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Diaspore structure and maternal environment shape seed dormancy in wild Rosaceae: a global meta-analysis

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Abstract

Seed dormancy regulates germination and plant regeneration. We analysed 1,894 effect-size observations from wild Rosaceae, expressed as log response ratios (lnR) between treated and control seeds. Meta-analysis, meta-regression, principal component analysis (PCA), SHAP-based feature importance, and Boundary Line Analysis (BLA) assessed treatment responses. Treatments increased germination (lnR = 0.766), although heterogeneity was high. Diaspore length was the strongest biological predictor. Precipitation was the leading environmental predictor, followed by aridity index and elevation; soil variables contributed less. Stratification after scarification or endocarp removal produced stronger responses than other treatments. BLA identified an effective stratification temperature range of 0.19–15.8 °C, with approximately 8 °C as the practical central temperature. Minimum and maximum duration thresholds averaged 40 days (range 0–79) and 210 days (139–280), respectively. Seed-source environments with moderate precipitation, intermediate elevations, well-drained sandy soils, and adequate phosphorus were associated with higher baseline germinability and stronger treatment responses. Dormancy release reflects interactions among seed traits, environmental history, and treatment requirements. We propose disrupting fruit coverings followed by moist cold stratification near 8 °C for 40–210 days, adjusted by species and seed origin, to support propagation, *ex situ* conservation, and ecological restoration of wild Rosaceae.

Keywords: Climate, conservation, dormancy loss, meta-analysis, scarification, stratification.

Introduction

The Rosaceae is one of the largest and most ecologically diverse angiosperm families, comprising approximately 3,000 species in 88-100 genera, mainly distributed across the temperate Northern Hemisphere [1]. Wild representatives of this family, including fruit-bearing trees, shrubs and herbs, play important roles in broad-leaved forests by providing food for frugivores, supporting pollinator networks, contributing to local livelihoods, and acting as reservoirs of genetic variation for crop improvement, forest restoration and adaptation to environmental change [2–4].

Despite these functions, wild fruit-bearing of Rosaceae remain underrepresented in both *in situ* and *ex situ* conservation programs, which have traditionally prioritized timber species [4,5]. Their populations are increasingly affected by habitat loss and fragmentation, land-use change, invasive species, pollution, overharvesting and climate change [6]. Even when widely distributed, they often occur as small, scattered populations, largely restricted to forest margins and ecotones [7]. Weak competitive ability, high light or specific edaphic requirements, slow growth, long juvenile phases and frequent clonal propagation all constrain sexual recruitment and long-term population persistence [5,8]. Gene flow can facilitate the spread of adaptive variants, but population differentiation for adaptive traits indicates that local adaptation remains important [9]. In addition, hybridization with cultivated relatives poses a serious threat, often leading to introgression, genetic swamping and the progressive loss of wild genotypes [10–12].

A major bottleneck for sexual regeneration is seed dormancy [13]. Seeds of Rosaceae are water-permeable and primarily exhibit physiological dormancy (PD), although nondormant seeds have also been reported [14,15]. Physiological dormancy occurs at non-deep, intermediate and deep levels, with deep PD being particularly common in genera such as *Crataegus*, *Sorbus* and *Prunus*, often requiring prolonged cold or sequential warm and cold stratification to enable germination [4,14,16–20]. Depending on the species and dormancy depth, germination can also be promoted by after-ripening, gibberellic acid (GA_3), scarification, or removal of covering structures [21–23]. Numerous species-level studies have

53 demonstrated these effects, but the responses are highly variable and often appear contradictory across
54 taxa [24–27].

55 Much of this variation is linked to the exceptional diversity of diaspores in the family. Rosaceae
56 fruits range from achenes, drupes and pomes to follicles, hips and berries, and the functional dispersal
57 unit differs accordingly [28–31]. In many woody taxa, the seed is enclosed within a lignified endocarp
58 that is permeable to water, but can impose mechanical resistance, restrict embryo expansion, delay
59 oxygen diffusion or inhibit the leaching of germination inhibitors [22,24,32–34]. Such resistance often
60 interacts with PD, and in some cases, removal of the endocarp or seed coat alone is sufficient to induce
61 germination without any stratification [24]. These structural traits can therefore strongly modify the
62 temperature, moisture and treatment requirements for dormancy release.

63 Diaspore structure alone, however, does not fully explain interspecific variation in dormancy. The
64 environmental conditions experienced by the maternal plant during seed development and maturation can
65 also influence embryo development, reserve accumulation, and the structure and permeability of the seed
66 coat and endocarp, thereby affecting the initial depth of primary dormancy [35–37]. At broader scales,
67 climatic attributes of the seed source, such as temperature seasonality, growing degree days and aridity,
68 may shape the physiological thresholds that determine when dormancy is released and germination can
69 occur [38–41]. Natural dispersal by frugivores can further modify these outcomes depending on seed size
70 and dormancy class [13,42–45].

71 Despite the large number of germination studies on Rosaceae, the factors underlying the wide
72 variation in dormancy-breaking responses remain poorly understood, particularly across species with
73 contrasting biological and environmental characteristics. Most studies focus on single species or
74 treatments, making it difficult to distinguish general patterns from taxon- or context-specific effects.
75 Meta-analysis offers a robust, quantitative approach to synthesize such heterogeneous data, to estimate
76 treatment effects, and to identify the moderators underlying this variability [46,47], as demonstrated for
77 the megagenus *Astragalus* [48] and alpine plants [49].

Here, we used a global quantitative synthesis integrating meta-analysis, meta-regression, Principal Component Analysis (PCA), SHAP-based feature importance analysis, and Boundary Line Analysis (BLA) to determine how biological traits, maternal environmental conditions, and dormancy-breaking treatments shape seed dormancy and its release in Rosaceae. Using a compiled dataset that integrates fruit type, endocarp structure, diaspore length, dispersal mode, life form, seed-source climate, soil properties, dormancy-breaking treatments, and germination-testing conditions, we address four interrelated objectives: (i) to test whether treatment effectiveness depends on diaspore length, fruit type, endocarp characteristics, dispersal mode, and life form; (ii) to assess whether maternal macroclimate and seed-source environment explain variation in response to dormancy-breaking treatments; (iii) to quantify the effects of the major dormancy-breaking treatments—cold and warm stratification, scarification, endocarp removal, heat treatments, and GA_3—on germination; and (iv) to develop a generalized, evidence-based framework for dormancy release and seed production in Rosaceae by integrating seed traits, environmental conditions, and treatment responses, and to identify a practical thermal and temporal range for stratification that can guide species-specific propagation and restoration protocols. We hypothesized that diaspore structure—particularly lignified covering layers interacting with PD—will explain substantial variation in germination responses, and that maternal climate will account for additional heterogeneity beyond taxonomy and treatment type. By identifying these interacting controls, this study provides a quantitative, predictive framework for improving propagation, restoration, and ex situ conservation of wild fruit-bearing plants of Rosaceae.

Results

The overall meta-analysis showed a significant positive treatment effect on seed germination (lnR = 0.766, 95% CI: 0.686–0.845, $z = 18.96$, $P < 0.001$; Fig. 2). Heterogeneity was substantial ($I^2 = 87.8\%$, $\tau^2 = 1.092$) and remained high across subgroup analyses ($I^2 = 79.9$–87.8%; $\tau^2 = 1.03$–1.12; Table S2).

Biological drivers of dormancy release

Diaspore length was associated with variation in germination responses (Fig. 2). Medium diaspores showed the strongest significant response (lnR = 1.200, 95% CI: 1.075–1.325, $P < 0.001$), while small and large diaspores also showed significant positive effects. Responses were nonsignificant for very large (lnR = 0.493, 95% CI: −0.156–1.142, $P = 0.136$) and very small diaspores (lnR = 0.190, 95% CI: −0.103–0.483, $P = 0.204$). Endocarp structure made little difference: lnR was 0.769 (95% CI: 0.650–0.889) for non-stony and 0.763 (95% CI: 0.657–0.869) for stony endocarps (both $P < 0.001$).

Most fruit types showed significant positive responses: achenes (lnR = 0.715), drupes (0.822), follicles (0.443), pomes (0.813), and hips (2.037; all $P < 0.05$; Fig. 2). Hips had the largest estimated effect, but this was based on only nine observations. Berries showed a significant negative response (lnR = −1.195, 95% CI: −2.183 to −0.207, $P = 0.018$; n = 5). All life forms showed significant positive effects, strongest in trees (lnR = 0.945), followed by shrubs (0.684) and herbs (0.488; all $P \leq 0.001$). Among dispersal modes, endozoochory (lnR = 0.797, 95% CI: 0.699–0.895) and synzoochory (1.095, 95% CI: 0.925–1.265) showed significant positive effects ($P < 0.001$), whereas the other modes did not.

Environmental drivers of dormancy release

Germination responses varied among Köppen–Geiger climate classes (Fig. S3). Significant positive effects occurred in Bsk (lnR = 1.226, 95% CI: 1.079–1.373), Cfb (0.990, 0.841–1.138), Csb (0.618, 0.287–0.948), Cwa (0.705, 0.342–1.068), Cwb (0.390, 0.020–0.759), Dfb (0.706, 0.409–1.002), and Dwb (2.524, 0.536–4.511); the remaining classes showed nonsignificant effects.

