

## The need for mechanistic explanations in (seed) ecology

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*"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"* J. Pearl (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 on 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 fueled 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 and 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 under-considered 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 this journal). 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, but instead take 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 (Figure 1). Experimental evidence also shows that scarification (simulating fire heat) greatly increases germination compared with changes in season (Ruiz-Talonia et al. 2023; Figure 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 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.

In 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, as a fire regime variable they considered a single parameter, potential fire season length (PFSL, defined as 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). PFSL 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.

Rosbakh et al. (2023) analysis is then developed from their contention that seed dormancy is most adaptive in areas with the longest fire season (i.e., tropical ecosystems, Figure 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 lifespan of the seeds (Keeley 1991, Lamont 2022, Pausas and 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 (Pausas & Lamont 2022, Lamont et al. 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 drivers 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 & Lamont 2022, Pausas et al. 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, Cohelo 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 36000 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 needs to be fully promoted (Nanglu et al. 2023).

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### Author contributions

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

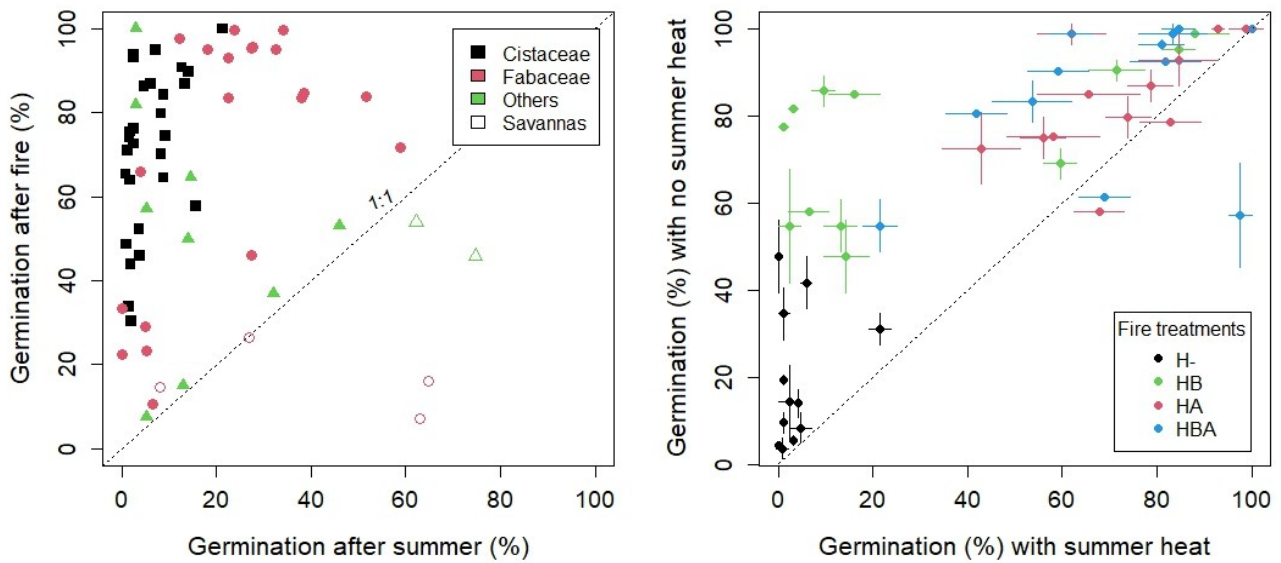
### References

- Archibald S, Lehmann CER, Gómez-Dans JL, Bradstock RA. 2013.** Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences, USA* **110**: 6442–6447.
- Baskin CC, Baskin JM. 2014.** *Seeds: ecology, biogeography, and evolution of dormancy and germination*. San Diego, California: Elsevier.
- Beckett, H., Staver, A.C., Charles-Dominique, T. & Bond, W.J. 2022.** Pathways of savannization in a mesic African savanna-forest mosaic following an extreme fire. *J. Ecol.*, **110**, 902–915.
- Bond WJ. 2019.** *Open Ecosystems: Ecology and Evolution Beyond the Forest Edge*. Oxford University Press.
- Brown PT, Hanley H, Mahesh A, Reed C, Strenfel SJ, Davis SJ, Kochanski AK, Clements CB. 2023.** Climate warming increases extreme daily wildfire growth risk in California. *Nature* **621**: 760–766.
- Brundrett MC. 2021.** One biodiversity hotspot to rule them all: Southwestern Australia—An extraordinary evolutionary centre for plant functional and taxonomic diversity. *Journal of Royal Society of Western Australia* **104**: 91–122.
- Calude CS, Longo G. 2017.** The deluge of spurious correlations in Big Data. *Foundations of Science* **22**: 595–612.

