed release) may also be viewed as an example of accumulating a seed bank as best-bet strategy.

The importance of fire does not mean that climate is unimportant in shaping seed dormancy in fire-prone ecosystems. For instance, summer temperatures determine the heat thresholds for dormancy release to ensure seed bank persistence – by avoiding germination before a fire (Zomer *et al.*, 2022). Under a warming climate, summer temperatures may cross thresholds for dormancy release and stimulate germination under suboptimal conditions, thus depleting the seedbank and jeopardizing the postfire recruitment. In that sense, species with heat-released dormancy may be more sensitive to climate change than species with smoke-released dormancy. In addition, final germination not only depends on (inherent) dormancy release, but also on the hydrothermal conditions for germination (imposed-dormancy release), and this makes seed-bank species sensitive to climatic change. For instance, higher temperatures may maintain imposed dormancy for longer, resulting in reduced postfire germination, despite receiving the appropriate stimulus for dormancy release (e.g. fire; Arnolds *et al*., 2015). Furthermore, many species with seed dormancy that form the seed bank have dry fruits that are dispersed at relatively short distances (myrmecochory, autochory) and thus their potential migration in a rapidly warming planet is limited.

Long-distance seed dispersal

'Bet-hedging' and 'best-bet' are two strategies that select for seed dormancy in order to accumulate a seed bank and thus delay germination until conditions become more suitable. There is a further driver that selects for seed dormancy that does not imply the formation of seed banks. Many seeds have acquired seed dormancy to facilitate long-distance dispersal and thus spread germination across the landscape. The clearest example is dispersal by vertebrate frugivores (endozoochory by birds, bats, mammals and reptiles; Levey *et al*., 2002, Traveset *et al*., 2007). Frugivores consume the fruit pulp and defaecate or regurgitate the seeds far from the mother plant. This means that seeds need to resist passage through the gut and remain intact until arriving at a new microsite for germination. In such a way, plants benefit from long-distance dispersal to a potentially optimal microsite, often including the faecal material acting as fertilizer (Dinerstein & Wemmer, 1988; Traveset *et al*., 2007). Thus, seeds of fleshy fruited species typically are dormant, and scarification through the gut releases their dormancy (chemical and/or mechanical scarification, and more rarely removal of inhibitors in the pulp; Traveset *et al*., 2007). Although bet-hedging spreads germination of seeds accumulated in the seed bank over time, this strategy spreads the annual seed crop across space and thus it could be viewed as a spatial bet-hedging strategy (Table 1).

Concluding remarks

Climate is by no means the only driver of seed dormancy, nor is bet-hedging the only mechanism that shapes dormancy. Correlative studies based on climate datasets are unlikely to capture the diversity of adaptive strategies plants acquired to maximize their fitness; disturbances and species interactions also need to be considered. Despite the ubiquitous presence of fire across the globe (Archibald *et al*., 2013) and through geological time (Scott, 2018), recent seed dormancy reviews (noted above) fail to consider fire as drivers for the evolution of seed dormancy. However, fire-prone ecosystems are hotspots of seed dormancy that allow seed banks to accumulate in both the soil and the canopy (Keeley, 1991; Lamont *et al*., 2020; Pausas & Lamont, 2022). We need to overcome the 'fire blindness' syndrome (*sensu* Pausas & Lamont, 2018) that still seems to prevail in much ecological research. Further studies are needed to understand and quantify the relative importance of the different strategies in various ecosystems across the globe. An interesting test of climate vs disturbance as selective factors would be to compare dormancy in closed forests that seldom burn with species in adjacent regularly burnt shrublands under the same climate. We predict that dormancy and seedbanks would be largely restricted to the fire-prone ecosystems. More research also is needed to understand the environmental conditions that maintain and release imposed dormancy (once inherent dormancy is released or does not apply) as changes in climate cues could be the key to plant success under a changing climate.

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Author contributions

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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 Examples of massive postfire recruitment from seed bank.

Key words: bet-hedging, fire ecology, germination, postfire recruitment, seed dormancy.