Among climatic predictors, lnR declined with increasing mean annual precipitation (estimate = −0.0005, 95% CI: −0.0007 to −0.0003, $z = -5.08$, $P < 0.0001$), elevation (−0.0002, 95% CI: −0.0004 to −0.0001, $z = -3.75$, $P = 0.0002$), and aridity index (−0.0004, 95% CI: −0.0006 to −0.0001, $z = -3.03$, $P = 0.0024$). Mean annual temperature was not significantly associated with lnR ($P = 0.368$; Fig. 3; Table S3).

Soil properties showed both positive and negative associations with lnR (Fig. 3; Table S3). Positive associations occurred for cation exchange capacity (estimate = 0.0192, $P = 0.0010$), sand content (0.0115, $P = 0.0001$), bulk density (1.0038, $P = 0.0002$), and Olsen P (0.0034, $P = 0.0028$). Negative associations

were observed for soil organic carbon (estimate = −0.0891, $P = 0.0007$), clay (−0.0278, $P < 0.0001$), and silt content (−0.0094, $P = 0.0332$). Soil pH ($P = 0.084$) and available water capacity ($P = 0.056$) were not significant. Relationships between seed dormancy and maternal environmental conditions broadly followed those observed for lnR (Fig. S4).

The PCA explained 45.5% of total environmental variation in the first two axes (PC1 = 27.4%; PC2 = 18.1%; Fig. 4). PC1 represented a macroclimatic gradient associated with elevation, precipitation, and aridity, while PC2 reflected soil-texture variation, with sand contrasting with clay and silt. Olsen P aligned with the sand-associated gradient, whereas soil organic carbon, mean annual temperature, and growing degree days were associated more strongly with the clay-rich gradient. When observations were plotted by diaspore length, smaller diaspores occurred across a broad range of environmental conditions, whereas larger diaspores were concentrated in the lower PCA quadrants, associated with greater thermal accumulation and heavier-textured soils (Fig. 4).

Treatment effects on dormancy release

Most treatment subgroups showed positive germination responses, although effect sizes differed among treatments (Fig. 5). Endocarp removal was associated with a larger effect (lnR = 1.335, 95% CI: 1.069–1.601) than its absence (0.713, 0.630–0.796). Scarified seeds also showed a stronger response (lnR = 0.982, 95% CI: 0.803–1.161) than non-scarified seeds (0.715, 0.626–0.803; all $P < 0.001$).

Cold stratification (lnR = 0.991, 95% CI: 0.885–1.097) and sequential stratification (1.305, 1.103–1.506) produced significant positive responses, whereas non-stratified (0.054, −0.089–0.198, $P = 0.459$) and warm-stratified seeds (0.157, −0.333–0.646, $P = 0.531$) did not. Germination responses were positive both without GA_3 (lnR = 0.845, 95% CI: 0.755–0.934) and with GA_3 (0.470, 0.298–0.643). Seeds without heat treatment showed a positive effect (lnR = 0.825, 95% CI: 0.743–0.907), whereas heat-treated seeds did not (−0.105, −0.402–0.193, $P = 0.490$). Both dark and light conditions showed significant positive responses (lnR = 0.638 and 0.775, respectively). Fresh seeds showed a larger effect (lnR = 1.280, 95% CI: 1.089–1.470) than stored seeds (0.615, 0.500–0.730; all significant effects $P < 0.001$; Fig. 5).

Combined treatments also showed significant positive effects. Applying SC × GA, SC × ST, SC × ST × GA, and ST × GA yielded lnR values of 0.990, 1.340, 1.635, and 0.958, respectively (all $P < 0.001$; Fig. 5). Their corresponding groups without these combinations also showed significant positive responses (lnR = 0.759, 0.702, 0.746, and 0.744, respectively).

The temperature BLA showed a strong relationship between stratification temperature and lnR (R^2 = 0.859, RMSE = 0.539, SSE = 5.817), based on 1,552 observations spanning 0–25°C, with 20 points defining the upper boundary (Fig. 6a). The estimated thermal limits were −0.17°C and 26.3°C, with an optimum interval of 0.19–15.8°C and midpoint of 7.9°C (Fig. 6a).

The duration BLA identified distinct lower and upper response boundaries (Fig. 6b). The lower-boundary model explained 80.2% of variation (R^2 = 0.802, RMSE = 1.021, SSE = 26.047; 25 boundary observations). Its estimated minimum effective duration was 138.7 days, with a breakpoint at 280 days. The upper boundary reached a plateau at lnR = 5.53 after 79 days; its unconstrained x-intercept (−2761 days) was constrained to zero. Thus, the upper response boundary increased rapidly and plateaued by 79 days, while the lower boundary indicated a longer duration range, from approximately 139 to 280 days (Fig. 6b).

Integrated drivers of dormancy release

SHAP analysis identified diaspore length as the most important predictor of lnR (mean absolute SHAP ≈ 0.175), followed by climate (≈ 0.170), storage (≈ 0.141), and stratification (≈ 0.125; Fig. 7a). Endocarp structure (≈ 0.105) and fruit type (≈ 0.088) had moderate importance, whereas dispersal mode, life form, scarification, GA_3, heat, and light each had mean absolute SHAP values below 0.050.

Among environmental predictors, mean annual precipitation had the highest importance (≈ 0.187), followed by aridity index (≈ 0.100) and elevation (≈ 0.085; Fig. 7b). Soil organic carbon (≈ 0.077), clay content (≈ 0.076), and cation exchange capacity (≈ 0.069) were also influential. Mean annual temperature had moderate importance (≈ 0.071), while sand, pH, Olsen P, bulk density, silt, available water capacity, $CaCO_3$, and growing degree days had comparatively low predictive importance (Fig. 7b).

Discussion

Our global quantitative synthesis showed that seed dormancy and its release in wild Rosaceae varied with biological traits, seed-source environmental conditions, and dormancy-breaking treatments. Across the full set of predictors examined, diaspore length emerged as the most influential predictor of variation in lnR, while climate was the second important predictor. Among climatic variables, lnR declined significantly with increasing MAP, elevation, and AI, whereas MAT was not significantly related to lnR. Edaphic variables showed both positive and negative associations with lnR. Treatment-related responses also varied substantially among treatment types and combinations. These findings suggest that dormancy in Rosaceae is not a uniform family-level characteristic, but rather reflects the combined influence of intrinsic biological traits, treatment conditions, and environmental context. In the following sections, we discuss how these factors contribute to variation in dormancy and its release across the family.

Biological drivers of dormancy release

Biological traits were key drivers of germination variation across Rosaceae (Fig. 2), with diaspore length contributing most prominently to SHAP importance (Fig. 7A). Stronger responses in medium and large than small diaspores (Fig. 2) support the view that seed size reflects life-history trade-offs rather than directly determining germination [35,50]. Although larger diaspores provide greater maternal reserves for embryo development, they do not necessarily germinate faster, as relationships among seed mass, dormancy, and germination vary with dormancy class and life form [51]. The nonsignificant response of very large diaspores likely reflects the small sample size in this category.

Fruit morphology and dispersal mode may shape these relationships by influencing the post-dispersal microenvironment [14,52]. Endozoochory, for example, can promote germination through pulp removal, scarification, and altered hydration, although its effects depend on seed size and dormancy class [44]. Stronger responses in endozoochorous and synzoochorous taxa (Fig. 2) may reflect both disperser

handling and deposition in favorable microsites, consistent with the co-evolution of dispersal and dormancy to spread recruitment across space and time [53].

Our results also distinguished structural coverings from true physical dormancy (PY). Although effect sizes were comparable between intact stony and non-stony endocarps (Fig. 2), experimental endocarp removal markedly enhanced germination (Fig. 5). However, the endocarp is maternal fruit tissue (pericarp), not seed-coat tissue, and its presence alone does not establish PY, which requires water impermeability (*sensu* [54]. Covering layers in Rosaceae may constrain embryo growth mechanically or limit gas exchange [55], as shown in *Prunus campanulata* [24] and *Rosa rugosa* [56]. These robust coverings also protect seeds from predators and environmental hazards, enhancing persistence [57,58].

Stronger effects in trees than in shrubs and herbs (Fig. 2) may reflect broader regeneration syndromes. Life form correlates with seed mass, longevity, and reproductive output [50,59]. Long-lived trees may tolerate prolonged recruitment delays, whereas shorter-lived species may favor opportunistic establishment during suitable periods [51,53].

Together, these findings suggest that diaspore length, fruit anatomy, dispersal mode, and life form jointly contribute to variation in dormancy and germination, consistent with broader evidence linking seed traits to ecological strategies [37,60]. Dormancy in Rosaceae can therefore be viewed in the context of the broader relationships among diaspore traits, dispersal, and seed persistence, rather than as an isolated trait [13].