- Coelho MTP, Barreto E, Rangel TF, Diniz-Filho JAF, Wüest RO, Bach W, Skeels A, McFadden IR, Roberts DW, Pellissier L, et al. 2023.** The geography of climate and the global patterns of species diversity. *Nature* **622**: 537–544.
- Curran TJ, Gersbach LN, Edwards W, Krockenberger AK. 2008.** Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. *Austral Ecology* **33**: 442–450.
- Cohen D. 1966.** Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**: 119–129.
- Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan J-F, Hawkins BA, Kaufman DM, Kerr JT, Oberdorff T, O'Brien E, et al. 2004.** Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**: 1121–1134.
- Dantas VL, Pausas JG. 2022.** The legacy of the extinct Neotropical megafauna on plants and biomes. *Nature Communications* **13**: 129.
- Farley SS, Dawson A, Goring SJ, Williams JW. 2018.** Situating ecology as a big-data science: current advances, challenges, and solutions. *BioScience* **68**: 563–576.
- Fick SE, Hijmans RJ. 2017.** WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**: 4302–4315.
- He T, Lamont BB, Pausas JG. 2019.** Fire as a key driver of Earth's biodiversity. *Biological Reviews* **94**: 1983–2010.
- Huston MA. 1994.** *Biological diversity. The coexistence of species on changing landscapes.* Cambridge University Press, Cambridge. 681 pp.
- Keeley JE. 1991.** Seed germination and life history syndromes in the California chaparral. *The Botanical Review* **57**: 81–116.
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW. 2012.** *Fire in Mediterranean ecosystems: ecology, evolution and management.* Cambridge, UK: Cambridge University Press.
- Lamont BB. 2022.** Historical links between climate and fire on species dispersion and trait evolution. *Plant Ecology* **223**: 711–732.
- Lamont BB, Burrows GE, Korczynskyj D. 2022.** High summer temperatures do not interact with fire to promote germination among seeds of Cistaceae: a reinterpretation of Luna (2020) with extra data on wet/dry conditions. *Plant Ecology* **223**: 141–149.
- Lamont BB, Burrows GE, Pausas JG. 2024.** Fire-type heat increases the germination of Cistaceae seeds in contrast to summer heat. *Fire Ecology* **20**: 20.
- Luna, B., Piñas-Bonilla, P., Zavala, G., & Pérez, B. 2023.** Timing of fire during summer determines seed germination in Mediterranean Cistaceae. *Fire Ecology* **19**: 52.
- Messeri L, Crockett MJ. 2024.** Artificial intelligence and illusions of understanding in scientific research. *Nature* **627**: 49–58.
- Moritz MA, Batllori E, Bolker BM. 2023.** The role of fire in terrestrial vertebrate richness patterns. *Ecology Letters* **26**: 563–574.
- Nanglu K, de Carle D, Cullen TM, Anderson EB, Arif S, Castañeda RA, Chang LM, Iwama RE, Fellin E, Manglicmot RC, et al. 2023.** The nature of science: The fundamental role of natural history in ecology, evolution, conservation, and education. *Ecology and Evolution* **13**: e10621.
- Yang H, Wang S, Son R, Lee H, Benson V, Zhang W, Zhang Y, Zhang Y, Kattge J, Boenisch G, Schepaschenko D, Karaszewski Z, Stereńczak K, Moreno-Martínez Á, Nabais C, Birnbaum P, Vieilledent G, Weber U, Carvalhais N. 2024.** Global patterns of tree wood density. *Global Change Biology* **30**: e17224.
- Owen-Smith N. 2021.** *Only in Africa: The Ecology of Human Evolution.* Cambridge: Cambridge University Press.
- Pausas JG. 2022.** Pyrogeography across the western Palearctic: a diversity of fire regimes. *Global Ecology and Biogeography* **32**: 1923–1932.
- Pausas JG, Bond WJ. 2019.** Humboldt and the reinvention of nature. *Journal of Ecology* **107**: 1031–1037.
- Pausas JG, Bond WJ. 2021.** Alternative biome states challenge the modelling of species' niche shifts under climate change. *Journal of Ecology* **109**: 3962–3971.

