New Phytologist

Correspondence

The need for mechanistic explanations in (seed) ecology

> *'I would rather discover one cause than gain the kingdom of Persia'.*
> Democritus (460–370 BC)

> *'Data do not understand causes and effects; humans do'.*
> Pearl & Mackenzie (2018)

Introduction

The increasing availability of global-scale data on plant traits (e.g. Kattge *et al.*, 2020), species distribution (e.g. GBIF.org), climate variables (e.g. Fick & Hijmans, 2017), sophisticated numerical methods (e.g. machine learning tools, R packages) and computing power (e.g. cloud computing) has enabled researchers to understand our biosphere in an unprecedented manner (Farley *et al.*, 2018). However, these techno-scientific advances come with a cost. Researchers with sufficient technical skills in data management can now study global patterns and produce numerically sophisticated and apparently robust papers, without a clear hypothesis to test nor attempt to interpret any patterns from a mechanistic perspective. In addition, these broad-scale analyses tend to use the most readily available data rather than necessarily the most relevant data. This is further fuelled by the growing culture that values 'fast' science over research that may take years to complete (the *publish-or-perish* culture; Sarewitz, 2016). As a consequence, there is an increase in research based on correlating 'everything' to see if any patterns emerge, instead of a hypothesis-driven approach (see Calude & Longo, 2017 for examples of spurious correlations). An outcome for plant ecology is that key factors in determining plant fitness, such as fire regime, light availability, herbivory, pollinator availability and other biotic interactions, are underconsidered in broad-scale studies, as they are less available than climate information, in particular. This is exacerbated by the long-standing belief that climate is the major factor shaping ecological patterns (Pausas & Bond, 2019; Brown *et al.*, 2023). Studying global-scale patterns also tends to hide biological mechanisms, as these act at local scales and may vary across environments; thus, broad-brush approaches may mask key local processes.

In this letter, we highlight the potential for broad-scale correlative studies that ignore mechanisms to hinder progress in ecology. We specifically focus on seed dormancy, but we also provide a few other recent examples to illustrate that this is currently a general problem in ecological studies.

Seed dormancy: patterns and processes

Recent studies using thousands of species and millions of records have concluded that seed dormancy is an adaptive strategy for plants living under seasonal climates (Rubio de Casas *et al.*, 2017; Wyse & Dickie, 2018; Zhang *et al.*, 2022; Rosbakh *et al.*, 2023 – all published in *New Phytologist*). Note here that the information available in large databases is for seed dormancy types that reflect prolonged (multi-year) dormancy (inherent or true dormancy; Baskin & Baskin, 2014) and not for temporary dormancy that may be imposed by within-year adverse environmental conditions. These studies have consistently emphasized that physical dormancy (hard seeds) is linked to strong seasonal fluctuations. This conclusion is derived from correlations between species-specific seed dormancy records from global databases and annual climatic data (precipitation and temperature seasonality from global climate maps) using species locations (from GBIF.org). However, there are problems in expecting dormancy to be selected for as an adaptive response solely to climate seasonality (i.e. predictable *intra-annual* variation). The question arises as to why seeds would adapt to survive for many years in the soil seed bank (seed dormancy) if there is predictable intra-annual variation? They could simply germinate once mild temperatures and soil moisture were restored in the next favourable season (environmentally induced dormancy; Pausas *et al.*, 2022; Pausas & Lamont, 2022) – but they do not.

Seed dormancy is not an adaptation to intra-annual variability but to the presence of strong and unpredictable *inter-annual* variability (Cohen, 1966; Philippi, 1993; Venable, 2007). In this case, dormancy functions as a bet-hedging mechanism that allows seeds to remain dormant over a number of years, reducing year-to-year variation in fitness should germination be induced every year, and instead taking advantage of exceptionally good years for seedling recruitment.