Environmental drivers of dormancy release

Macroclimatic and edaphic variables were consistently associated with dormancy and lnR (Fig. 3, Fig. S4). Maternal environments can influence embryo differentiation, hormonal balance, seed-coat thickness, and physiological sensitivity during maturation [61,62]. These associations likely reflect geographic and climatic filtering of regeneration strategies rather than direct effects of individual abiotic factors.

Mean annual precipitation and AI were negatively related to dormancy and lnR, identifying water availability as a major climatic correlate of seed dormancy in Rosaceae (Fig. 3). In water-limited

ecosystems, seasonal drought favors stronger dormancy, preventing germination under unfavorable conditions [63]. Conversely, seeds from wetter environments exhibited lower dormancy and smaller gains in lnR following dormancy-breaking treatments. Maternal conditions may also affect embryo development before dispersal; for example, embryo size at maturity can vary among populations and environments depending on the species and environmental factor [37,64]. The parallel relationships of precipitation with dormancy and lnR suggest that long-term adaptation to moisture availability shapes seed physiological status before experimental treatments.

Mean annual temperature was not significantly related to lnR (Fig. 3), but higher MAT was positively associated with dormancy in the separate environmental regression (Fig. S4). This divergence suggests that temperature may influence dormancy thresholds more than the relative magnitude of treatment responses. In warmer climates, deeper dormancy may prevent germination after transient rainfall that precedes severe drought or heat [14,62,63]. These patterns align with the climate-dependent germination niche hypothesis, whereby dormancy evolves to synchronize emergence with predictable favorable periods [38,49,65].

Elevation was negatively related to lnR (Fig. 3), indicating weaker responses to dormancy-breaking treatments among seeds from higher elevations. Elevation integrates changes in temperature, growing-season length, and frost risk [66]. High-elevation habitats offer narrow establishment windows, selecting against unpredictable or poorly timed emergence [67,68]. Seeds from these environments may require specific combinations of natural cues to break dormancy that standard laboratory protocols rarely reproduce [49].

Edaphic variables had lower predictive importance than macroclimate but acted as secondary environmental filters. Higher sand content and AWC were associated with greater dormancy, whereas SOC was associated with lower dormancy (Fig. S4). Sandy soils drain rapidly and experience greater moisture fluctuations, potentially favoring deeper dormancy, whereas high SOC can improve moisture retention, nutrient availability, and microbial buffering [69,70].

PCA confirmed that climatic and edaphic predictors aligned along broad environmental axes, particularly water availability and soil texture, rather than acting independently. Overall, environmental origin strongly shapes germination responses to dormancy-breaking treatments [37,60], suggesting that dormancy in Rosaceae reflects maternal conditions, seasonal predictability, and post-dispersal hazards. However, individual abiotic variables explained relatively little variation, indicating that environmental filtering interacts with biological traits and treatment-specific constraints.

Treatment effects on dormancy release

Our meta-analysis demonstrated that dormancy release in Rosaceae depended strongly on the treatment applied and its combinations (Fig. 5). The largest effect sizes were associated with cold stratification, scarification, and combined treatments, whereas heat treatment had no significant effect. These patterns indicate that dormancy breaking rarely follows a universal mechanism; efficacy depends on whether the primary constraint is physiological, structural, or combined, as well as on dormancy depth and seed physiological state [54].

Cold stratification is consistently effective for breaking PD by providing moist chilling cues that stimulate metabolic and hormonal shifts [14,55]. Longer stratification was associated with higher lnR across an effective range of 0–280 days in Rosaceae (Fig. 6b), although requirements are species-specific. Duration varies with dormancy depth [14,54,71]: approximately 45 days sufficed for *Aruncus dioicus* [72], whereas prolonged stratification was required for *Prunus spachiana* [34], *P. serotina* [25], and *Sorbus alnifolia* [73]. This duration-dependent response reflects the progressive completion of biochemical processes, including the decline in covering-layer ABA and increase in embryo GA_4 documented in *Prunus campanulata* [24].

Sequential warm–cold stratification is particularly effective for morphophysiological dormancy, as warmth promotes embryo differentiation or growth before chilling releases PD [54,60]. Warm followed by cold stratification substantially enhanced germination in *P. campanulata*, *P. spachiana*, *S. alnifolia*, *Rosa canina*, and *Crataegus laevigata* compared with cold stratification alone (Bujarska-Borkowska,

2006; Chen et al., 2007; Kim et al., 2024; Pawłowski et al., 2020; Tang et al., 2019). In Rosaceae with mechanically restrictive endocarps, the warm phase may weaken the endocarp, while the subsequent cold phase releases PD. However, warm stratification is not universally beneficial: excessive warm exposure reduced germination in *Prunus mahaleb* [23], highlighting the need to match treatments to species-specific embryo developmental windows. Inappropriate warm treatments may also induce secondary dormancy in *Prunus*, *Crataegus*, and *Rosa* species [74–76].

Boundary Line Analysis identified a broad stratification temperature range (−0.17 to 26.3 °C), with an optimal window of 0.19–15.8 °C (Fig. 6a). This range encompasses temperatures commonly experienced during seasonal chilling in temperate habitats and accords with the diverse thermal requirements of species with different dormancy levels and types [14]. The broad range likely reflects differences in dormancy depth, embryo growth requirements, and thermal adaptation. Stratification duration also showed substantial variation: the upper response boundary extended to 79 days (with a breakpoint at 40 days), whereas the lower boundary extended to 280 days (with a breakpoint at 210 days; range 139–280 days). This separation suggests considerable variation among seeds and species in the duration needed for effective dormancy release, likely reflecting differences in dormancy intensity and chilling requirements. These temperature and duration boundaries provide a quantitative framework for defining effective stratification conditions in Rosaceae.

The pronounced response to endocarp removal highlights the prevalence of structural constraints across Rosaceae. Removal reduces mechanical resistance and improves gas and water exchange, potentially allowing underlying PD to be released. It markedly enhanced germination and sensitivity to exogenous GA_3 in *P. campanulata* [24] and *P. spachiana* [34], with comparable benefits reported in *P. mahaleb* [23], *P. azorica* [22], *P. yedoensis* [77], and *Rosa rugosa* [56]. These covering effects therefore represent mechanical and chemical constraints rather than true PY (*sensu* [54].

Exogenous GA_3 elicited more variable responses. Increasing its concentration did not systematically increase effect sizes (Fig. S5), and non-GA_3 treatments often achieved comparable or superior results (Fig. 5). GA_3 mainly promotes germination when hormonal imbalance is the primary constraint, but may

be ineffective when coverings restrict uptake or the embryo is underdeveloped [78,79]. It did not substitute for cold stratification in *A. dioicus* [72] or dormant *Potentilla* spp. [80], but acted synergistically with chilling or endocarp removal in *Prunus* species [23,25]. Inappropriate GA_3 concentrations can also inhibit germination [81], and laboratory success does not guarantee subsequent vigor: GA_3-treated *Prunus ulmifolia* seedlings showed poor field survival [82].

Scarification and multi-step protocols were among the most effective treatments because they alleviate multiple germination barriers [78]. By weakening structural coverings, scarification allows stratification or GA_3 to act on physiological constraints. This synergy was evident in *Rubus*, where mechanical or acid scarification combined with GA_3 maximized germination [83], and in *R. rugosa*, where simulated endozoochory fractured the endocarp and facilitated radicle emergence after stratification [56].

Finally, background seed conditions also mediated treatment outcomes. Light and dark conditions produced comparable effect sizes across the family, suggesting that light was not a dominant source of family-wide variation despite species-specific exceptions. Storage duration was not significantly associated with lnR in the meta-regression (Table S2), indicating that duration alone did not consistently explain treatment responses. Nevertheless, differences between fresh and stored seed lots suggest that storage history may influence responses through changes in viability, membrane integrity, or physiological sensitivity to germination cues [4]. Seed physiological status and post-dispersal history may therefore contribute to variation in dormancy release, although this cannot be attributed simply to storage duration.

An integrated view of Rosaceae dormancy

The integrated SHAP analysis shows that variation in lnR was more strongly associated with diaspore characteristics and environmental context than with most individual experimental treatments. The high contributions of diaspore length and climate suggest that seed responses to dormancy-breaking conditions are substantially conditioned before treatment. Treatments therefore act on a physiological state already shaped by seed development, morphology, and environmental history. The strong contribution of

precipitation within the environmental subset further suggests that water availability is a major axis of this pre-existing variation. This interpretation is consistent with the view that dormancy is established during seed development and subsequently shapes how seeds respond to environmental cues, rather than being an independent state readily removed by standardized treatments [53,54,63].

The relatively low SHAP contributions of individual treatments, including scarification, GA_3, heat, and light, do not imply that they are biologically unimportant. Rather, their global predictive contributions may be limited because their effectiveness depends on the biological and environmental context. A treatment can be highly effective for a specific dormancy mechanism yet contribute less to overall prediction across species with different dormancy states. This distinction is important when interpreting the contributions of storage and stratification, which represent aspects of seed physiological history that can modify the state from which germination begins. Overall, the integrated analysis suggests a hierarchical process in which seed phenotype and environmental history establish germination constraints, while post-dispersal treatments influence how effectively these constraints are overcome. Dormancy thus represents a dynamic interface between developmental history and environmental opportunity, with germination occurring when seed physiology becomes compatible with prevailing or experimentally supplied cues. This framework helps explain the substantial heterogeneity across Rosaceae and supports viewing dormancy as part of a broader regeneration strategy linking seed development, dispersal, environmental filtering, dormancy release, and establishment [13,44,63].