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The following Supporting Information is available for this article:

Fig. S1 Examples of massive postfire recruitment from seed bank

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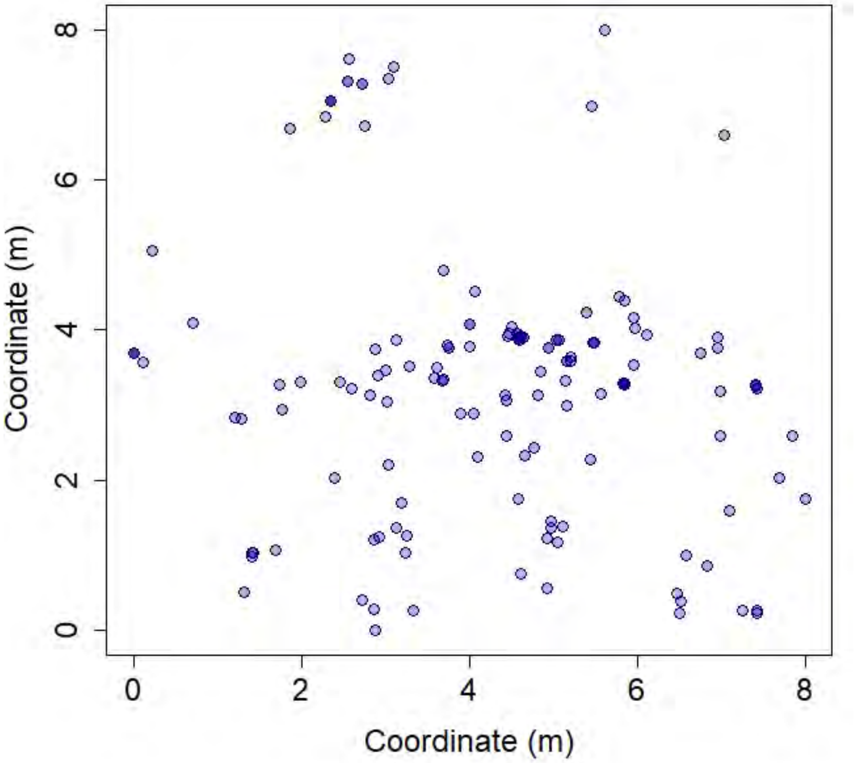
Massive germination from a soil seed bank 3 month after the 2021 fires fire in Marmaris, SW Turkey. Seedlings are mostly of Fabaceae species, and the shrubs are *Arbutus* (just starting to resprout). Photo: Gökhan Ergan.

Coris monspeliensis (Primulaceae) seedlings 8 months postfire, eastern Spain. Smoke-released dormancy. Photo by JG Pausas.

Ulex parviflorus (Fabaceae) seedlings, 1 year postfire in a burned *Pinus halepensis* forest, Beneixama, eastern Spain. Heat-released dormancy. Photo: JG Pausas

Convolvulus lanuginosus (Convolvulaceae) 1 month postfire, eastern Spain. Note that the fire was so intense that it fragmented the limestone rock and the same time that broke seed dormancy. Photo taken the same day and location as the photo in Fig. 1 (upper) of the main text. Photo: JG Pausas

Cistus albidus (Cistaceae) 9 months postfire, eastern Spain. Heat-released dormancy. Photo: JG Pausas



Spatial distribution of 200 seedlings of *Stachystemon axillaris* (Euphorbiaceae) 10 months postfire. Clumps of seedlings (darker colour from overlapping symbols) likely arise from ant nests. Midwest sandplains Perth, Australia. Data collected by Byron B. Lamont.

Seedlings of about 15 shrub species in and around a postfire litter microsite into which serotinous seeds (Proteaceae, Myrtaceae) released by the fire have been blown, and soil-stored seeds already present (Ericaceae, Fabaceae, Proteaceae). Midwest sandplains, Australia. Photo by Byron B. Lamont.

Pinus attenuata (Pinaceae) 2 years postfire in southern Oregon, USA. Serotinous species. Photo: Skye Greeler.

Pinus cortata (Pinaceae), Yellowstone N.P.; serotinous population. Photo: Brian J. Harvey

Pinus muricata (Pinaceae), California. Serotinous species. Photo: Brian J. Harvey

Pinus brutia (PInaceae), Marmaris, SW Turkey, 3 months after fire. Serotinous species. Photo: Gökhan Ergan.