- Pausas JG, Lamont BB. 2022.** Fire-released seed dormancy - a global synthesis. *Biological Reviews* **97**: 1612–1639.
- Pausas JG, Lamont BB, Keeley JE, Bond WJ. 2022.** Bet-hedging and best-bet strategies shape seed dormancy. *New Phytologist* **236**: 1232–1236.
- Pausas JG, Ribeiro E. 2017.** Fire and plant diversity at the global scale. *Global Ecology and Biogeography* **26**: 889–897.
- Pearl J, Mackenzie D. 2018.** *The Book of Why: The New Science of Cause and Effect*. New York.
- Pellegrini AFA, Refsland T, Averill C, Terrer C, Staver AC, Brockway DG, Caprio A, Clatterbuck W, Coetsee C, Haywood JD, et al. 2021.** Decadal changes in fire frequencies shift tree communities and functional traits. *Nature Ecology & Evolution* **5**: 504–512.
- Philippi T. 1993.** Bet-hedging germination of desert annuals: Beyond the first year. *The American Naturalist* **142**: 474–487.
- Rosbakh S, Carta A, Fernández-Pascual E, Phartyal SS, Dayrell RLC, Mattana E, Saatkamp A, Vandeloos F, Baskin J, Baskin C. 2023.** Global seed dormancy patterns are driven by macroclimate but not fire regime. *New Phytologist* **240**: 555–564.
- Rubio de Casas R, Willis CG, Pearse WD, Baskin CC, Baskin JM, 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.
- Ruiz-Talonia L, Whalley RDB, Gross C, Carr D, Reid N. 2023.** Overcoming limitations to propagation from seed of 40 Australian species important for restoration. *New Forests* **54**: 993–1012.
- Sarewitz D. 2016.** The pressure to publish pushes down quality. *Nature* **533**: 147–147.
- Senande-Rivera M, Insua-Costa D, Miguez-Macho G. 2022.** Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nature Communications* **13**: 1208.
- Schwilk DW, Keeley JE. 2012.** A plant distribution shift: temperature, drought or past disturbance? *PLoS ONE* **7**: e31173.
- Venable DL. 2007.** Bet hedging in a guild of desert annuals. *Ecology* **88**: 1086–1090.
- Venter ZS, Cramer MD, Hawkins HJ. 2018.** Drivers of woody plant encroachment over Africa. *Nature Communications* **9**: 2272.
- Wyse SV, Dickie JB. 2018.** Ecological correlates of seed dormancy differ among dormancy types: a case study in the legumes. *New Phytologist* **217**: 477–479.
- Zhang Y, Liu Y, Sun L, Baskin CC, Baskin JM, Cao M, Yang J. 2022.** Seed dormancy in space and time: global distribution, paleo- and present climatic drivers and evolutionary adaptations. *New Phytologist* **234**: 1770–1781.

## Figures



**Figure 1.** Germination (%) in experiments comparing fire and summer treatments. *Left:* Germination of 68 populations or species subjected to both fire- and summer-type heat treatments. Colours (in filled and empty symbols) refer to Cistaceae (black), Fabaceae (red), and others (white). Filled symbols refer to mediterranean and warm temperate ecosystems, empty symbols refer to savannas. Dotted line gives the 1:1 relationship, i.e. points above the line have higher germination levels after fire-type heat than after summer-type heat. Adapted from Pausas & Lamont (2022). *Right:* Germination with no high temperatures in summer (1 month at 20°C, control, y-axis) vs germination with summer heat (1 month at 50/20°C for 12/12 hours, 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), d) fire-heat before and after summer (HBA; the most ecologically unrealistic scenario). Variability represents SE. Dotted line is the 1:1 relationship, i.e. 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).