Implications for seed conservation and restoration

Diaspore morphology, particularly length, fruit type, and covering structures, was the strongest predictor of dormancy intensity and treatment response across Rosaceae, exceeding climatic and edaphic variables in predictive importance. Dispersal mode and life form made additional contributions. These findings support a trait-based approach to seed management rather than the use of generic germination protocols. For most Rosaceae taxa, evaluating and, where appropriate, removing or weakening the endocarp and persistent pericarp layers before thermal or chemical treatments may improve dormancy

362 release [14,55]. Mechanical scarification or endocarp removal, particularly when followed by cold
363 stratification, produced some of the largest effect sizes.

364 Our results suggest an initial stratification temperature of approximately 8 °C (effective range ≈0.2–16
365 °C) following scarification. The BLA indicated a response range of 0–280 days, with the minimum
366 duration associated with a positive response averaging 40 days (range 0–79 days) and the maximum
367 duration extending to 210 days (range 139–280 days). These estimates provide a framework for tailoring
368 stratification to species and seed lots, but should not be treated as universal optima. The desired degree of
369 dormancy release also depends on seed use. In nurseries, rapid and uniform germination may be the
370 priority, whereas direct seeding for ecological restoration may benefit from retaining some dormant seeds
371 to spread recruitment across seasons and provide insurance against unfavorable post-sowing conditions
372 [84].

373 Environmental patterns also inform seed sourcing and collection-site selection. Because maternal
374 conditions shape seed physiological status before storage and germination [61,62], seed lots from
375 different provenances may respond differently to the same nursery protocol [85]. Restoration programs
376 should therefore consider provenance climate as well as species identity when adjusting stratification
377 duration and pretreatment intensity. This is increasingly important under climate change, when source-
378 population climates may diverge from those at restoration sites [86,87]. In our dataset, source sites
379 associated with stronger germination responses tended to have moderate precipitation, intermediate
380 elevations, and well-drained sandy soils with adequate phosphorus availability.

381 Treatments that increase laboratory germination do not necessarily improve field establishment. In
382 *Prunus ulmifolia*, GA_3 increased laboratory germination but produced weak, etiolated seedlings with poor
383 field survival, underscoring the need to evaluate treatment outcomes beyond germination percentage [82].
384 The interaction between diaspore structure and treatment type supports a practical sequence that first
385 addresses fruit-covering constraints and then applies moist stratification to provide seasonal temperature
386 cues associated with winter [55]. Conservation protocols should balance dormancy release with seed
387 viability, seedling quality, and the preservation of source-population genetic diversity [88–90].

Considering dormancy throughout the restoration process—from collection and storage to sowing—may improve the predictability of seed performance and the success of seed-based restoration [85,90].

Conclusion

This global synthesis shows that dormancy in Rosaceae is not a uniform family-level trait but an integrated component of regeneration shaped by diaspore characteristics, fruit coverings, life form, and environmental conditions. Diaspore length was the strongest biological predictor of germination response, while fruit morphology, dispersal mode, and life form provided additional ecological context. Climatic and edaphic variables were also associated with dormancy and treatment response (lnR), highlighting the contribution of seed provenance and maternal environment to seed physiological status.

Our findings support a trait-informed approach to dormancy release in wild Rosaceae. An initial protocol is to disrupt or remove restrictive fruit coverings, followed by moist stratification at approximately 8 °C, within the effective range identified by our analysis (0.2–16 °C). The BLA indicated an average minimum effective duration of 40 days (range: 0–79 days) and an average maximum duration of 210 days (range: 139–280 days). These estimates provide a general framework, but treatment duration should be tailored to species, provenance, fruit-covering properties, treatment combinations, and dormancy depth.

Integrating diaspore traits with environmental and provenance information can improve seed collection, *ex situ* conservation, nursery propagation, and ecological restoration. In our dataset, moderate precipitation and elevation, well-drained sandy soils, and greater phosphorus availability were associated with lower dormancy or stronger treatment responses. More broadly, wild Rosaceae seed management should move beyond trial-and-error toward trait- and environment-informed strategies that recognize dormancy as an ecological mechanism regulating recruitment timing.

Materials and Methods

Data sources and dataset compilation

We searched the Web of Science (WoS) database for international research articles published before July 2026 using the keywords “seed dormancy + Rosaceae”, “seedling recruitment + Rosaceae”, “seedling establishment + Rosaceae”, and “seed germination + Rosaceae”. The search identified 171 publications, which were screened for eligibility (Fig. S1; Table S1). An additional 25 publications were identified from their references. Studies were included if they (1) investigated seed germination or seedling emergence in wild Rosaceae species, excluding cultivated plants; (2) compared a dormancy-breaking treatment with an untreated control; (3) tested germination under controlled conditions, including incubators, germinators, or greenhouses; and (4) reported mean germination values and the number of replicates. Hereafter, *germination* refers to both seed germination and seedling emergence. Mean values and replication counts were extracted from eligible studies. When studies included multiple experiments, locations, populations, or dormancy-breaking treatments, each treatment–control comparison was treated as a separate observation.

To characterize the ecomorphological attributes of the selected taxa, we compiled a plant functional trait database using the TRY Plant Trait Database [91], Kew’s Plants of the World Online (POWO), the Flora of North America, the Flora of China, and FloraVeg.EU [29]. Morphological and ecological traits were standardized into mutually exclusive functional categories to support multivariate analyses while avoiding excessive taxonomic subdivision [30,31,91].

Fruit type: Fruits were classified into six categories based on their structure and developmental origin: achenes (e.g., *Potentilla*, *Polylepis*), drupes (e.g., *Prunus*, *Rubus*), pomes (e.g., *Malus*, *Sorbus*, *Cotoneaster*), follicles (e.g., *Spiraea*, *Kageneckia*), hips (restricted to *Rosa*), and berries, including fleshy, indehiscent fruits without a stony core (e.g., *Sarcopoterium*).

Endocarp structure: Fruits with a distinct, hard endocarp were classified as “stony”, whereas those with a leathery or cartilaginous core were classified as “non-stony”.

Diaspore length: Diaspores were classified into five size categories: very small (<1.5 mm), small (1.5–5.0 mm), medium (5.1–10.0 mm), large (10.1–20.0 mm), and very large (>20.0 mm). Measurements were compiled from the LEDA Traitbase, the Digital Seed Atlas of the Netherlands, and published

sources [28,30]. We measured the functional dispersal unit rather than the seed alone: the seed in dehiscent fruits and the entire protected unit in indehiscent fruits. Wings and trichomes were excluded.

Primary dispersal mode: Dispersal syndromes were classified into seven categories based on field observations and published sources [13,31,44]: anemochory (wind), autochory (self-dispersal or gravity), endozoochory (ingestion by animals), epizoochory (external animal attachment), hydrochory (water), myrmecochory (ant dispersal), and synzoochory (animal caching).

Life form: Species were classified as trees, shrubs, or herbs. For plastic or thicket-forming taxa (e.g., *Prunus angustifolia*, *P. scoparia*), species with predominantly multi-stemmed, suckering growth were classified as shrubs, whereas those consistently forming a single woody trunk exceeding 4–5 m were classified as trees, following the phanerophyte framework [29,30].

Environmental data: Latitude, longitude, and elevation were extracted from the original publications. Köppen–Geiger climate types were obtained from Climate-Data.org (https://en.climate-data.org/). When site-specific values were unavailable in the original studies, climatic variables (growing degree days [GDD], with a 0 °C base; aridity index [AI]; and temperature seasonality [TS]) were obtained from WorldClim [92], plant-water variables from CropWater [93], and soil properties (pH, soil organic carbon [SOC], clay content, and bulk density) from ISRIC SoilGrids at 250 m resolution (https://data.isric.org/).

Experimental conditions: We recorded seed-storage conditions before testing, including duration, temperature, and use of fresh seeds, as well as dormancy-breaking treatments: scarification, endocarp removal, dry or wet heat, warm or cold stratification (including sequential treatments), and gibberellic acid (GA_3), including its concentration. Combined treatments were also identified. Stratification duration and temperature, germination-test duration, incubation temperature, and light regime were recorded. For alternating stratification temperatures (e.g., 16/8 h regimes), a duration-weighted mean temperature was calculated. The database therefore captured both pre-test conditions and germination-test environments.