Since the correlation between seed dormancy and seasonal climates has no clear causal basis, one must consider what other factors might drive this relationship. For example, many ecosystems with seasonal climates are fire-prone. Fire provides both a mechanism for dormancy release (via heat or smoke) and creates conditions (postfire) that are optimal for germination and establishment (low competition, high resource availability, minimal predation, low pathogen load). There is much experimental evidence to show that fire-type temperatures (i.e. greatly exceeding summer temperatures) increase germination of many species with physical dormancy, whereas hot summers do not (Fig. 1). Experimental evidence also shows that scarification (simulating fire heat) greatly increases germination compared with changes in season (Ruiz-Talonia *et al.*, 2023; Supporting Information Fig. S1). Thus, fire-induced dormancy release increases plant fitness as it is uniquely synchronized with optimal germination conditions (best-bet strategy; Pausas *et al.*, 2022). Therefore, the

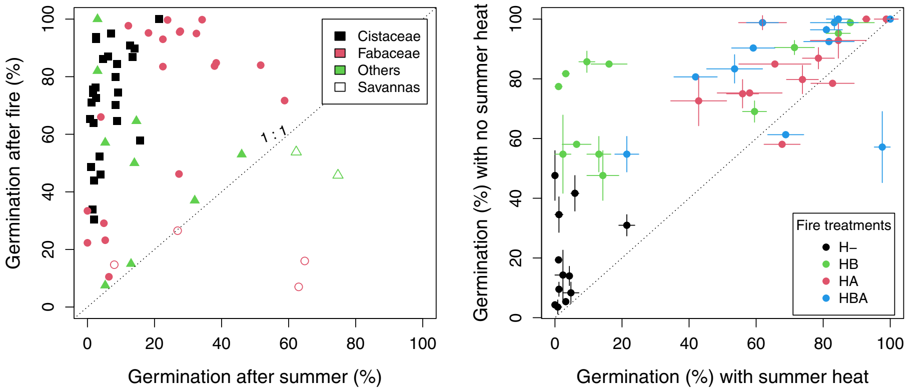

Fig. 1 Germination (%) in experiments comparing fire and summer treatments. Left panel: germination of 68 populations or species subjected to both fire- and summer-type heat treatments. Colours (in closed and open symbols) refer to Cistaceae (black), Fabaceae (red), and others (green). Closed symbols refer to Mediterranean and warm temperate ecosystems, open symbols refer to savannas. Dotted line gives the 1 : 1 relationship, that is, points above the line have higher germination levels after fire-type heat than after summer-type heat. Adapted from Pausas & Lamont (2022). Right panel: germination with no high temperatures in summer (1 month at 20°C, control, *y*-axis) vs germination with summer heat (1 month at 50°C : 20°C, 12 h : 12 h, *x*-axis) for 12 Cistaceae species. Different colours represent different fire-type heat treatments: no fire heat (H−), fire heat after summer (HA; the most ecologically realistic scenario), fire heat before summer (HB), fire heat before and after summer (HBA; the most ecologically unrealistic scenario). Variability represents SE. Dotted line is the 1 : 1 relationship, that is, points above the line indicate that the heat of summer does not contribute to germination (summer heat reduced germination in most fire treatments and species). Elaborated from Luna *et al*. (2023) and Lamont *et al*. (2024).

underlying driver of the correlation of seed dormancy with a seasonal climate may be because the vegetation in strongly seasonal climates is also the most fire-prone (Keeley *et al.*, 2012; Lamont, 2022); thus, fire provides a more plausible mechanism to select for prolonged seed dormancy than climate seasonality.

By contrast, a recent correlative study concluded that the fire regime has little to do with seed dormancy and that macroclimate variables were the most (statistically) significant (Rosbakh *et al.*, 2023). However, this study has several conceptual drawbacks. Specifically, for the fire regime variable they considered a single parameter, potential fire season length (PFSL, defined as the average number of months with climatic conditions prone to fire, obtained from Senande-Rivera *et al.*, 2022), a variable not considered as a standard descriptor of the fire regime as it is indirect. It is unclear which of the components of the fire regime this variable is supposed to represent; furthermore, fire regime components are not necessarily correlated, preventing use of a single descriptor (Archibald *et al.*, 2013; Pausas, 2022). Potential fire season length provides no clues about such important components as fire frequency and season in which it occurs, nor about postfire conditions and seedling fitness. The authors do not provide a mechanism linking PFSL with dormancy release. Thus, the use of the term 'fire regime' in the title of Rosbakh *et al.* (2023) is misleading; they have not considered the range of fire variables that are known to describe the fire regime, whereas they used a wide range of variables to describe the climate regime.