## New Phytologist Supporting Information

Article title: The need for mechanistic explanations in (seed) ecology

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The following Supporting Information is available for this article:

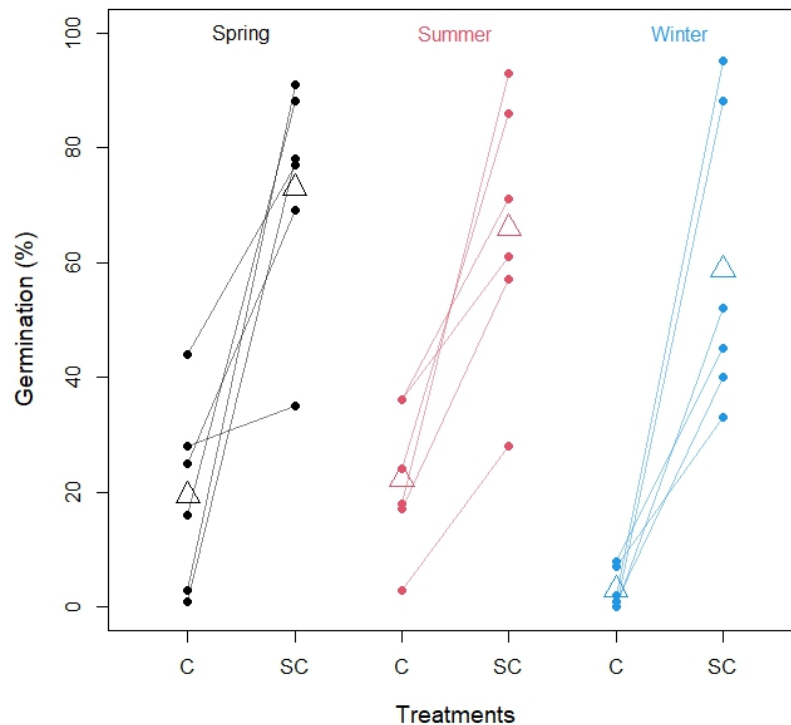
**Fig. S1** Germination of six hard-seeded Australian species under control conditions and after scarification

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

**Fig. S3** Many ecological patterns depend on the scale.

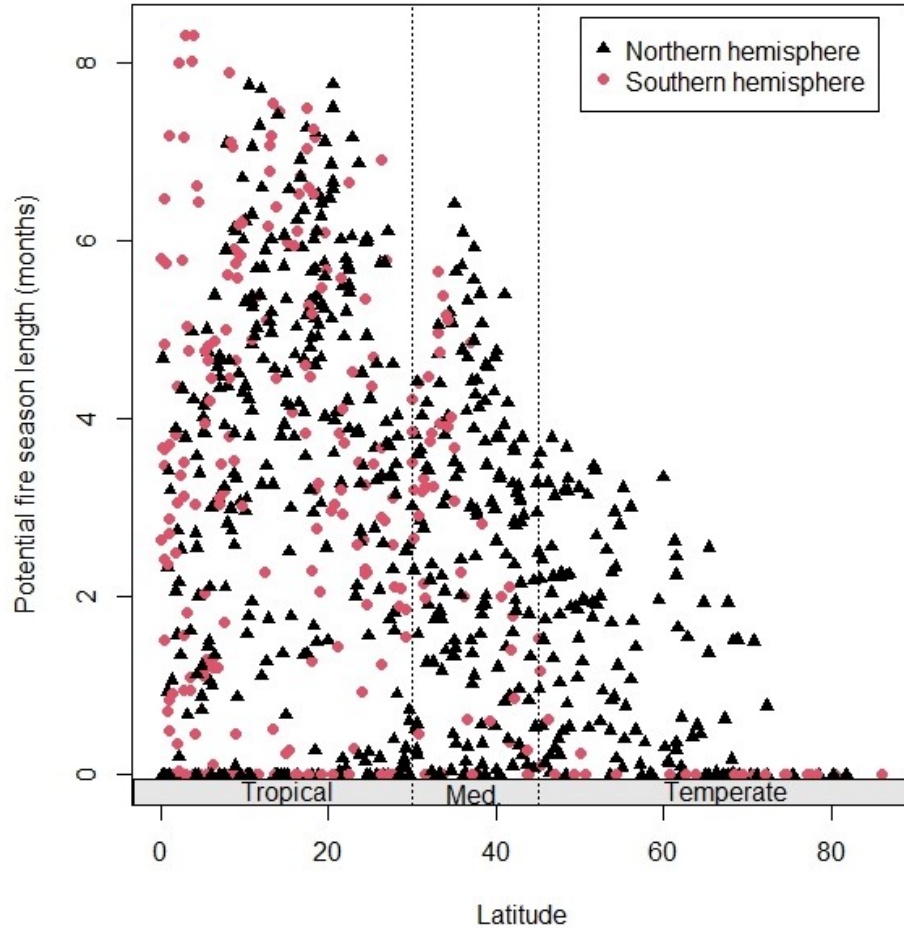
**Notes S1** References used in the Supporting Information