Dataset overview

The final dataset comprised 1,894 observations from 61 references, covering 86 Rosaceae species across 29 countries and 106 geographical locations (Fig. 1). The dataset captured substantial ecological and morphological variation, although observations were unevenly distributed among trait categories (Fig. S2). Trees (931 observations, 49.2%) and shrubs (849, 44.8%) predominated, whereas herbs accounted for 6.0% (114). Drupes were the most common fruit type (945, 49.9%), followed by achenes (467, 24.7%) and pomes (412, 21.8%); follicles, hips, and berries were uncommon. Medium-sized diaspores dominated (952, 50.3%), followed by small (494, 26.1%) and large (344, 18.2%) diaspores, while very small and very large diaspores were rare. Stony endocarps accounted for 62.1% of observations (1,177), compared with 37.9% for non-stony endocarps (717). Endozoochory was the predominant dispersal mode (1,377, 72.7%), followed by synzoochory (330, 17.4%); all other dispersal modes each accounted for 3.1% or less.

Control germination varied across trait categories (Fig. 1b–f), with most distributions concentrated near zero and extending toward higher values. Higher mean germination was observed for very large diaspores (approximately 36%), epizoochorous species (38%), anemochorous species (22%), and follicles (20%). Herbs showed a broader germination distribution, with substantial density between 20% and 50%, whereas trees and shrubs were concentrated near zero. Stony and non-stony endocarps showed broadly similar, strongly right-skewed distributions. Hips and berries, represented by few observations, generally had germination below 10%.

Data analyses

Meta-analysis

We used random-effects meta-analysis in the *metafor* package in R [94] to quantify treatment effects on Rosaceae seed germination. For each treatment–control comparison, we calculated the natural log response ratio (lnR) and its sampling variance [47]. Positive lnR values indicate increased germination, whereas negative values indicate inhibition. Models were fitted using restricted maximum likelihood

(REML) to account for biological and methodological heterogeneity [95]. We estimated pooled effect sizes, 95% confidence intervals (CIs), between-comparison variance (τ^2), I^2, and 95% prediction intervals.

Sources of variation were examined using categorical subgroup analyses and intercept-free meta-regressions fitted with REML [94,95]. Moderators included plant functional traits (life form, fruit type, diaspore length, endocarp structure, and dispersal mode), individual treatments (storage, scarification [SC], endocarp removal, heat, light, GA_3, and stratification [ST]), combined treatments (SC × ST, SC × GA_3, ST × GA_3, and their three-way combination), and climate type. For each subgroup, we extracted the number of comparisons (k), pooled lnR, standard error, 95% CI, test statistics, P-values ($\alpha = 0.05$), and I^2. Effect sizes were visualized using forest plots, and funnel plot asymmetry was assessed for potential small-study effects and publication bias (Fig. S2).

Multivariate and regression-based analyses

Meta-regression analysis

We used random-effects meta-regression with REML in *metafor* to examine associations between germination responses and continuous experimental, climatic, and edaphic variables [47,95]. Each model incorporated lnR and its sampling variance (Var_{lnR}):

$$\ln R_i = \beta_0 + \beta_1 X_i + u_i + \varepsilon_i \quad (1)$$

where lnR_i is the effect size for observation i, β_0 is the intercept, β_1 is the slope for continuous moderator X_i, $u_i \sim N(0,\tau 2)$ accounts for between-comparison heterogeneity, and $\varepsilon_i \sim N(0, Var_{lnR,i})$ is the within-study sampling error.

We first examined the relationship between seed-storage duration (days) and lnR. Environmental heterogeneity was assessed using separate univariate models for 13 variables: mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), aridity index (AI), elevation (m a.s.l.), soil organic carbon (SOC, g kg^{-1}), cation exchange capacity (CEC, cmol(+) kg^{-1}), clay, silt, and sand contents (%), pH, bulk density (g cm^{-3}), available water capacity (AWC, mm m^{-1}), and Olsen phosphorus (Olsen P, mg

514 kg^{-1}). Separate models allowed each environmental gradient to be evaluated without jointly including
515 potentially collinear predictors.
516 For each model, we extracted the intercept and slope, their standard errors and 95% CIs, and
517 associated P-values. Moderator significance was assessed using the omnibus test (QM), while residual
518 heterogeneity was evaluated using QE, τ^2, and I^2. Because environmental conditions may covary with
519 geographic distribution, species traits, and experimental protocols, these associations were interpreted as
520 correlational rather than causal.
521
522 **Estimation of potential stratification thermal thresholds**
523 Boundary Line Analysis (BLA) was used to estimate the thermal and temporal boundaries of
524 germination responses to stratification. The response variable was lnR, and the predictors were duration-
525 weighted mean stratification temperature (T) and stratification duration. BLA characterizes the
526 boundaries of a response distribution across an explanatory gradient [96].
527 For temperature, we fitted a three-segment dent-like function to the upper response boundary,
528 representing an increase, an optimum plateau, and a decline [97,98]:

$$lnR = \left(\frac{T - T_b}{T_{o1} - T_b}\right) \times lnR_{max} \quad if \quad T_b < T < T_{o1} \tag{2}$$

$$lnR = \left(\frac{T_c - T}{T_c - T_{o2}}\right) \times lnR_{max} \quad if \quad T_{o2} < T < T_c$$

$$lnR = lnR_{max} \quad if \quad T_{o1} < T < T_{o2}$$

$$lnR = 0 \quad if \quad T \leq T_b \ or \ T \geq T_c$$

529 where lnR_{max} is the maximum boundary response, T_{o1} and T_{o2} are the lower and upper bounds of the
530 optimum interval, and T_o is their midpoint. Observations were sorted by weighted mean stratification
531 temperature and divided into 25 equal-width intervals; the maximum lnR in each interval was retained as
532 an upper-boundary point. The model was fitted to these points by nonlinear least squares. To ensure $T_b <$
533 $T_{o1} < T_{o2} < T_c$, the model was parameterized using positive intervals between successive temperatures.

These estimates describe the thermal range associated with stratification-related dormancy release, not the cardinal temperatures for germination itself [65].

For stratification duration, observations were sorted into 25 equal-width intervals, and the minimum and maximum lnR values in each interval were retained to define the lower and upper boundaries. Each boundary was modelled independently using a segmented function with an increasing linear phase and a horizontal plateau. The x-intercept of the increasing segment estimated the minimum effective duration (Tmin), at which the fitted boundary reached lnR = 0. The breakpoint marked the maximum effective duration (Tmax), beyond which the boundary response no longer increased systematically; the plateau represented the estimated maximum boundary response (lnR_{max}). Negative unconstrained Tmin estimates for the upper boundary were set to zero. Candidate breakpoints were evaluated across the observed boundary points, and the model with the lowest residual sum of squares (SSE) was selected for each boundary. Together, the fitted boundaries describe the observed range of germination responses associated with different stratification durations.

Analyses were conducted in R using *readxl* [99], *dplyr* [99], *minpack.lm* [100], *ggplot2* [101], and *openxlsx*. Model fit was evaluated using SSE, the coefficient of determination (R^2), and root mean square error (RMSE), where applicable.

Principal Component Analysis

Principal Component Analysis (PCA) was used to summarize environmental gradients and visualize relationships among climatic, topographic, and soil variables [102]. The analysis included 19 standardized variables: five climatic variables (growing degree days [GDD], temperature seasonality [TS], AI, MAT, and MAP), two topographic variables (elevation and slope), and 12 soil variables (bulk density, Olsen P, pH, exchangeable sodium percentage [ESP], electrical conductivity [EC], CEC, calcium carbonate [$CaCO_3$], AWC, clay, silt, SOC, and sand). PCA was based on singular value decomposition in R [103].

The first two principal components (PC1 and PC2) were retained for visualization, with their explained variance calculated from the eigenvalues. Neither lnR nor dormancy status was included as a

PCA variable. Instead, lnR observations were plotted on the environmental ordination and coloured by diaspore-length class, allowing germination responses to be examined across environmental gradients. Observations from the same location consequently shared similar environmental coordinates.

Environmental variables were displayed as vectors, with direction indicating their association with the principal components and length representing their contribution to the ordination [102]. Vectors were grouped by function (water-related, temperature, soil, and topographic variables), and the variance explained by PC1 and PC2 was reported on the respective axes.

SHAP-based feature importance analysis

SHAP-based feature importance analysis was used to quantify the relative contribution of biological, experimental, climatic, and soil-related predictors to the prediction of germination effect size (lnR) [104]. Random Forest regression models were fitted using the *ranger* package in R, with lnR as the response variable [105]. The first Random Forest model included life form, fruit type, diaspore length, endocarp, dispersal mode, storage, scarification, endocarp removal, climate type, heat treatments, light, GA, stratification, and the interactions SC × ST, SC × GA, ST × GA, and SC × ST × GA. Categorical predictors were treated as factors. Because the observations differed in their sampling variances, inverse-variance weights were calculated as $1/Var_{lnR}$ and standardized to a mean of one before fitting the Random Forest model. The model was fitted using 1,000 trees, with the number of randomly selected predictors at each split (*mtry*) set to the square root of the total number of predictors. Permutation-based variable importance was calculated, and unordered categorical predictors were handled using the ordering approach implemented in the *ranger* package.