The analysis by Rosbakh *et al.* (2023) is then developed from their contention that seed dormancy is most adaptive in areas with the longest fire season (i.e. tropical ecosystems, Fig. S2). However, fires in tropical grasslands are so frequent that fire-released seed dormancy is almost redundant, whereas it is common in Mediterranean shrublands where fire is highly stochastic but guaranteed within the lifespan of the seeds (Keeley, 1991; Lamont, 2022; Pausas & Lamont, 2022). Fire type (crown or surface) and season of the fire (e.g. after the dry winter in savannas; after the wet spring in Mediterranean regions) are likely to be more important than the length of the fire season, as they are related to both fire frequency and intensity; and fire season matches with the germination phenology of the corresponding floras (Lamont *et al.*, 2022; Pausas & Lamont, 2022).

It is also important to note that different species in fire-prone vegetation may have different strategies for surviving and reproducing at a given site. For instance, the fact that physical seed dormancy is strongly linked (causally, not just statistically) to high-intensity fires does not mean that all or most species in fire-prone ecosystems must possess physical seed dormancy. Only a subset of Mediterranean species has this trait, whereas many have other strategies for dealing with fire (e.g. smoke-released dormancy, resprouting, thick bark, serotiny). Therefore, physical seed dormancy does not need to be dominant nor the only trait adapted to the historical fire regime. Of course, high-intensity fires are not the only driver selecting for physical seed dormancy as it increases seed longevity generally (e.g. for ensuring survival of frost, exceptional summer heat, digestion), and global analyses may well fail to capture fire regime as a key variable. But what is important is that there is a mechanism that explains the selection for seed dormancy in seasonal ecosystems with intense crown fires: in ecosystems with prolonged hot, dry summers and intense crown fires that create huge swathes of colonizable patches, physical dormancy of seeds whose dormancy can be broken by heat is clearly adaptive (Pausas *et al.*, 2022; Pausas & Lamont, 2022).

We are not against broad-scale analyses and synthesis, nor against correlative studies as an essential first step in research, but when the results lack a biological basis (e.g. inherent seed dormancy is adaptive in seasonal climates) then they may impede the identification of key ecological processes.

Beyond seed ecology

The overemphasis on climate and lack of testing alternative hypotheses to environmental factors is not exclusive to seed ecology. For instance, global patterns of species diversity are often based on correlative analyses with climate (Currie *et al*., 2004; Peters *et al*., 2016; Coelho *et al*., 2023). This is despite the presence of other possible candidates, that may or may not be correlated with climate, that directly affect the fitness of species (e.g. stochastic disturbances, soil fertility, physiographic features, mutualists and herbivores) and contribute to explaining species richness at both local (Huston, 1994; He *et al*., 2019) and broad scales (Pausas & Ribeiro, 2017; Brundrett, 2021; Moritz *et al*., 2023). Trait ecology is also prone to these pitfalls (Fig. S3). For instance, wood density in trees is a trait likely shaped by multiple factors; increased wood strength as a response to disturbances, such as cyclonic winds, could be a key factor in some regions (Curran *et al*., 2008; Dantas & Pausas, 2022), and the role of dense wood in fire tolerance and epicormic bud insulation appears important among some fire-prone lineages (Burrows, 2002). However, a recent global analysis (based on 36 000 samples and sophisticated machine learning methods) failed to consider any disturbance-related variable among the 79 examined (Yang *et al*., 2024).