**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 Notes S1.

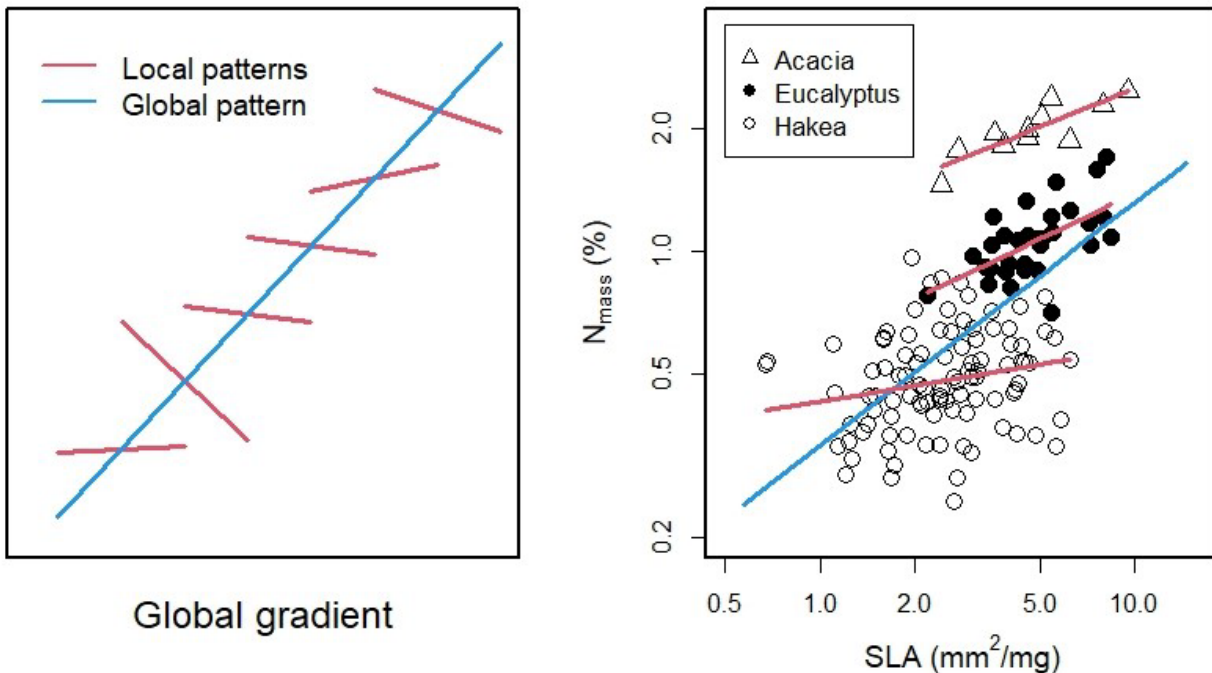




**Fig. S2** Relationship between the potential fire season length (in months; as used by Rosbakh et al. 2023) and latitude for the Northern and Southern hemispheres (black triangles and red circles, respectively). Potential fire season length (PFSL) was extracted from Senande-Rivera et al. (2022) and 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 Notes S1.



**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 Notes S1.



**Notes S1** References used in this Supporting Information

**Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, et al. 2017.** An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* **67**: 534–545.

**Lamont BB, Groom PK, Cowling RM. 2002.** High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. *Functional Ecology* **16**: 403–412.

**Senande-Rivera M, Insua-Costa D, Miguez-Macho G. 2022.** Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nature Communications* **13**: 1208.

**Wright IJ, Groom PK, Lamont BB, Poot P, Prior LD, Reich PB, Detlef E, Veneklaas EJ, Westoby M. 2004.** Leaf trait relationships in Australian plant species. *Functional Plant Biology* **31**: 551–558