SHAP values were estimated using the *fastshap* package with 100 Monte Carlo simulations and adjustment for the estimated baseline prediction. For each predictor, the mean absolute SHAP value was calculated and used as a measure of its relative contribution to the model predictions. Predictors with larger mean absolute SHAP values were considered more influential in predicting lnR. Because absolute

SHAP values do not retain the direction of individual contributions, the resulting rankings were interpreted as measures of predictive importance rather than as evidence of positive or negative effects. A second, independent SHAP analysis was conducted to evaluate the relative contribution of climatic, edaphic, and topographic variables to lnR. The predictors included bulk density, Olsen P, soil texture, GDD, TS, AI, pH, ESP, EC, CEC, $CaCO_3$, AWC, slope, clay, silt, SOC, sand, MAT, MAP, and elevation. Soil texture was treated as a categorical predictor, whereas all other environmental variables were entered as continuous predictors. The same Random Forest and SHAP procedures were applied to this model.

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Author contributions

ES and PC conceived the original idea. ES collected and extracted the data from the literature. ES assembled and managed the database, analyzed the data and drafted the manuscript. PC supervised the work. ES, MW and PC interpreted the findings and revised the manuscript. All authors approved the final version.

Data availability

The data supporting the findings of this study are provided in the main manuscript and its Supplementary Materials. Additional data or information may be obtained from the corresponding author upon reasonable request.

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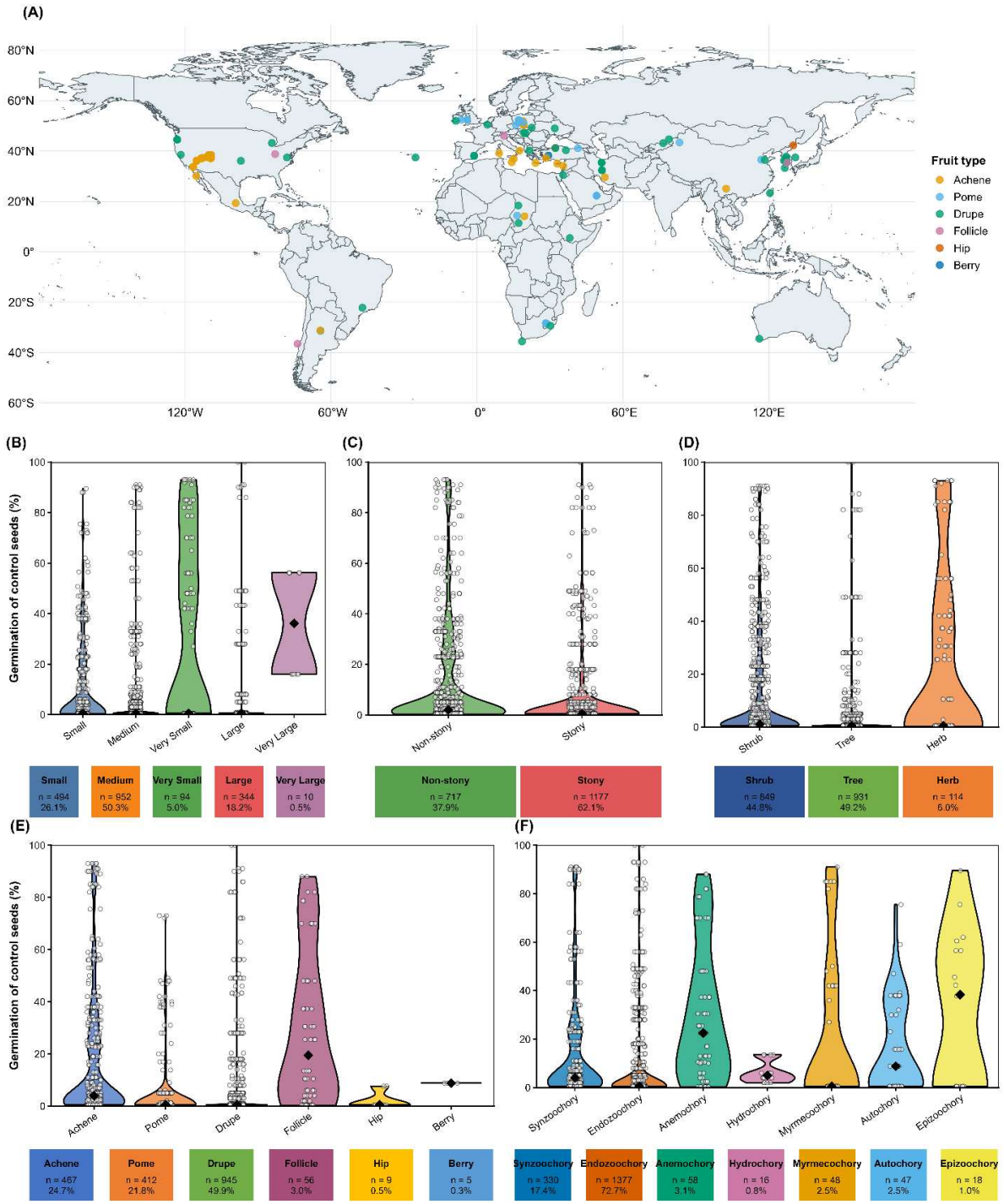


Figure 1. Global distribution of the study locations and variation in initial germination of control seeds across biological traits. (A) Map shows the geographic distribution of study locations, with points colored according to fruit type at each location. (B–F) Violin plots show the distribution of initial germination (%) of control seeds across biological trait categories: (B) diaspore length, (C) endocarp type (stony vs. non-stony), (D) life form, (E) fruit type, and (F) seed dispersal mechanism. The number of observations (n) and their percentage of the total observations are shown below each category in the respective panel.