Species distributions are also typically explained at the macroclimate scale only, despite the existence of alternative drivers (Schwilk & Keeley, 2012; Pausas & Bond, 2021). A recent example is the prediction of African vegetation using a plant growth model applied to species distribution and climate variables (Higgins *et al*., 2023). While the model may correctly predict some current vegetation, it fails to incorporate the most important ecological mechanisms that shaped African vegetation, such as large herbivores and frequent fires (Bond, 2019; Owen-Smith, 2021). Exclusion experiments show that these massive plant consumers drastically change vegetation composition and structure (Venter *et al*., 2018; Pellegrini *et al*., 2021; Beckett *et al*., 2022). We need mechanistic models that incorporate understanding of how ecosystems work in order for such models to be useful predictive tools.

Global analyses are an ambitious endeavour to find universal rules, but it needs to be appreciated that such rules may fail at identifying mechanisms that create broad-scale patterns if likely causal variables are not included in the first place, and when they are defined by multiple factors. Most critically, such a broad-scale approach may even hide key local ecological processes (Fig. S3); more integration between broad-scale description and hypothesis-based studies is needed. Furthermore, hypothesis-driven science cannot be replaced by computer mining of immense databases; the scientific method can be enriched by the use of large databases but not replaced by it. If ecology aims to be a predictive science, we should focus more on a mechanistic understanding than on describing correlations with vast amounts of data. And this is important as technologies become more accessible to everyone. The current rise of artificial intelligence (AI) tools may exacerbate this problem through the illusion of understanding (Messeri & Crockett, 2024). Alternatively, AI may help to investigate critical variables that differ from climate and soils at broad scales and to overcome some of the research biases. In addition, carefully crafted, comparatively based and prolonged field observations are the key to understanding natural phenomena and need to be fully promoted (Nanglu *et al*., 2023).

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Competing interests

None declared.

Author contributions

JGP initiated the project, analysed the data, and wrote the first version of the manuscript. BBL, JEK and WJB contributed ideas, examples and edits to the final text.

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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 Germination of six hard-seeded Australian species under control conditions and after scarification.

Fig. S2 Relationship between the potential fire season length and latitude for the Northern and Southern hemispheres.

Fig. S3 Many ecological patterns depend on the scale.

Key words: correlative science, fire ecology, germination, large data sets, mechanistic understanding, seed dormancy.

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The following Supporting Information is available for this article:

Fig. S1 Germination of six hard-seeded Australian species under control conditions and after scarification for the Northern and Southern hemispheres.

Fig. S2 Relationship between the potential fire season length and latitude.

Fig. S3 Many ecological patterns depend on the scale.

Fig. S1 Germination of six hard-seeded Australian species (paired symbols) under control conditions (C) and after scarification (SC). The experiment was performed in three seasons (spring, summer, and winter; different colors). Triangles are the mean values for the treatment and season across species. A variance component analysis indicates that treatment explains 78% of the total variability in germination, i.e., differences in germination between the two treatments are more important than differences between seasons. Elaborated with data from Ruiz-Talonia et al. (2023); see References below.

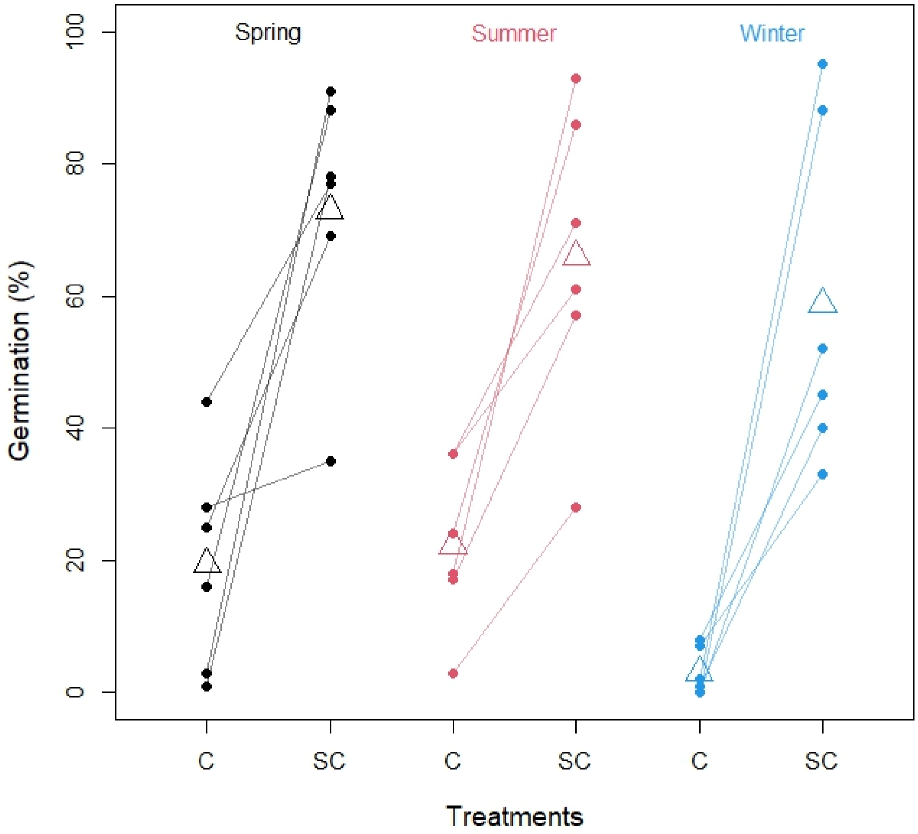


Fig. S2 Relationship between the potential fire season length (in months; as used by Rosbakh et al. 2023) and latitude for the Northern and Southern hemispheres (black triangles and red circles, respectively). Potential fire season length (PFSL) was extracted from Senande-Rivera et al. (2022) and averaged for each ecoregion (sensu Dinerstein et al. 2017) to reduce spatial autocorrelation. PFSL is highest in tropical ecosystems with little fire-released dormancy, whereas PFSL is intermediate where fire-released dormancy and postfire recruitment are dominant in mediterranean (Med.) ecosystems (Pausas and Lamont 2022). See References below.