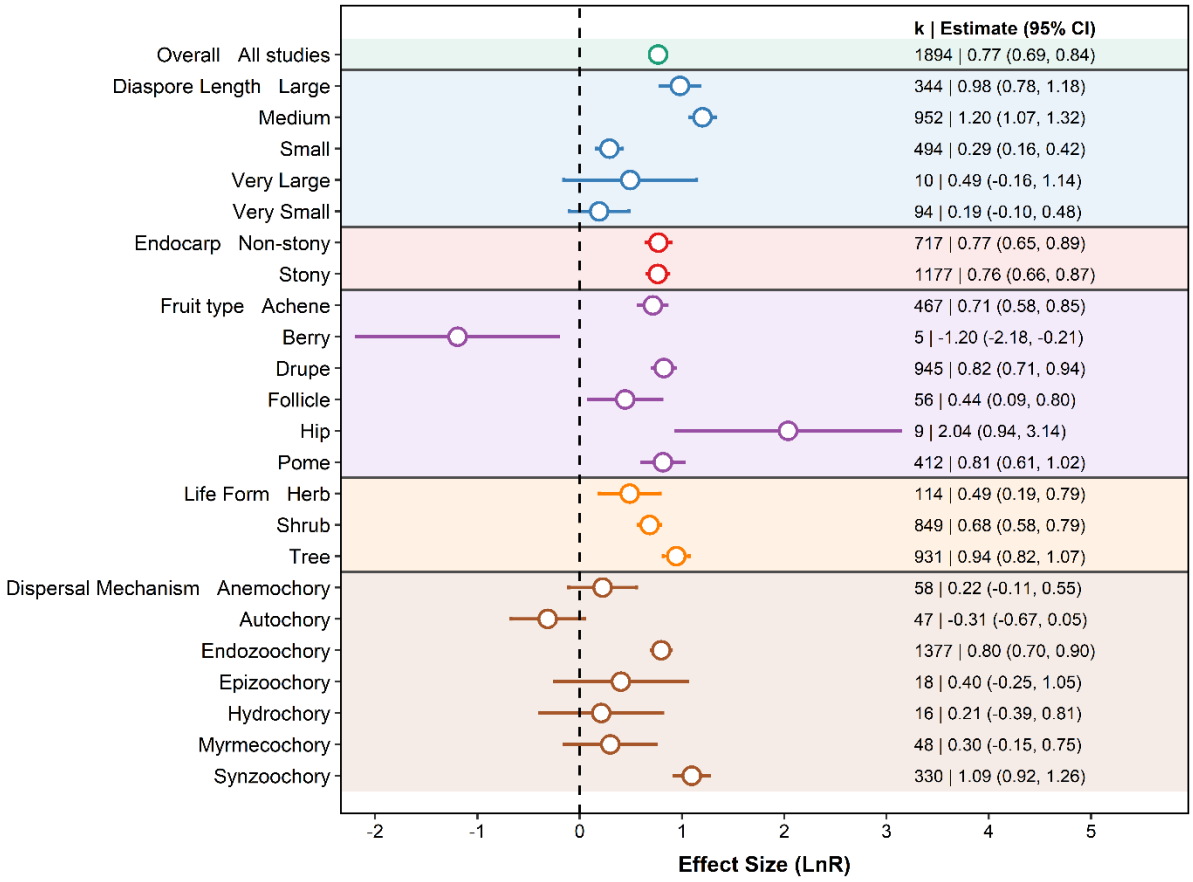
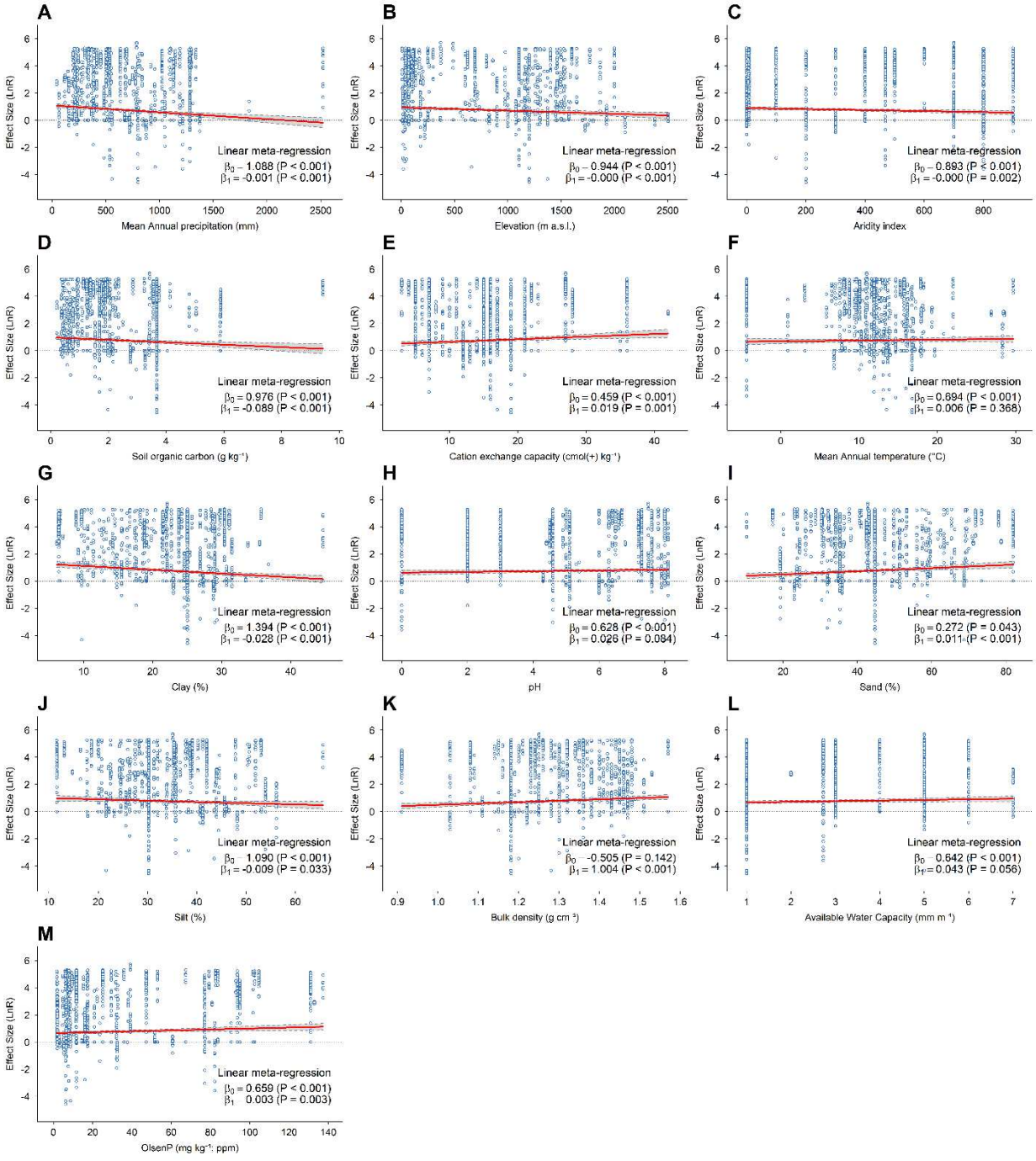
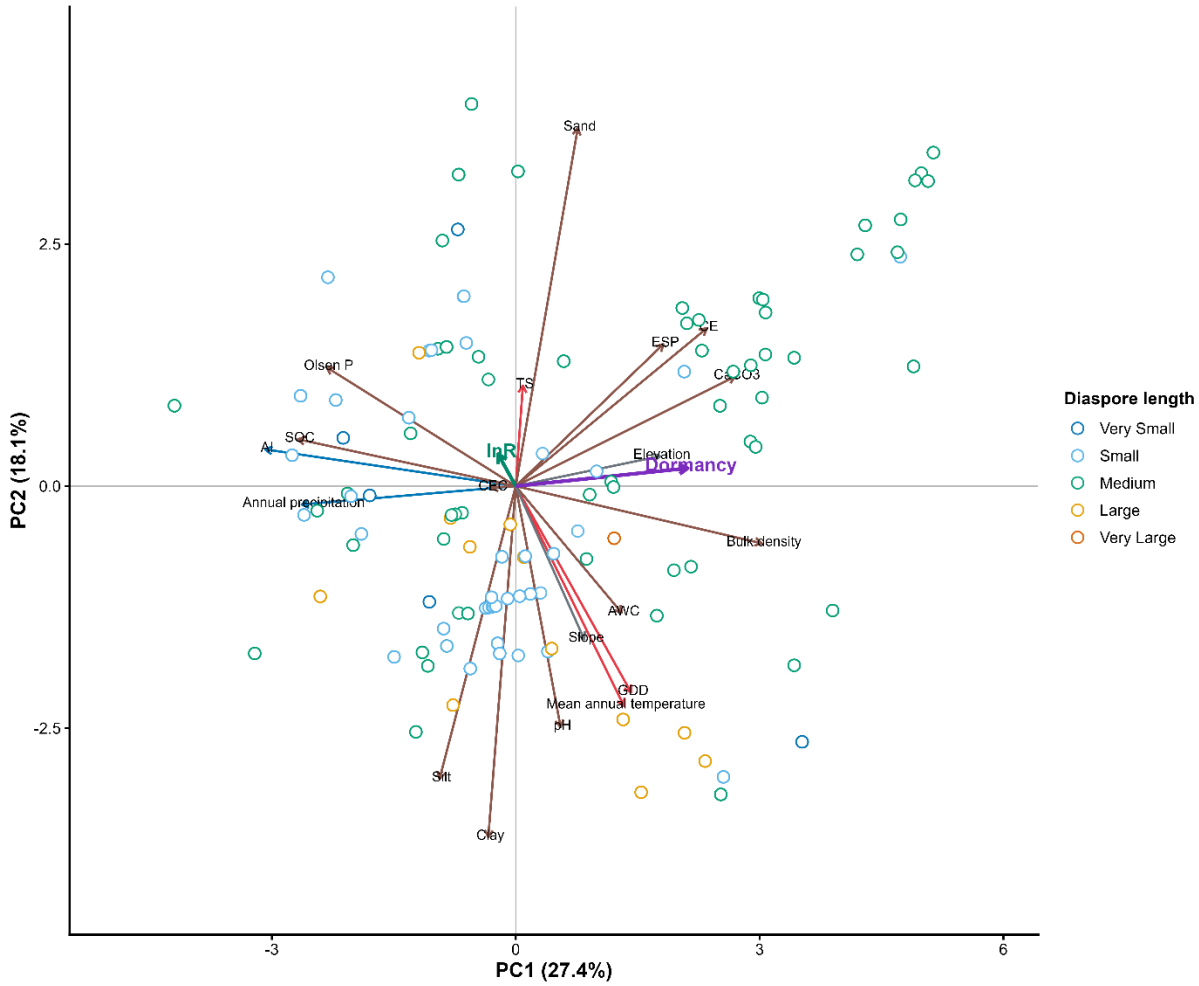


Figure 2. Overall meta-analysis and subgroup analyses of biological drivers of dormancy release in Rosaceae. The forest plot presents the overall effect size and subgroup estimates for diaspore length, endocarp type, fruit type, life form, and dispersal mechanism. Points represent pooled effect sizes (lnR), horizontal lines indicate 95% confidence intervals, and the corresponding number of observations (k), effect size estimates, and 95% confidence intervals are reported for each subgroup.



873

874 **Figure 3.** Univariate random-effects meta-regression of effect size (lnR) against climatic and
875 environmental variables across Rosaceae. The 13 continuous predictors are presented in separate panels
876 (A–M): mean annual precipitation (MAP), elevation, aridity index (AI), soil organic carbon (SOC), cation
877 exchange capacity (CEC), mean annual temperature (MAT), clay content, pH, sand content, silt content,
878 bulk density, available water capacity (AWC), and Olsen phosphorus (Olsen P). Points represent
879 individual observations, solid lines indicate fitted meta-regression relationships, and shaded areas
880 represent the corresponding 95% confidence intervals.



881

882 **Figure 4.** Principal Component Analysis (PCA) of climatic and environmental variables and seed
883 functional traits across the study observations. The ordination illustrates the multivariate relationships
884 among environmental gradients and biological characteristics of the diaspores, with observations
885 positioned according to their scores on the principal components. Variables with longer vectors contribute
886 more strongly to the corresponding environmental gradients, while the direction and angle between
887 vectors indicate their associations within the ordination space.

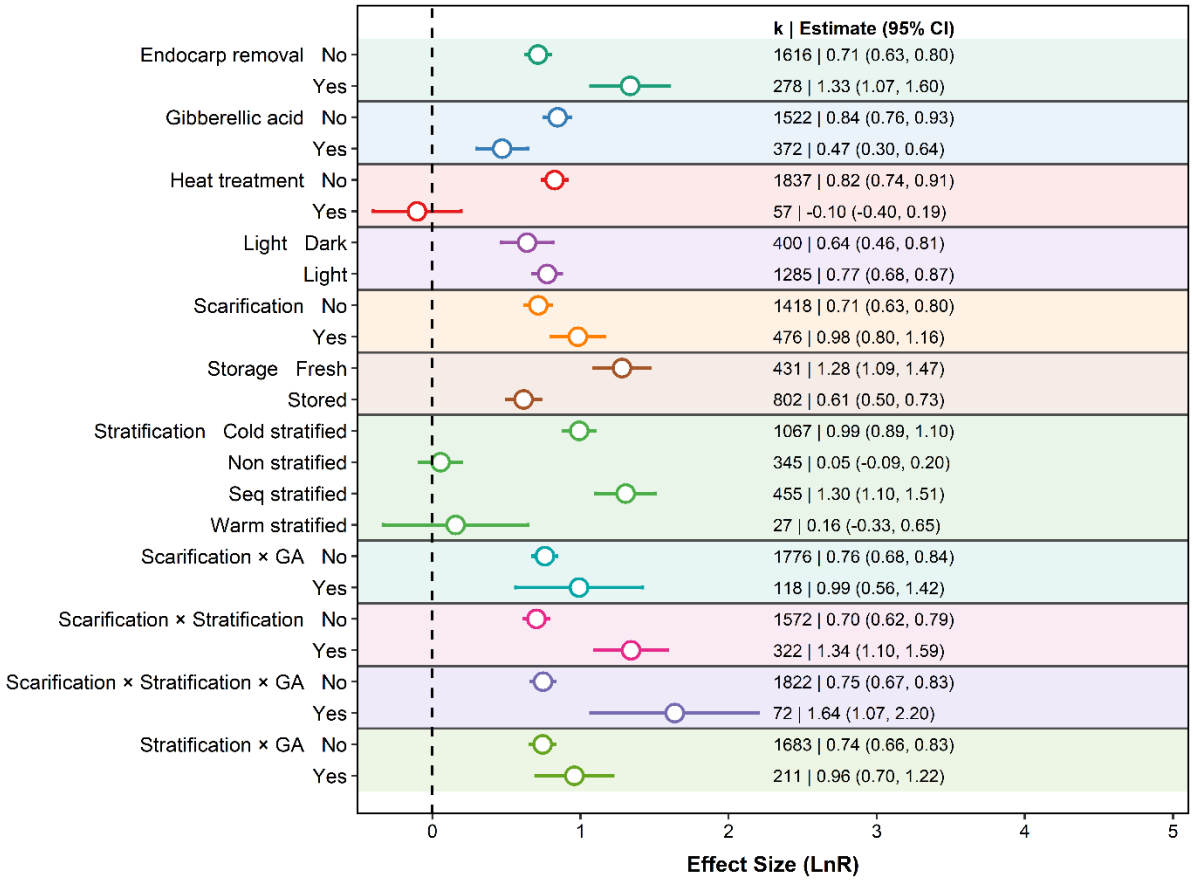


Figure 5. Meta-analysis of dormancy-breaking treatments in Rosaceae. The forest plot presents pooled effect sizes (lnR) for endocarp removal, gibberellic acid (GA_3), heat treatment, light, scarification, storage condition, stratification, and their combinations. Points represent pooled effect-size estimates, horizontal lines indicate 95% confidence intervals, and the corresponding number of observations (k), effect sizes, and confidence intervals are shown for each treatment category and level.

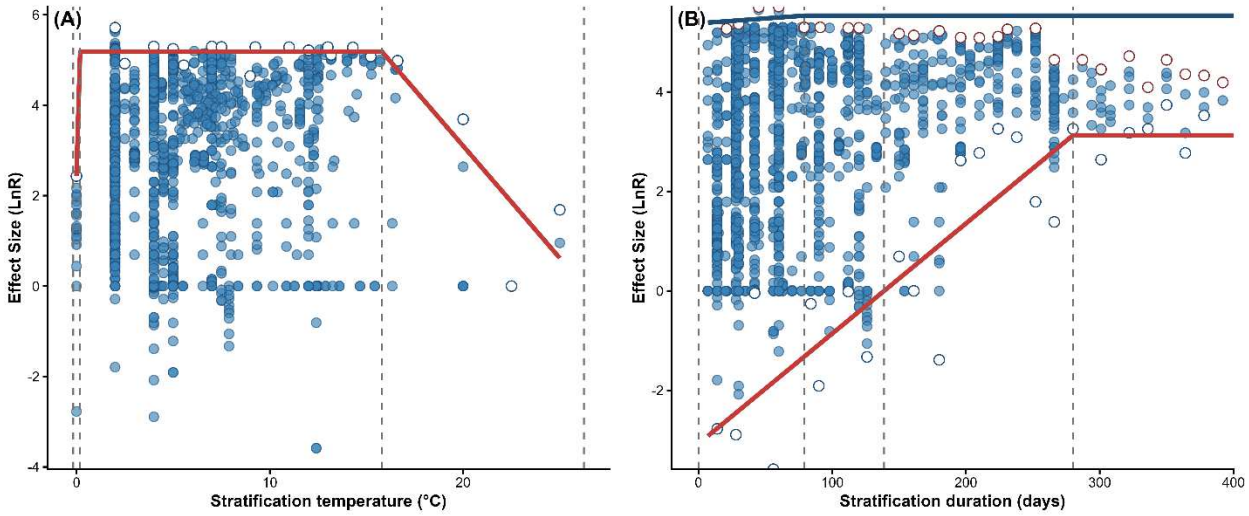


Figure 6. Boundary Line Analysis (BLA) of stratification temperature and duration in relation to effect size (lnR; dormancy release) in Rosaceae. (A) Relationship between stratification temperature and lnR, showing the upper boundary and the estimated thermal window associated with effective stratification. The observed temperature range was 0–25°C. (B) Relationship between stratification duration and lnR, showing the lower and upper boundaries and the corresponding temporal ranges of the observed response. Stratification duration ranged from 0 to 280 days.

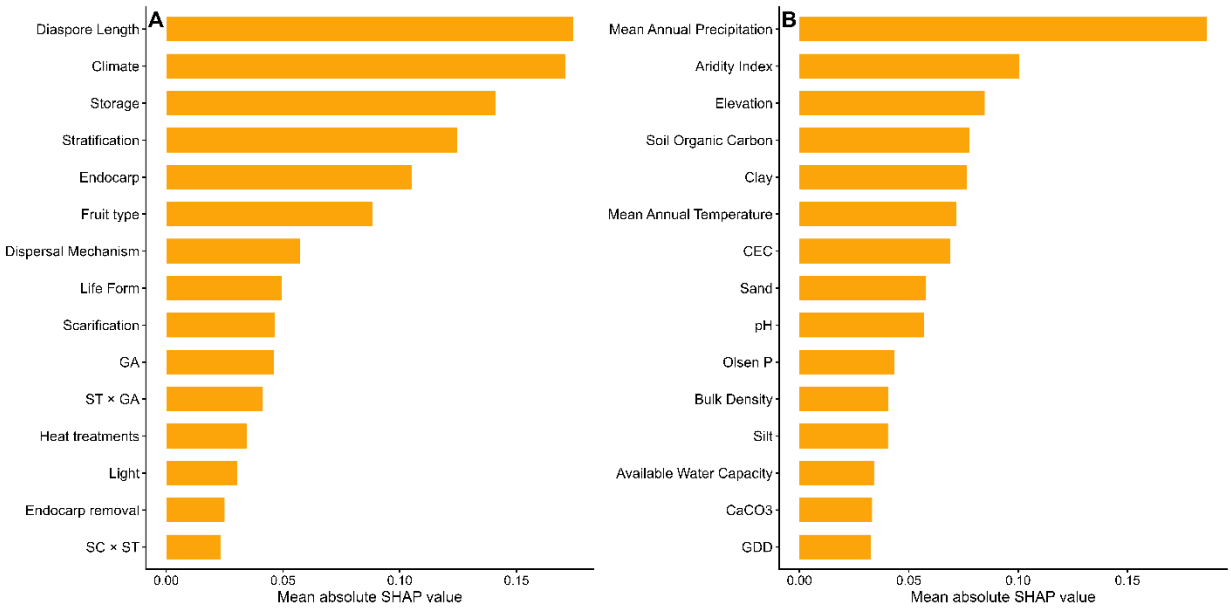


Figure 7. SHAP-based assessment of the relative contribution of biological, environmental, and experimental predictors to variation in dormancy release in Rosaceae. (A) Mean absolute SHAP values for all evaluated moderators, showing their relative importance in predicting the treatment–control effect size (lnR). (B) Mean absolute SHAP values for the climatic and edaphic predictors evaluated separately. Higher mean absolute SHAP values indicate a greater contribution to model prediction.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Suppfile.docx
- Supptables.docx
- RosaceaeMetaanalysisDataset.xlsx
- Suppfigs.docx