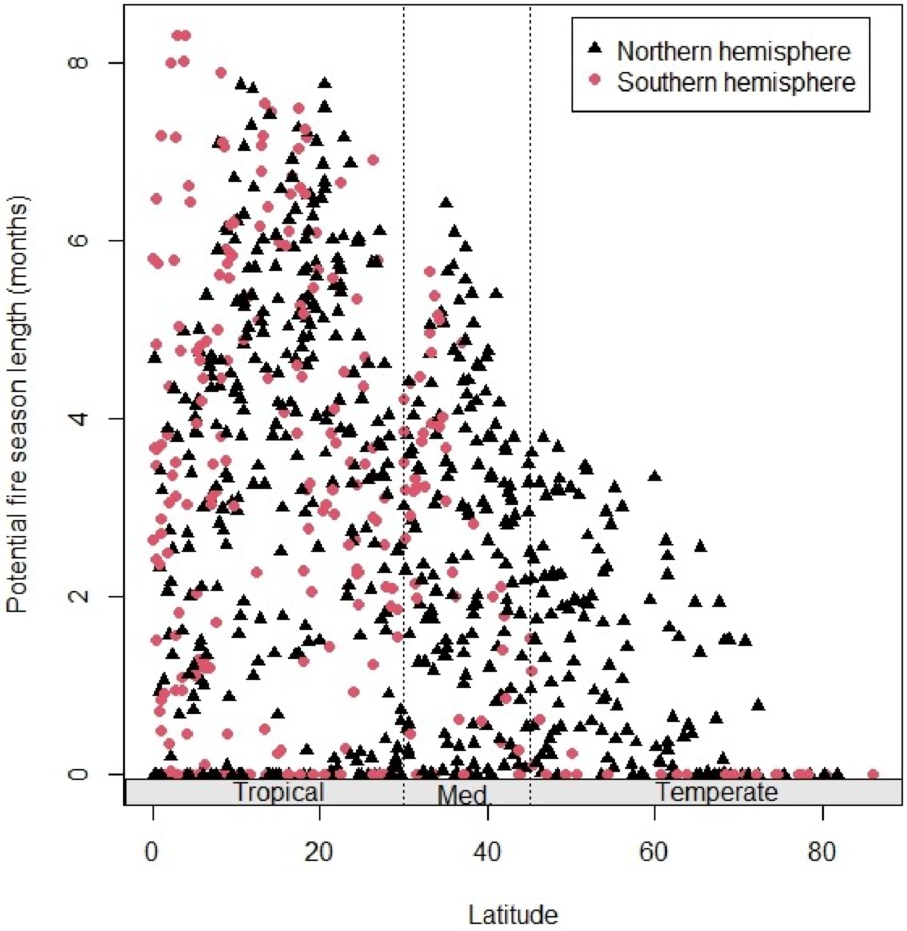
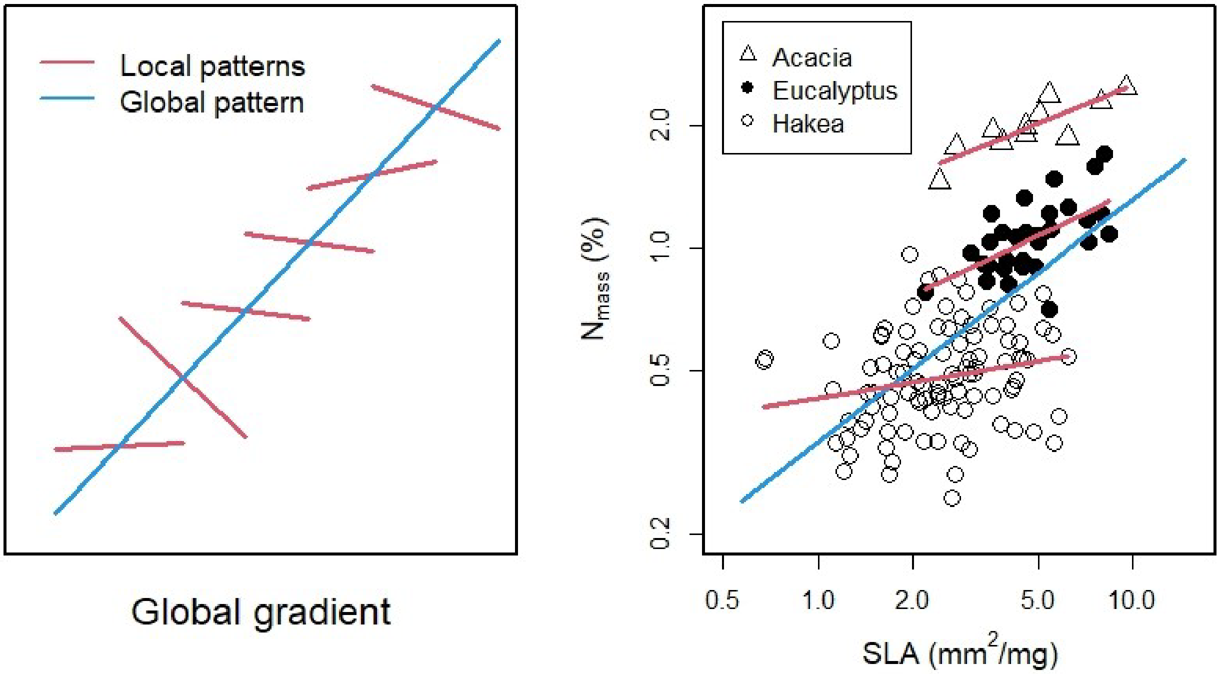


Fig. S3 Many ecological patterns depend on the scale. A global study that does not consider the local scale processes or biota may fail to find the actual patterns that exist in different regions (hypothetical example to the left). An example for leaf traits (specific leaf area vs leaf N concentration; right) showing how none of the component genera conforms to the overall relationship, even though the data are taken from the same continent (from Wright et al. 2004). Lamont et al. (2002) showed that rainfall largely accounted for variations in SLA among Hakea species. See References below.



Supporting Information References

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